Bachelor thesis

Population variation in early growth of brown trout inhabiting different climates: Evidence for countergradient growth?

Av Sandra Marie Paulsen

Redaksjonen ønsker å publisere vannrelaterte studentoppgaver på bachelor, master- og doktorgradsnivå. Oppgavene som tas til vurdering skal være publisert ved de respektive studiestedene, og kandidatene skal være ferdig eksaminert før den aksepteres for publisering. Disse oppgavene har gjennomgått god faglig kvalitetskontroll gjennom veiledning og sensur, og publiseres derfor som fagfellevurderte artikler i VANN. Denne gangen har vi gleden av å presentere bacheloroppgaven til *Sandra Marie Paulsen*, som avla sin eksamen ved daværende Høgskolen i Hedmark, campus Evenstad, i mai 2014.

Abstract

Current climate change scenarios predict warmer temperatures within the next 100 years. In ectotherm species an increase in temperature will directly affect the metabolic rates and the life history strategies since they are controlled by temperature. A freshwater fish population is highly

exposed to the climate changes since they have a restricted ability to counteract the environmental variation by dispersing. A key life history trait directly influenced by temperature for ectotherms is growth and growth rates at early life stages seem to be of particular importance for the population dynamics. How is the growth in the early life stages between populations from locations with different climates? In this study we studied the growth of the yolk-sac larvae of brown trout, *Salmo trutta,* from four different populations where the climate varies considerably between the location of the populations due to dissimilarities in temperature and precipitation throughout the seasons. The study of the growth was preformed in a hatchery under controlled situations where the temperature was the same for all populations. Measurements of growth were done by using photographs of larva, were length of larva and perimeter of the yolk sac was measured in millimetre in the analysis software ImageJ. Five necessary variables; population, degreedays after hatching, period, length and size of yolk sac have been used to present results from this study. The study showed a difference in growth and absorption of yolk sac to length increment (i.e. growth efficiency) between the four populations of brown trout, where the cold climate populations had the fastest growth and the highest growth efficiency.

Sammendrag

Nåtidens senarioer for klimaendringer predikere varmere temperaturer innen de neste 100 årene. For ektoterme arter vil en økning av temperatur direkte påvirke stoffskiftehastighet og livshistorie strategier siden dettte blir kontrollert av temperatur. En fiskepopulasjon i ferskvann er svært utsatt for klimaendringer siden den har en begrenset mulighet til å motvirke variasjonen i miljøet ved å forflytte seg til et nytt område. Et viktig karaktertrekk hos ektoterme arters livshistorie er vekst, noe som blir direkte påvirket av temperatur, og vekstrater i tidlige livsstadier ser ut til å være spesielt viktig for populasjonsdynamikken. Hvordan er veksten i tidlig livsstadier mellom populasjoner fra ulike lokaliteter med ulikt klima? I dette studiet har vi sett på veksten til plommesekk yngel av stasjonær ørret, *salmo trutta*, fra fire ulike populasjoner hvor klimaet varierer mye mellom de ulike populasjonene grunnet ulikheter i temperatur og nedbør gjennom året. Studiet av vekst ble utført på et settefisk anlegg under kontrollerte forhold hvor temperatur var den samme for alle populasjonene. Målinger av vekst er gjort gjennom å ta bilder av plommesekk yngel hvor lengde og omkrets av plommesekk er målt i millimeter gjennom analyseverktøyet ImageJ. Fem nødvendige variabler; populasjon, døgngrader etter klekking, periode, lengde og størrelsen på plommesekk har blitt brukt for å presentere resultatene fra studiet. Studie avslørte forskjeller i vekst og utnyttelse av plommesekken til lengdevekst mellom de fire populasjonene av ørret. Populasjonene fra et kaldt klima hadde den raskeste veksten og den høyeste utnyttelsen av plommesekk til lengde vekst.

Acknowledgements

This is my bachelor thesis after three years with wildlife management on Hedmark University College, campus Evenstad. I have chosen to write about differences in growth and relation between growth and size of the yolk sac between four populations of brown trout in relation to climatic differences between the populations in the intragravel process as yolk-sac larvae. This thesis has given me a great joy and I have learned a lot during the process of writing a bachelor thesis; from fieldwork, writing the thesis in English and reading a lot of research papers.

First of all I am very grateful for the support and really super good guidance I have received from my supervisor Kim Magnus Bærum. Thanks for letting me tag along your PhD project, letting me use the electro-fish apparatus (it was a blast), helping me with my fieldwork, statistical analyses and models, correcting my sometimes really bad English and thanks for all the inspiring feedbacks since you are always so optimistic!

I also have to give thanks to my boyfriend Torkil for support and pushing me to write on my thesis when I really didn't want to.

Introduction

Current climate change scenarios (IPCC, 2013) predict warmer temperatures within the next 100 years. In Fennoscandia a general temperature increase of as much as 4°C might be expected. Thus, as temperature has a large potential to affect biota, the climate change is expected to influence multiple species at different levels. In particular, ectotherms will be directly affected as metabolic rates and life history strategies (Stearns, 1992) often are controlled by temperature (Sandström, Neuman & Thoresson, 1995). Further, ectotherms with restricted ability to counteract the environmental variation by dispersing, such as many freshwater fish populations, are highly exposed to the climate changes. In such systems, the populations might respond by adaptive processes to counteract possible extinctions. A key life history trait directly influenced by temperature for ectotherms is growth. Growth has the potential to affect size at age, maturation and longevity (e.g., Blueweiss et al. 1978; Stearns, 1992; Sogard, 1997). Moreover, growth rates at early life stages seem to be of particular importance for the population dynamics (Ottersen & Loeng, 2000). Hence, growth rates at early life stages are expected to be under selection and affected by the environment. However, knowledge of when, how and if populations and ecosystems will be affected by the predicted changes is restricted to a minimum for most systems. Consequently, further research on climate effects on populations and related adaptive responses is highly relevant and encouraged (e.g. Crozier & Hutchings, 20014). (e.g. Crozier & Hutchings 2014)

In general, the Bergmann's Rule states that the body size of endothermic species increases with increasing latitude and with decreasing temperature (Belk & Houston, 2002). The characteristic of Bergmann's rule is also documented for ectotherms species (Ray, 1960). However, for ectotherms this is rather counter intuitive as growth rates in general are expected to decrease with metabolic rates as temperature decreases with latitude. This has lead to the theory of "countergradient variation " where growth capacity could be developed to counteract the negative impact of the physical environment on growth (Levins, 1969). The theory thus predicts that populations from high latitude areas would grow faster than populations from low latitude areas when compared against each other at the same temperature. This theory is supported by e.g. a study of Atlantic silversides where fish from high latitudes grew faster than conspecifics from lower latitudes in an experimental setting, and that the pattern had a genetic basis since it was present at several laboratory generations during the study (Conover & Present, 1990). Further, it's shown that poikilotherm species in high latitude areas have a higher metabolic rate at certain temperature than the populations in lower latitudes (Bullock, 1955).

Knowledge about possible adaptations to specific climatic conditions could have implications for fish management (e.g., stocking effort, harvest and quotas) to reduce the footprint of the climate change on the population dynamics. However, such adaptation in freshwater fish systems appears modestly explored in the literature, with ambivalent results. A study on local adaptation in brown trout early life-history traits to their local environments and temperature showed high quantitative genetic differentiation values for alevin and swim-up lengths. There were also differences in phenotypic plasticity between the populations in the study that reflect a pattern of genetically based local adaption (Jensen et al. 2008). The study also showed that the population who originated from a tributary with average winter temperatures of 3-5°C had the largest alevin length at 2 and 5°C and the alevin length were smaller at 8°C, while the population who originated from a tributary with average winter temperatures of 6 - 7°C were larger at 8°C than at 5°C (Jensen et al. 2008). Contrary, Forseth et al. (2009) found no evidence for thermal adaption when studying growth performance in eight populations of anadromous and lake-feeding brown trout.

In this study I will use the yolk-sac larvae of the brown trout, *salmo trutta,* to explore adaptive growth rate variations among population of brown trout originating from different altitudes and climatic regions in Norway. The climate regions used represent variations in both temperature and precipitations.

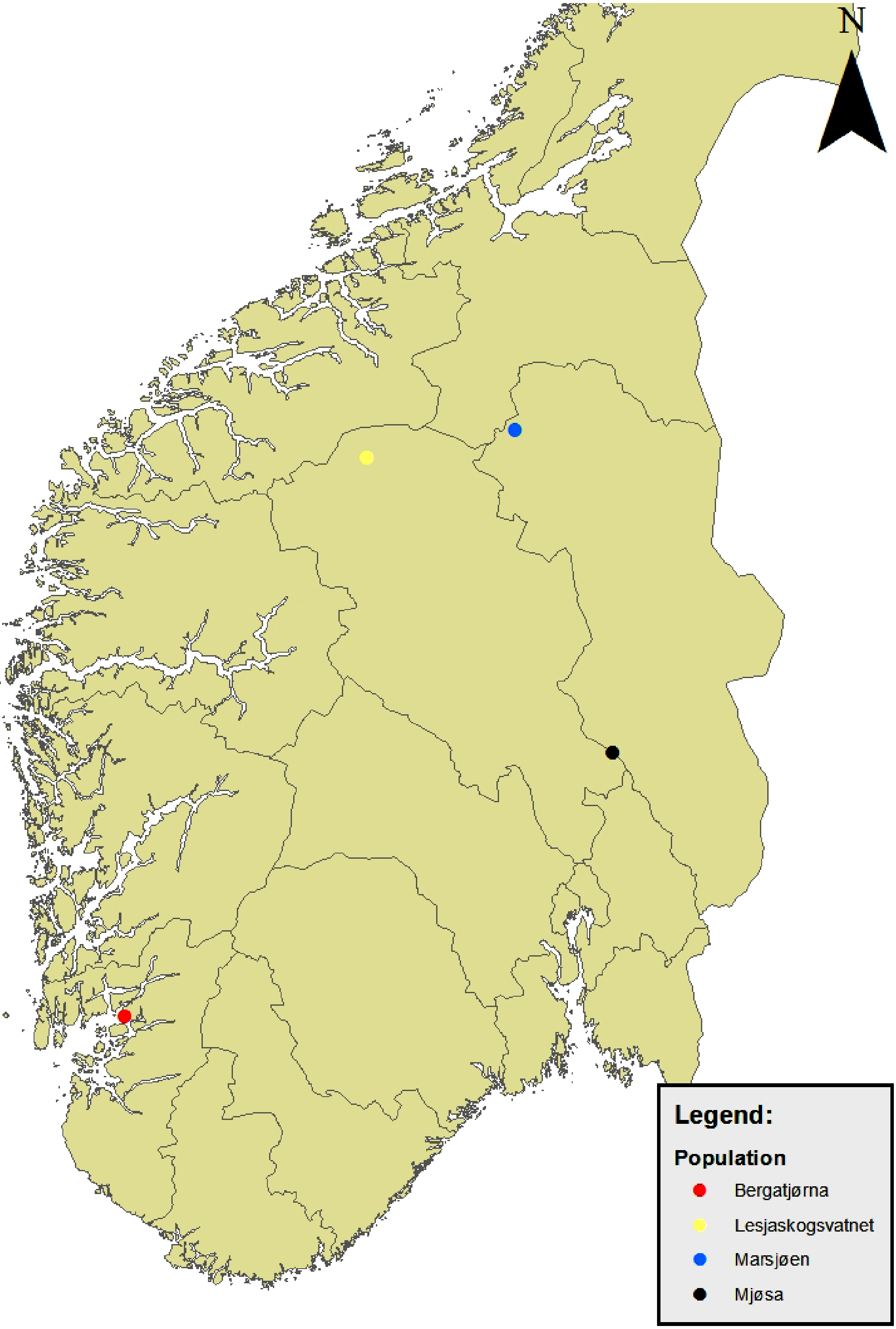
The brown trout was one of the first fish species in Norway after the last ice age, and it is widespread throughout Norway (Borgstrøm & Hansen, 2000). The trout is a specie in the salmonidae family and the can be divided in two different types; sea trout, which is anadromous, and freshwater resident trout that live the entire life in lakes, rivers and brooks. The brown trout can vary in growth and colour based upon differences in life strategies, locality and climate (Borgstrøm & Hansen, 2000). The Norwegian landscape varies from warm low altitude areas with eutrophic lakes to cold high altitude areas with oligotrophic lakes. The fish communities in the lakes can be allopatric (only one fish specie) or sympatric (more than one fish species) (Borgstrøm, Jonsson, & L'Abée-Lund, 1995). These variables can contribute to the brown trout's life strategies for growth between different brown trout populations. The main nourishment for the brown trout are invertebrates (Borgstrøm & Hansen, 2000), conditioned by the livelihoods of the lake the brown trout can also start preying on fish when they reach a length of 20-25 cm (Borgstrøm et al. 1995). Brown trout that prey on fish have a greater growth than the trout that only lives on invertebrates and animal plankton (Borgstrøm & Hansen, 2000). The brown trout that lives in lakes are usually potamodromous; meaning that the brown trout use the inlet tributaries for spawning- and nursery habitat and the lake as nourishment habitat (Jonsson, 1989). The brown trout spawns in the autumn and the spawning period for the Norwegian brown trout varies geographically (Taugbøl, Museth, Berge & Borgerås, 2004). In the colder high altitude areas they spawn from in the middle of September to the start of November, while in warmer low altitude areas they spawn from October throughout November (Sømme, 1948). When the spawning starts the female makes a nest in the gravel and after she have laid her roe and the male have fertilised them, the female covers the roe up with the gravel by making a new nest over the first nest (Minnesota Department of Natural Resources, 2014). The water temperature will determine the survival of the roe, Jungwirth & Winkler (1984) claimed that 16°C and 4°C was the upper and lowest temperature for roe survival, while Crisp (1989) claimed the lowest temperature for roe survival were 0°C. After the roe is buried down in the gravel, the intragravel development process starts and it can be divided into three stages; eying, yolk-sac larvae and fry. The stage eying is when the fully pigmented eyes can easily be seen in the roe (Crisp, 1993). When the roe hatches after 400-450 degreedays, the yolk-sac larvae stage starts and the larvae gets nourishment by absorptions of the yolk sac while living in the gravel (Crisp, 1993). When the yolk sac is fully absorbed the larvae starts it way up from the gravel as a fry and fills the swim bladder with air and then it can start feeding on external foods, this is called "swim-up" (Crisp, 1993).

In this study I will focus on the intragravel development process of the yolk-sac larva from four different populations located in the southern Norway with different climates; high/low altitude, cold/warm. In particular I will look for adaptive variations in growth (i.e. length at age). It's anticipated a presence of countergradient variation for growth between the populations in this study as shown in the studies of Conover & Present (1990). I will also explore the relation between size of yolk sac and growth efficiency.

Material and methods

Study area

The four populations used in this study are spread out in southern Norway from Bergatjørna in the south to Lesjaskogsvatnet in the north. The climate varies considerably between locations due to dissimilarities in temperature and precipitation throughout the seasons. The four populations are Bergatjørna in Rogaland county, Mjøsa in Akershus, Hedmark and Oppland county, Marsjøen in Hedmark county and Lesjaskogsvatnet in Oppland county.



Picture 1. The location of the brown trout populations used in this study.

Picture 2. Bergatjørna

Bergatjørna

Lake Bergatjørna is located in the southwest of Norway and is located at 8 m.a.s.l (Picture 2). In this part of Norway the precipitation is very high, and the average total precipitation at the nearest weather station in the period May-October is at 1050.8 ± 192.3 mm (from 1960-2000). The average daily air temperature in the period May-October is 12.7 ± 3.8 °C and the duration of period without snow cover are 8-9 months (from 2006 - 2012) (www.ekilma.no, station number: 46910). The mature brown trout in Bergatjørna has a low accessibility to tributaries for spawning and nursery habitat for the trout fry, since its only one or two know spawning tributaries. We sampled spawning trout for stripping from the tributary Sandbekken. Further in this study the Bergatjørna population will be referred to as the "Strand" population.

Mjøsa

Mjøsa is a major lake in southern Norway and is located at 123 m.a.s.l. It has a typical inland climate where the weather is quite stable during the summer season. The average total precipitation in the period May-October is at 363.6 ± 79.0 mm at the nearest weather station (from 1960-2000). The average daily air temperature in the period May – October is 11.9 ± 5.2°C, and the duration of period without snow cover are 6-7 months (from 2006-2012) (www.eklima.no, station number 12200). The mature brown trout from Mjøsa have access to numerous tributaries for spawning and nursery habitat for the trout fry. We sampled spawning trout for stripping from the tributary Måsabekken. Further in this study the Mjøsa population will be referred to as the "Måsabekken" population.

Picture 3. The spawning tributary Måsabekken

Marsjøen

Marsjøen is a mountain lake in southern Norway and are located at 1064 m.a.s.l. Like the major lake Mjøsa it also has a typical inland climate where the weather is stable during the summer season. The average total precipitation is 249 ± 50.9 mm in the period May – October at the nearest weather station (from 1960-200). The average daily air temperature is 6.2 ± 4.9°C in the period May - October and the duration of period without snow cover is 4 months (from 2006-2012) (www.eklima.no, station number 9100). The mature brown trout from Marsjøen have access to several tributaries for spawning and nursery habitats for the trout fry. We sampled spawning trout for stripping in the tributary Sandtjørnbekken.

Picture 4. Marsjøen with the spawning tributary Sandtjørnbekken

Picture 5. Lesjaskogsvatnet and the spawning tributaries Brandliåe and Hyrjon

Lesjaskogsvatnet

Lesjaskogsvatnet is a lake that lies in a high altitude area and are located at 611 m.a.s.l. Lesjaskogsvatnet is oriented to the west in southern Norway and therefore the weather can be very unstable in the summer season. The average total precipitation is 273 ± 82.2mm in the period May – October (from 1960-2000) at the nearest weather station. The average daily air temperature in the period May – October is 8.8 ± 4.6°C and the duration of period without snow cover is 4-5 months (from 2006 – 2012) (www.eklima.no, station number 61770). The brown trout in Lesjaskogsvatnet have access to several tributaries for spawning and nursery habitat for trout fry. We sampled spawning trout from the tributaries Brandliåe and Hyrjon. Further in this study the Lesjaskogsvatnet population is called the Lesja population.

Sampling and stripping process

Mature males and females were sampled during spawning (mid September –mid October, depending on location) with a backpack electro-fisher apparatus in selected spawning tributaries. During sampling we emphasised fish close to 500 grams, as it was not guaranteed that we would catch larger fish in all population. Thus standardizing the size of the parental fish. We used the same amount of mature males and females from each population for the stripping process. The sampled fish was weighted to the nearest gram and put down before we started on the stripping process to collect roe and milt from the trout. For the stripping process we used a weight, plastic bags and paper towel. The stripping process was performed by wiping off water around and under the abdomen, especially around the vent. This was done to avoid water mixing with the roe and the milt under the stripping process. This is a crucial step as the most important precaution detail with the stripping process is to avoid getting water into the plastic bags with roe or milt, because the roe will start swelling in contact with water and then you can't use it for fertilisation (Stefansson, Holm, & Taranger, 2002). The milt is gets activated by water and its only active in 15-20 second before it gets exposed for osmosis and then you can't use it for fertilisation of roe (Stefansson, Holm, & Taranger, 2002.

We stripped the trout by putting the fish on the side with a little bend on the spine with the head as the highest point. Further, thumb and index finger was pulled along the abdomen of the fish, facilitating roe or milt will flow out from the vent and into the plastic bag. After stripping, we ensured that a suitable amount of oxygen was left in the plastic bag before we closed it. The plastic bags with roe and milt was stored in a lightproof styrofoam box with cooling elements, such that the temperature was held low during transportation back to the fish hatchery at Evenstad for fertilisation.

Roe treatment

The fertilisation of roe from the selected populations was performed at Evenstad fish hatchery immediately upon arrival. To ensure random crossings within each population, the roe from all population specific females was mixed together and the whole batch was divided into smaller batches according to number of respective males. Pre fertilisation the roe was carefully rinsed with physiologic saline solution (9 gr salt/l water) twice where the saline solution was filtered completely out between each time. We did this to remove potassium from potential crushed roe, as potassium can reduce the fertilisation results

(Veterinærinstituttet, s.a.). The saline solution was used to prevent roe from swelling during the process. The actual fertilisation was carried out by pouring the roe over in small bowls and then the milt from one male was added in each bowl. We then stirred around cautiously in the bowl so that every roe had the same probability to get fertilised. After the fertilisation we rinsed the milt of the roe in a strainer with physiologic saline solution to remove organic substances, which can reduce the coming disinfection of the roe in the next step. We put the strainer with the roe in a bowl with the disinfection solution made from physiologic saline solution and iodine solution (10 ml buffodine pr. l), and it's important that the whole strainer in the bowl covers with the disinfection solution. The roe will have to lie in the disinfection solution for ten minutes. Then we move the fertilised roe in to the hatchery where we put the roe in a hatchery tray, its important to not fill the tray to full since the roe swells gradually.

Hatchery

We had four hatchery trays that each contained a population. We measured 10 roe from each population to get an average weight of the roe for each population (table 1).

The hatchery trays were carefully monitored and it was a routine to pick out "dead" unfertilised roe at least once a week. When the roe reached the life stage as eyed roe we performed a physical shock to the roe by pouring the roe from the hatchery tray at hip height down into a bucket with water. We performed the shocking treatment since the unfertilised roe change colour so its easy for us to sort out the unfertilised roe for the fertilised before we put it back into the hatchery trays. Normally trout will hatch 400-450 degreedays after fertilisation, it depends on the temperature in the water. In this experiment we used only non-heated water, so it had the same temperature as the stream the hatchery gets water from. We used a hobo data logger to keep track of the temperature in the hatchery trays. Hatching after how many degreedays after fertilisation is shown in table 2.

Since the experiment is about growth and utilisation of the yolk-sac in the trout early fry stage as yolk-sac larvae we had to come up with a plan to do the measurements without damaging the very fragile yolk-sac larvae. We choose to use a program called ImageJ in this program we can do measurements by taking photos of the yolk-sac larvae, and then calibrate how many pixels it is in one mm. This way we will not be exposing the yolk-sac larvae for unnecessary damage. The photos of the yolk-sac larvae was taken by putting ca. ten larvae in a petri dish with water in, we put an mm paper under the petri dish before we take the photos with a

Table 1. Average roe dry weight (g)±SD for the populations Strand, Måsabekken, Lesja and Marsjøen.

Strand	Måsabekken	Lesja	Marsjøen
0.034±0.008	0.023±0.004	0.024±0.004	0.023±0.005

Table 2: Hatching time for the different populations used in the study, in degreedays after fertilisation.

Marsjøen	Måsabekken	Lesja	Strand
417	375	409	417

Table 3: Photos taken for each population, degreedays after hatching

Photo nr.	Marsjøen	Måsabekken	Lesja	Strand
1.	5.42	5.03	14.38	4.76
2.	36.83	38.96	71.24	23.98
3.	135.19	174.20	160.82	151.93

Picture 6: A photo taken of the Marsjøen population

camera standing on a tripod(picture 1). We took three photos of the populations in different degreedays after hatching with three duplicates each time (table 3).

Picture 7. Measurements of yolk-sac larvae in ImageJ.

ImageJ

ImageJ is a processing and analysis tool that makes it possible for to perform measurements on the yolk-sac larvae by converting pixels to mm. We convert pixels into mm by setting a scale by marking up 10 mm in the photo by using the mm paper under the petri dish, and select that the measured length is 10 mm and then the program convert the pixels into mm each time I do a measurement in the photo. I did measurements of length and perimeter of the yolk sac on ten ± yolk-sac larvae in photo one and two; in the photo three we only measured length since the yolk-sac larvae had nearly fully absorbed the yolk sac. I measured length from the root of the caudal fin and to the end of the snout (picture 7). Measurements of the perimeter of the yolk sac was done by drawing a segmented line around the part of yolk-sac that was lying upwards in the photos (picture 7).

Data material

The data materials are based on measurements of length and the perimeter of the yolk sac in Image J. We took three photos during the study of each population with three replicates for each session, with measurements for 10± yolk-sac larvae in each photo, N_{total}=290. The data sett has five necessary variables that have been used to get results from the study; population, degreedays after hatching, period (an organisation of when pictures have been taken, photo 1 is period 1), length and size of yolk sac.

Statistical analysis

All statistical analysis is done in analysis software RStudio v0.98.501 (RStudio, 2014). The data used in the statistical models is checked for normal distribution before the statistics are made. I fitted a set of linear models with length as response variable and combinations of degreedays after hatching, population and size of yolk sac as explanatory variables (allowing for interactions) to explore variations in length at age (i.e., growth). The best model, which is represented in the results, was chosen based on AIC-values.

Results

A linear regression model (summary in table 4) revealed significant differences between the populations, both in intercepts and slopes, in predicted length at degreedays after hatching and size of yolk sac ($F_{15,274}$=191.8, $p<0.05$, r^{2just}= 0.908).

Table 4: Summary of estimates for length in relation to degreedays after hatching and size of yolk sac for the four populations; Lesja, Måsabekken, Marsjøen and Strand with standard error, t-value and p-value.

	Estimate	Std. Error	t value	Pr(>ltl)
Population Lesja (intercept)	4.933512	1.789221	2.757	0.00622
Degreedays after hatching	0.102624	0.011269	9.107	< 2e-16
Size of yolk sac	0.732271	0.118637	6.172	2.41E-09
Population Marsjøen	6.03244	2.512876	2.401	0.01703
Population Måsabekken	2.575629	2.460631	1.047	0.29614
Population Strand	4.974255	2.472711	2.012	0.04523
Degreedays after hatching:Size of yolk sac	-0.004264	0.000844	-5.052	8.01E-07
Degreedays after hatching:Population Marsjøen	-0.026204	0.017358	-1.51	0.13229
Degreedays after hatching:Population Måsabekken	-0.027445	0.01489	-1.843	0.06639
Degreedays after hatching:Population Strand	-0.03082	0.015969	-1.93	0.05464
Size of yolk sac:Population Marsjøen	-0.403454	0.163799	-2.463	0.01439
Size of yolk sac:Population Måsabekken	-0.255661	0.160622	-1.592	0.11261
Size of yolk sac:Population Strand	-0.358317	0.148828	-2.408	0.01672
Degreedays after hatching:Size of yolk sac:Population Marsjøen	0.001282	0.001311	0.978	0.32905
Degreedays after hatching:Size of yolk sac:Population Måsabekken	0.002253	0.001111	2.028	0.0435
Degreedays after hatching:Size of yolk sac:Population Strand	0.004397	0.00139	3.163	0.00174

Specifically, Strand had the highest length at start (table 4) but also the slowest growth in the predicted model for growth (figure 1). Marsjøen had the second lowest length after Måsabekken at start (table 4) but the most rapid growth (figure 1). The Lesja population had the second highest length at start and Måsabekken population had the lowest length at start, both showing medium growth with no significant variation among the two (table 4). A significant interaction between the populations Marsjøen, Lesja and Strand, and numbers of degreedays after hatching and size of yolk sac are present (table 4). This means that length at age varies differently according to the size of yolk sac across the populations. Predicted length in relation to size of yolk sac over the experimental time, or in other words, how much of the yolk sac is transferred into length increment (a proxy for growth efficiency related to size of yolk sac) is shown in figure 2. Måsabekken and Marsjøen had similar and highest growth efficiency, while Lesja and Strand had lower efficiency with Strand showing the lowest.

Discussion

The four populations of brown trout showed differences in growth trajectories, and growth in relation to size of yolk sac in the early life stage as yolk-sac larvae in an experimental setting. These four populations lives in different climate regions; Marsjøen and Lesja lives in a cold climate while Strand and Måsabekken lives in a warmer climate. The cold climate population Marsjøen had the most rapid growth in the study while the warm climate population Strand had the slowest growth. Måsabekken and Lesja both had medium and similar growth in the prediction model. There was also a large variation in growth efficiency according to size of yolk sac. Måsabekken and Marsjøen utilized seemingly more of their yolk sac into length increment compared to Lesja and Strand.

The populations who live in a cold climate have a shorter growth season due to a cold water temperature and the duration of snow cover than the ones who live in a warmer climate. It is documented that the optimum water tempera-

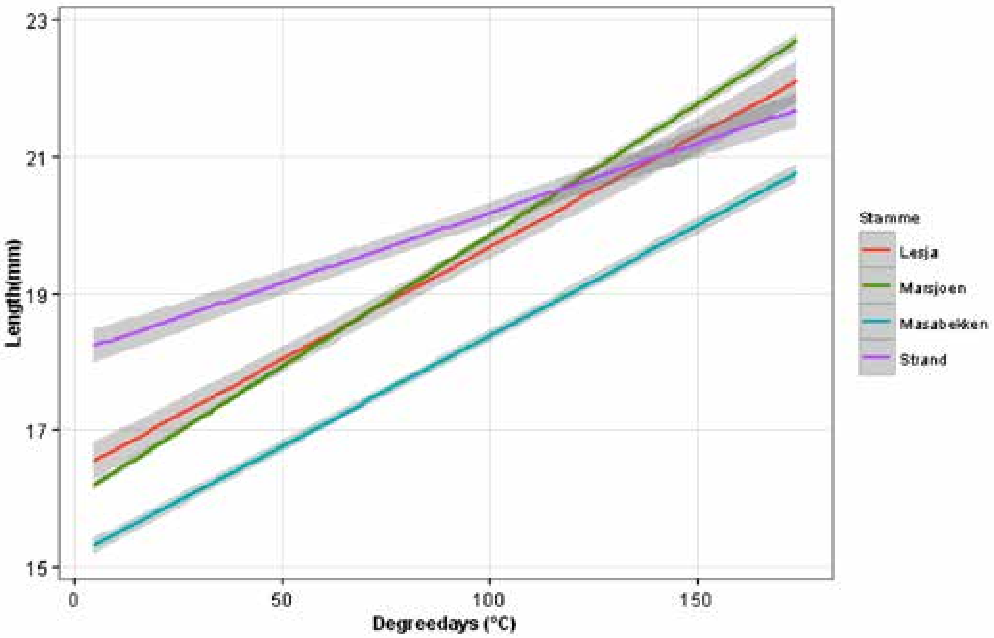


Figure 1: Prediction of length in accordance to numbers of degreedays after hatching

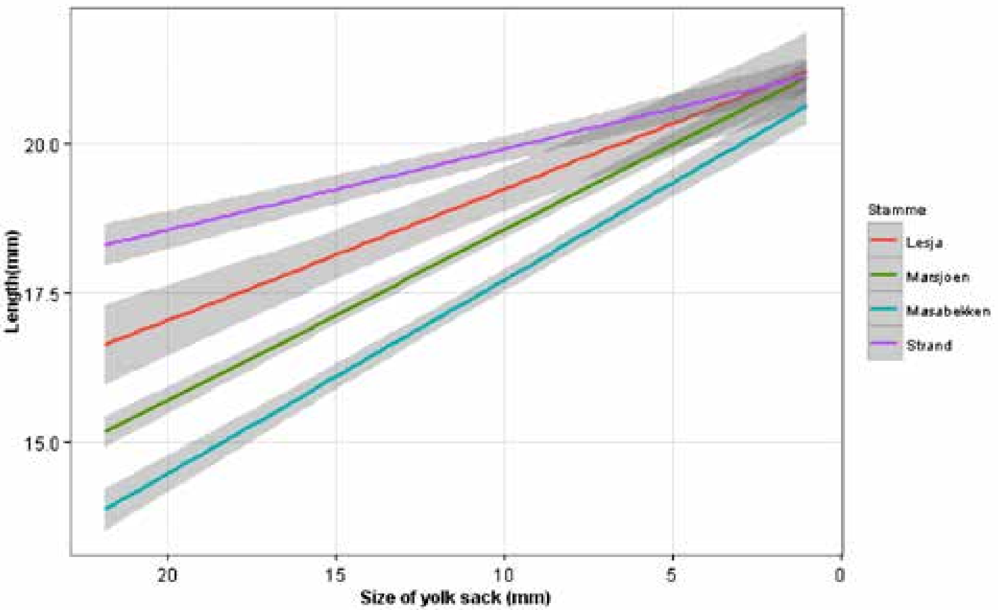


Figure 2: Predicted fish length in relation to size of yolk sac over the experimental time. Left on the X-axis represent predicted size of yolk sac volume at hatching, while moving right on the axis represent a temporal movement towards yolk sac depletion at the end of the experiment.

ture for growth is between 7-9°C and 16-19°C for two year old brown trout (Brown, 1946). The competition for food and the predation stands for nearly 90 per cent mortality rates in the early life stages in salmonids (Elliot, 1994), and large fry is in general more resistant to starvation

(Einum & Fleming, 1999), predators (Werner & Gilliam, 1984; Pedersen, 1997) and able to eat larger food items (Wankowski, 1979). This means that the yolk-sac larvae from a cold climate have to set an greater foundation for body size before the emergence from the nest to withstand the heavy predation and competition for food in the nursery habitat to achieve a further greater body size quickly because of the short and cold growth season. Other studies have shown that growth increases with increasing latitude. In Levintons (1983) study on the latitudinal compensation hypothesis of the *Ophryotrocha* it was showed that there was a difference in somatic growth rate between populations from high (cold) and low latitude (warm). The population from a cold climate had a greater somatic growth rate and that the growth rate decreased with increasing temperature. When they reached a certain high temperature the difference in somatic growth rate between the cold and warm climate populations was non-existent and the cold climate population showed a very high mortality. In Conover and Present (1990) study on countergradient variation in growth rate in Atlantic silversides showed that fish from high-latitude areas had a greater growth than those from low-latitude areas first and foremost at high temperatures. This suggests that fish from high-latitude areas are adapted to grow fast during the small amount of time high water temperatures occurs (Conover & Present, 1990). The importance of a rapid growth for the cold climate populations can also be explained by the fact that a larger fish have an higher winter survival than small fish and that this pattern increases with latitude (Conover & Present, 1990).

The more rapid growth of Marsjøen could thus be explained by an adaptation to the population's geographical location (i.e. high altitude) as this has the shortest and coldest growth season (see introduction). On the contrary, Strand has relaxed growth season duration stress and a warmer growth season in general and thus also more relaxed growth rates. It is also striking that the two populations found on medium altitudes (thus medium temperature regimes) in this study, Måsabekken and Lesja, also showed medium growth rates. Taken together, this strongly indicates some sort of growth adaptation to local environment and I think that the four populations show the pattern of Levins (1969) countergradient variation, since the cold climate populations have a faster growth than the warm climate populations when compared at the same temperature.

Måsabekken population had the lowest length at the start of the study and the highest growth efficiency. I think that the yolk-sac larvae from Måsabekken have developed some sort of "compensatory growth". Compensatory growth is a way for the underprivileged larvae to reach the same size as the privileged, larger larva through attain a full locomotor to utilize the energy contained in the yolk before the exogenous feeding starts (Kamler 2008), but to what cost of fitness? Studies have shown that fast growth in fish may reduce the swimming performance (Billerbeck, Lankford & Conover, 2001), strength of the skeletal (Arendt & Wilson, 2000) and decrease starvation endurance (Stockhoff, 1991) since the larva use high rates of energy to growth there will be less energy for body components and all these factors contribute to a reduced survival (Pedersen, 1997). In contrast to these factors, being large is also a way to reduce mortality and all the benefits that comes with being large as discussed above. Based on my dataset I cannot say that compensatory growth is present, but I think it can be one of the reasons for the high growth efficiency in the population.

During the study the Strand population had the highest length at start and slowest growth and the lowest growth efficiency in the predicted models. During the stripping process we experienced that mature females had less and bigger roe in their ovaries, 0.034g dry weight compared with 0.024g and 0.023g in the other populations. We have no information about the density of fry and predators in the nursery habitat, but by producing less and bigger roe we get bigger yolk-sac larvae at hatching that might have a higher fitness in high density and small nursery habitats, where competition for space is high. In general large fry have a huge benefit in competition for food because they can exploit larger food sources (Wankowski, 1979) and they are also less vulnerable to predators (Pedersen, 1997).

In the study we revealed a difference in growth efficiency between the populations based on how much of the yolk sac is transferred into length increment. The yolk sac contains yolk, and yolk is the source of nutrients and energy for the yolk-sac larvae under the endogenous feeding (Kamler, 2008). Marsjøen and Måsabekken had the highest growth efficiency while Lesja and Strand had lower efficiency with Strand showing the lowest. In the predicted model for length in relation to age (i.e., growth) Marsjøen population had the most rapid growth and in the predicted model for growth efficiency also the highest growth efficiency. Marsjøen population high growth efficiency can be related to the rapid growth and that Marsjøen come from a cold climate where a fast growth is necessary to counteract the negative effects of a cold climate (i.e., shorter season for growth). My findings of higher growth efficiency related to yolk sac size in the "cold" populations vs. the "warm" populations could thus indicate that the growth adaptation is related to how the fry use energy from the yolk during ontogeny (i.e. into length increment or other developmental processes). This might involve processes such as epigenetic inheritance (Auer *et al.* 2012; Salinas & Munch 2012) and the proximate cause is outside the scope of this thesis.

In Norwegian freshwater fish management it is common to use stocking fish as a measure to help fish populations in poor conditions. And the Norwegian government encourages the freshwater fish management to use fish from local populations to produce stocking fish if used as a management measure (Direktoratet for naturforvaltning, 1991). In my study of the yolk-sac larvae from different populations of brown trout it is shown that the populations have different local adaptions for growth, and if this pattern last in later life stages we must see the importance of using local adapted stocking fish, since the local adapted fish is the "best" for that precisely environment it originates from. E.g. we have a lake in connection to a larger water system where the freshwater fish management shall use stocking fish as a management measure. They collect broodstock fish from a lake that is located at 300 m.a.s.l under and close to the lake where the management is going to preform the measure. Since the two lakes are located close to each other and are connected in the same water system the two brown trout populations "originate" from the same stock of brown trout. My study has shown different local adaption between different populations of brown trout that are located in different climates, and by using stocking fish that originates from a population that is located at 300 m.a.s.l under the lake where the management measure is preformed you risk using stocking fish that is poorer adapted to the environment. If the local adaption to growth is an effect of plasticity, meaning that growth is a direct effect of what kind of temperature the mature female experience before spawning (Mousseau & Fox, 1998). May usage of broodstock fish that lives in a hatchery year after year under the "wrong" temperature regime spoil the effect of local adaption to growth.

If climate changes occur and a temperature increase of as much as 4°C in Fennoscandia as predicted by IPCC (2013), how will freshwater fish species react since based on this study there are local adaptions between different populations, especially warm and cold climate populations? Study of two year old brown trout showed optimum growth in water temperatures at 7-9°C and 16-19°C (Brown, 1946), while in an other study on adult brown trout there was high mortality above 20°C and the mortality was complete above 25°C (Gardner & Leetham, 1914). Climatic change with an increase of temperature will effect the warm climate populations more than the cold climate populations since the cold climate populations is located in area with average summer season (May – October) temperature of 6.2±4.9°C (Marsjøen) and 8.8±4.6°C (Lesja), an increase of temperature by as much as 4°C

(IPPC, 2013) will still keep them in the temperatures for optimum growth (Brown, 1946). The warm climate populations have an average summer season (May – October) temperature of 11.9±5.2°C (Måsabekken) and 12.7±3.8°C (Strand), the increase of temperature can have an negative impact on the growth and mortality of these two warm climate populations since the water temperature might be higher than the temperature for optimum growth. So climatic changes, especially higher temperatures will effect warm climate population's more than cold climate populations.

Sources of error

The result from this study can just be seen as indication for growth and yolk sac absorption for the Norwegian brown trout yolk-sac larvae as I only used four populations. Further, the study is only based on three photos (x 3 replicas) of length and two photos (x 3 replicas) of size of the yolk sac at different degreedays after hatching per population. Ideally, it should have been a more carefully monitoring of degreedays for each population to get more data points and thus better solution in the data. However, as the data is derived from a standardised experimental set up, I believe that the results to be trusted even with the data obtained.

Since the yolk-sac larvae were to be used in another study as fry, I think that the method of using the software ImageJ to analyse the photos were the best solution to get data on length and size of yolk sac from the yolk-sac larvae without killing each larva used in this study. If I would had chosen another method for sampling the data I would have used the method in the study of hatching performance and yolk sac absorptions of Caspian brown trout (Kocabaş et al. 2012) and the study of hatching performance and yolk sac absorptions of Abant trout (Kocabaş et al. 2011). In these studies they sampled ten yolk-sac larvae for each sampling period, the larvae was anesthetized and then preserved in 10% formaldehyde. After being preserved for a time the larvae was dissected to remove the yolk sac from the body of the larvae and then dried separately and weighed individually (Kocabaş et al. 2012). This way its possible to get exact measurements of length before the larva is preserved, and you can se the relation between the dry weight of yolk sac and dry weight of larva in context of length growth after degree-days after hatching.

Conclusion

My study has shown that populations of brown trout located in different climate regimes have a difference in growth in the early life stage as yolk-sac larvae. The cold climate populations had the most rapid growth and that the fast growth can be explained by local adaptions to the environment. The study has also shown that the cold climate populations utilize the yolk sac faster for length growth than the warm climate populations. For freshwater fish management it is of importance that we only use fish from the same population as stocking fish since they are directly adapted to the environment the populations live in. And that the usage of broodstock fish that lives in an hatchery may produce stocking fish that is poorer adapted to the environment then if they were sampled as roe by stripping in the spawning tributaries. If climate changes occur and we get a increase of temperature it will have an negative impact on the warm climate populations of brown trout.

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