Growth and smolting in anadromous brown trout (*Salmo trutta*) from Lærdalselva: Responses to hydropower and *Gyrodactylus salaris*
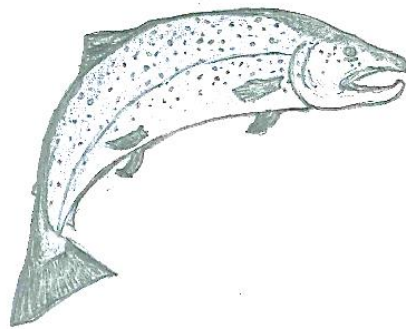
Figure 1: Anadromous brown trout in Lærdalselva. Foto: Torstein Kristensen

Preface

This master thesis was written for the Department of Ecology and Natural Resource Management at the Norwegian University of Life Sciences (NMBU). The study was carried out in collaboration with NIVA (Norwegian Institute for Water Research) and the KUSTUS project. This project objective is to survey and increase the knowledge base on salmonoids in Sognefjorden, and is financed by both public sector and private companies. Human induced environmental amendments, and the following effect on wild salmonid populations is highly relevant. I hope my study can contribute by increasing our understanding of these complex systems, and be a fresh breath of air in the further management of the anadromous brown trout population of Lærdalselva and Sognefjorden. Unless otherwise mentioned, all fotos are taken by me.

I would like to take the opportunity to thank my supervisor Thrond O. Haugen for his excellent mood, statistics-skills and good help. I also want to thank my co supervisors Torstein Kristensen for good discussions and input, and Bjørn Olav Rosseland for providing me scales. Atle Rustadbakken and Reidar Borgstrøm also deserves a thank for evaluation my scale readings, and good discussions around scale reading theory. NIVA and KUSTUS-people Henning A. Urke and Morten Bergan for skilfully and educational guiding me through fieldwork in the deep valleys of Lærdal. Håvard Lo, from the veterinary institute in Trondheim, for providing me scales. My parents also deserves a thanks for just being there, calling me every Sunday for five years. And last but not least my girlfriend Marte, the "breakfast-club", and all my fellow students and good friends at Ås for bringing joy and happiness into my university life!

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CONTENTS

Abstract

Lærdalselva has faced many environmental alterations caused by anthropogenic activity over the last four decades. This study has categorized these into four different treatment periods: "Before hydropower " (1954-1974), "After hydropower" (1974-1996), "Hydropower, *Gyrodactylus salaris* and *Gyrodactylus salaris* treatments" (1996-2011) and "present times" (2012-2014). The objective of this study was to determine if these treatment periods have imposed growth alternations and altered age- and size at smolting in the anadromous brown trout population (*Salmo trutta* L.) of Lærdalselva.

These objectives were analyses using scale analyses of scales sampled from all treatment periods. From the scale readings, freshwater- and sea age as well as age at smolting were determined at individual level along with back-calculated sizes at all ages. These size-at-age and smolting trajectory data were subjected to statistical analyses designed for elucidating the research objectives.

There were no significant differences in May-October mean water temperature among treatment periods. The May-October mean water discharge has changed significantly among treatment periods, with less water discharge after hydropower.

Back-calculated length at first year was significant reduced after launching hydropower compared to the preceding period. Back-calculated specific growth rate during second year in freshwater, showed no evidence of treatment period effect. There was a positive correlation between summer low-water discharge and second-year specific growth rate. There has been a significant shift in smolt reaction norms (SRN) where the anadromous brown trout during the hydropower period delayed smolting by almost a year and larger size than during the preceding period. During the more recent periods, the SRN has gradually shifted towards the original pattern. The marine growth has changed significantly among the treatment periods. First sea year back-calculated specific growth rate has significantly declined during the period after hydropower compared to the preceding period. However, Second-sea-year back-calculated specific growth rate has significantly improved after hydropower when compared to the before period. For the hydropower, *G. salaris* and *G. salaris* treatment period, a decline in second-sea-year back-calculated specific growth rate was found – after correcting for the positive effect of mean summer air temperature. My study indicates that the anadromous brown in Lærdalsleva is capable of rapid adaptions to anthropogenic-induced environmental change.

1. Introduction

Different populations within the same species can show considerable variation in life-history traits. Mortality rate, migration patterns, age at maturity and longevity, as well as the timing and expression of these traits throughout an individual's life can vary within populations that genetically belong to the same population. Life-history traits are considered to be evolutionary compromises between costs and benefits, thus tightly linked to fitness at an individual level (Stearns 1992). Natural selection favours those genotypes whose life-history traits generate the highest per capita rate of increase, in response to their living environment. (Roff 2002). Within populations, life-history related genotype frequencies may change in response to the stochasticity and/or gradual change of the environment (Champell et al 2008). Natural- or anthropogenic-induced alternation of the environment will change the selective landscape, and result in changing adaptations. Intraspecific variation in body size, age and size at migration and longevity, may partly be a proximate response to environmental conditions, especially within species with intermediate growth such as fishes (Stearns 1992). Due to this, fishes often express considerable phenotypic plasticity, i.e., a genotype's variation in phenotypic expression across environmental gradients, that in itself may constitute adaptations (Schlichting & Pigliucci 1998). The phenotypic response pattern across environmental variation constitutes a reaction norm and knowledge about the shape of such reaction norms is pivotal for understanding and interpreting phenotypic variation observed in the wild (Schlichting & Pigliucci 1998). Typical reaction norms observed in fishes are growth and developmental traits in relation to temperature (Hutchings 2011). However, traits like growth is also known to influence the expression of other life-history traits, for instance when to mature or when to smolt (Roff 1984). Therefore these life-history traits will also get affected by the thermal reaction norm of growth. When making management decisions it is thus important to have a profound knowledge about an organism's life history, and the local adaptions in the involved population.

Brown trout (*Salmo trutta*) has a complex and diverse life history, and the complexity varies with the environmental conditions (Klemetsen et al. 2003). The typical pattern is populations consisting of small resident, and larger migratory individuals (Jonsson 1985).
Anadromous brown trout are known to be locally adapted to their natal rivers, in which they show a strong homing behaviour when returning back from feeding in the ocean to their home

river for spawning (Jensen 1968). Lake-spawning populations occur, and the species may also spawn successfully in brackish water (Limburg et al. 2001; Brabrand et al. 2002). Unlike Atlantic salmon (*Salmo salar*) the anodromous brown trout feed primarily in estuaries and along coasts. Only large individuals are sometimes observed in the open ocean (Jonsson & Jonsson 2006b). This migratory strategy is regarded as an adaptive behaviour to increase growth and fitness, in seasonal temperate regions (Jonsson & Jonsson 2011). There are also costs associated with migration, and the decision to move depends on what yields the highest fitness after benefits and costs have been balanced (Jonsson & Jonsson 2006a). Growth, energetic status and metabolic rate in the juvenile phase influence this decision (Forseth et al. 1999; Boel et al. 2014). Progeny of anadromous brown trout are not initially adapted to a life in the ocean, and can complete their whole lifecycle in fresh water. However, there is a general pattern that they grow up in fresh water, but can move to saltwater and adapt to a marine life in pelagic waters, after a physiological transformation called smolting (Hoar 1988; Jonsson & Jonsson 2006b). Photoperiod, temperature and water discharge are all important factors, controlling timing and development of this process (Jonsson 1991 ; Hembre et al. 2001). Borgstrøm and Heggenes (1988) found particularly young and small smolt in a South Norwegian stream. They hypothesized that this was an adaption to the low water discharge, and periods of drought during summers. Growth and body size influence almost all life-history traits (Roff 2002). Size and growth is considered the most important life-history traits of brown trout, likely due to the close association with survival and fitness (Jonsson & Jonsson 2011). For instance, longevity is observed to increase with larger body size (Jonsson et al. 1991). Temperature is the abiotic variable with the most extensive effect on growth of salmonids (Elliott, J. A. et al. 1995; Jonsson & Jonsson 2011). Annual growth is highly linked to water temperature both in freshwater and coastal waters (L´Abée-Lund et al. 1989). Other factors such as flow and depth, bottom substrate, barriers to migration, nutrient richness, habitat coherence and consistency also influence growth and life-history traits in anadromous brown trout (Klemetsen et al. 2003). Biotic functions, such as intracohort, intercohort and interspesific competition can also influence life history traits and growth both negative and positive (Klemetsen et al. 2003; Jonsson & Jonsson 2011).

Brown trout biology and migratory behaviour make them highly responsive to landscape alternation, exploitation and external inputs (Jonsson & Jonsson 2011). There is a general consensus that river regulation has a strong negative effect on brown trout by altering migration opportunities, and degrading valuable spawning and juvenile habitats (Johnsen

B.O. et al. 2011). The abiotic changes river regulations entails, such as changed water discharge, can potentially affect the demography of a brown trout population. Among other by altered selection on growth and thereby important life history traits (Saltveit 1990b; Ugedal et al. 2002; Sandlund & Jonsson 2014). For instance, salmonids from the river Surna has experienced reduced growth and thereby delayed smolting due to the presence of cold water and altered water discharge, after hydropower regulation (Saltveit 1990a). In addition altered water discharge can directly affect smolting by interfering with various stimuli associated with behaviour and development during this process (Hembre et al. 2001; Jonsson & Jonsson 2009a). The introduction of novel parasites such as *Gyrodactylus salaris* (Monogenea, Gyrodactylidae) and other pests, can be regarded as a massive environmental change in the freshwater. *G. salaris* infect Atlantic salmon in freshwater, and has proven a serious treat to wild salmon, by eradicating stocks in several Norwegian rivers (Johnsen & Jensen 1992; Bakke et al. 2007). The management strategy in Norway is to eradicate *G. salaris* by killing the host with the use of rotenone (Johnsen et al. 2014). The massive mortality among the populations living in the river at the time of treatment, can result in genetic drift, and thereby reduced genetic variability (Johnsen et al. 2014). In addition, *G. salaris* infection itself and the efforts to eradicate it can lead to considerable changes in the inter- and intraspesific competitive relationships between Atlantic salmon and anadromous brown trout (Johnsen et al. 2014). A population's response to bottleneck situations arising from anthropogenic causes, depends heavily on its genetic variability and phenotypic plasticity.

Over the past decades the anadromous brown trout along the Norwegian coast has experienced a serious decline in population size (Finstad et al. 2011). Populations of Central Norway and Western Norway have had the strongest decline. The Norwegian environment agency points out ecosystem changes in the sea, increased salmon lice (*Lepeophtheirus salmonis*) infection due to increased open net pen salmon aquaculture, climatic changes and other diseases as the most causal relationships. Growth conditions in the rivers are also considered to be a crucial factor affecting the decline (Jonsson et al. 2009). Ecosystem changes can be due to climatic changes, which in turn can affect the occurrence of nutrients and prey such as fishes. Climatic changes may also cause changes in the migration patterns of anadromous brown trout, which can lead to migration at unfavourable times in the context of the nutrient conditions in the sea (Jonsson & Jonsson 2009a). The fjords in Western Norway are characterized with a lot of salmon farming. Furthermore the salmon lice infection is

considered to be a decisive factor for the decline of the resident salmonids in recent years (Bjørn et al. 2009).

The river Lærdalselva is one of Norway´s best-known angling rivers on an international level. Historically the anadromous brown trout of Lærdalselva is known for its large size (Nall 1932), and plays an important role in local value creation, with its fine reputation as fine food and good sport. The watercourse of Lærdalselva were in the period 1971-88 exploited to hydropower regulation with three large power plants (Røvik 2014). In addition to the regulation, there has been built fish ladders expanding the anadromous stretch with 20 km, as a mitigating measure. The river was in 1996 infected by the parasite *G. salaris* (Ziętara et al. 2008). As early as the following year after the infection, Lærdalselva was treated twice with rotenone (Bakke et al. 2007). The treatment did not succeed, and in 1999 *G. salaris* was re-confirmed in Lærdalselva. A new treatment was locally not desirable because of the enormous fish death rotenone had led to. In 2005 an alternative to rotenone came: acidic aluminium. This is a much less invasive way to treat an infected river, however more complicated and demanding. The processing involves that the river is applied an aluminium solution, which in correct concentrations is lethal to *G. salaris*, but not fish (Pettersen et al. 2007). Unfortunately the treatment failed to succeed and *G. salaris* was detected in Lærdalselvi again in 2007 (Mo 2007). In 2011, a large-scale treatment with acidic aluminum supplemented with rotenone in inaccessible places, was conducted. The efforts kept going until the end of 2012, and at present the treatment appears to be successful (Hindar 2014).

Anthropogenic-induced environmental factors affecting anadromous brown trout may have severe consequences on growth, thus important life-history traits. This study compare life-history trait values in anadromous brown trout in Lærdalselva during four periods with differential human-influenced environmental regimes: Before hydropower (1954-1974), after hydropower regulation (1974-1996), hydropower regulation and *G. salaris* (1996-2011, i.e., including the flawed *G. salaris* treatments) and present times (2012-2014). I frame these periods as treatment periods, and, in particular, I explore the following research questions:

- Are there changes in growth patterns between treatment periods, both in the river and the marine environment?
- Are there changes in age and size at smolting among treatment periods?

Eventual changes will be discussed in relation to environmental factors that have changed over the treatment periods and whether the changes can be attributed to adaptation processes.

2. Materials and methods

2.1 Study Area

2.1.1 Sognefjorden

Sognefjorden is located in Sogn og Fjordane county in Norway, and extends from Skjolden in Luster municipality, to Ytre Sula in Sollund municipality. It is 205 kilometres long and 1308 meter deep, and this makes it the longest and deepest fjord in Norway (Kristensen et al. 2011). There are several fjords in connection with Sognefjorden, upon which Lærdalsfjorden is one of them. This fjord is approximately 9 kilometres long, and located on the south side of the Sognefjord, in the municipality of Lærdal. Lærdalselva runs ino Lærdalsfjorden at the city centre of Lærdal municipality, Lærdalsøyri. In addition to Lærdalselva, 18 rivers holding salmonids runs into Sognefjorden, which makes the fjord some of Norway´s main areas for salmonids. The significance of these watercourses is stipulated through the establishment of Sognefjorden as a national salmon-fjord by the Norwegian parliament. Furthermore five rivers with particular significance is determined as national salmon rivers; Vikja, Nærøydalselva, Flomselva, Lærdalselva and Årøyelva (Stp. 32 2006-2007)

2.1.2 Lærdalselva

The river Lærdalselva is located in Lærdal municipality in Sogn og fjordane countie, and is formed by the tributarities Mørkedøla and Smedøla. These rivers have their origin respectively from Hemsedalsfjellene and Fillefjell (Solbakken et al. 2012). The river is in total 44 kilometres and has its outlet in Sognefjorden by Lærdalsøyri. The river catchment is 1183 km^2, of which 1000 km^2 is above 900 meters above sea level. The river was regulated to hydropower in 1974 by the construction of Borlaug power plant. The hydropower regulations initiated the construction of four fish ladders in Lærdalselva as a mitigating measure in 1972 (Romundstad 1984). These ladders expand the anadromous stretch from Skjurhaugfoss to Heggfoss (41 kilometres) (Romundstad 1984). However, the lowermost fish ladder in Skjurhaugfoss has been closed since 1996 due to the *G. salaris* infection (Kristensen et al. 2011).

2.1.3 Water discharge and temperature

The average water discharge in Lærdalselva is at 36,4m^3/s, with a general low water discharge <20 m^3/s in winter. Spring floods occur in order to the snowmelt in May and June, and stabilizes below 30 m^3/s by august. Water from Mørkedøla and southern parts of the catchment is piped down to Borlaug power plant (*Figure 2*). This means that the water discharge above Skjurhaugfoss is greatly reduced on this stretch (Saltveit & Styrvold 1983). Until 1988 the outlet from Borlaug powerplant was below and in Skjurhaugfoss, which resulted leveled water discharge on this strech (Saltveit 1986). Stuvane Power plant came into operation in 1988, and utilizes water from Borlaug power plant. There is a defined minimum water discharge between Borlaug and Stuvane powerplant, and in periods of drought the water from Borlaug has it outlet in Skjurhaugfoss. Stuvane powerplant is preferably intended to run in the winter, but can also run in summer if the water discharge constitutes a salmonoid migration barrier. These power plants has a direct cause in lower water discharge, and has reduced flood events in Lærdalselva greatly (Holmquist 2000). In general it can be argued that Lærdalselva has received a greater water discharge in winter and less water discharge in summer (Brooks et al. 1989; Johnsen & Jensen 1997).

Lærdalselva is a cold river, as it drains high mountain areas. Temperatures vary greatly between years, especially in the summer. The highest temperatures occur in july, august and September, but rarely obtains temperatures above 15 ºC (**Figure 7**).
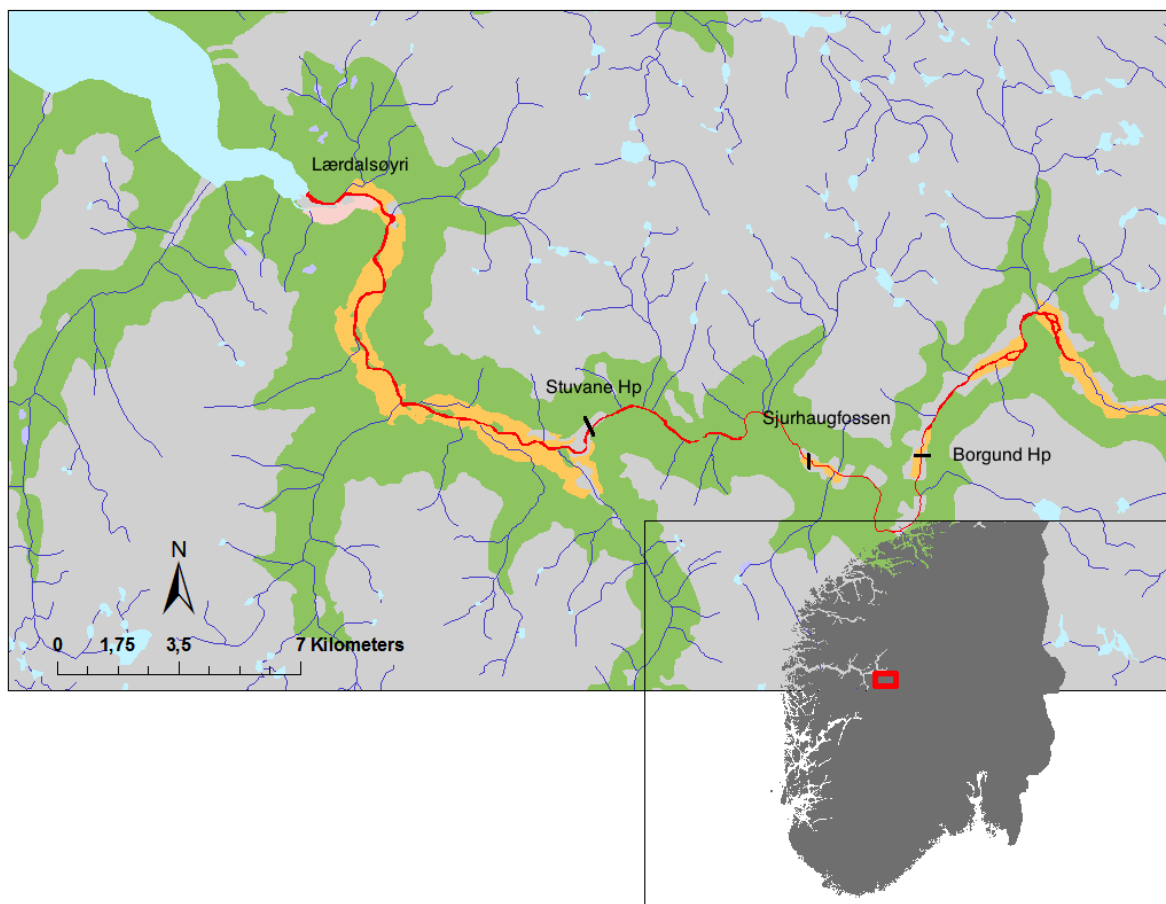
Figure 2. Map showing large parts of the anadromous stretch of Lærdalselva.

2.2 Study species

In this study on growth patterns, and variation in age and size at smolting my study species is the anadromous brown trout (**Figure 1**). My study system, Lærdalselva runs into coastal areas, and holds both resident Brown Trout and migratory anadromous brown trout. In the nineteenth century, these two were distinguished as separate species, but Dahl (1904) observed that inland resident brown trout could move downstream and develop into anadromous brown trout. In addition, numerous field observations has shown that non-anadromous and anadromous trout can spawn together, which is also documented by genetic studies (Jonsson 1985; Hindar et al. 1991). Although we are speaking of the same species, it can be reasonable to distinguish the species into different forms, depending on the habitat they are exploiting. The brown trout living their entire life in their natal stream: Resident brown trout (*S. trutta* forma fario). The brown trout migrating to a downstream lake, laketrout (*S. trutta* forma lacustris) or the brown trout migrating to the sea, anadromous brown trout (*S.trutta* forma *eriox*)(Klemetsen et al. 2003; Jonsson & Jonsson 2011).

The anadromous brown trout has its natural distribution chiefly in the East Atlantic, where it ranges from Iceland in the North West, the tributaries of the White Sea in the North East, and the river Douro on the border between Spain and Portugal, in the South. However, wide environmental tolerance and migratory behaviour, and human introduction, has made the distribution worldwide. It is now present in all major parts of the world except the Antarctic regions (Klemetsen et al. 2003).

2.2.1 Temperature

Temperature is the most important factor affecting the energy budget and success in exothermic fishes (Jonsson & Jonsson 2011), and the major factor that constraints the distribution of brown trout (Elliott 1994). Metabolic processes and growth, as well as the timing and duration of most life-history traits in brown trout are related to temperature (L´Abée-Lund et al. 1989; Jonsson & Jonsson 2011). It is proven seasonal changes in growth in anadromous brown trout populations from rivers at different latitudinal clines, which are circumstantial evidence of the temperature effect on growth (L´Abée-Lund et al. 1989). The anadromous brown trout is poikilothermic, and their metabolic energy costs increase with water temperature (Jonsson & Jonsson 2011). Development and growth takes place within

thermal limits, whereupon little evidence suggest local adaption in thermal tolerance (Elliott 1994; Jonsson & Jonsson 2011). Thermal performance curves for several brown trout populations have been constructed to predict responses to changes in temperatures. The Elliot Growth model suggests lower- and upper temperature limits for growth between 3.8 °C and 21.7 °C (Elliott, J. M. et al. 1995), with an optimum temperature for growth between 12.8 – 13.6 °C. These are studies from England, and Norwegian studies has shown that the optimum temperature for growth in anadromous brown trout may be higher (L´Abée-Lund et al. 1989; Forseth et al. 2009). Using 15 °C as an optimum temperature, the variation in parr growth in 34 Norwegian anadromous brown trout populations could be explained by temperature (L´Abée-Lund et al. 1989). As a concluding remark different studies on growth rate of brown trout has proved to be increasing with temperatures from 5 °C to 13-17 °C, and has decreasing growth to no growth at temperatures over 23 °C (Elliott, J. M. et al. 1995; Forseth et al. 2009; Jonsson & Jonsson 2011). Growth analyses on resident brown trout from Lærdalselva showed that maximum growth and nutrient absorption was obtained at 16 °C (Forseth & Jonsson 1994). Brown trout are oxygen demanding species and requires a sufficient oxygen saturation in the water, especially during embryo development (Jonsson & Jonsson 2011). in general brown trout shows low tolerance to high water temperatures, because warm water has low solubility of oxygen.

Figure 3: Anadromous brown trout from Sogn wintering in the river.

2.2.2 Life histories and habitat preferences

The anadromous brown trout spawns in the autumn, typically from September to December (Klemetsen et al. 2003). Females dig their nests on stone and gravel bottoms, and cover the fertilized eggs in their nest after spawning. The temperature is an important factor for incubation-time and endogenous larval feeding, nevertheless the hatching of the eggs takes place the subsequent spring (Klemetsen et al. 2003). Environmental disturbance and stress may cause earlier egg-hatching at unfavourable times (Næsje & Jonsson 1988). The Alevin stage lasts from hatching of the egg, to the end of dependence on the yolk sac as the primary nutrition source. The fry now starts the real fight for resources, and are aggressive and territorial (Klemetsen et al. 2003). They have to start external feeding and need food items of the correct size at the right time. This period is therefore characterized with high mortality rates (Jonsson & Jonsson 2011). The fry utilize shallow areas in the river, roaming around for food and shelter against predators and high water currents (Heggenes 1989; Klemetsen et al. 2003). As the fry grow larger they disperse, and take larger food items such as insect larvae and surface arthropods. This juvenile migratory trout is often called a parr (Klemetsen et al. 2003). The most important habitat variable is water depth, whereupon brown trout smaller than 7 cm is most common in shallow areas up to 20-30 cm (Heggenes et al. 1999). Brown trout parr is known to be more shy than Atlantic salmon (Bremset & Heggenes 2001), and access to river beds, vegetation, stones or riffles are all important factors in their choice of habitat (Borgstrøm & Hansen 2000). When the parr have reached a certain length and age, they can smolt and move to sea for feeding (L´Abée-Lund et al. 1989). Energetic status and growth in the juvenile freshwater phase seems to be an important individual factor affecting the decision to become a seaward migrant (Jonsson 1985; Forseth et al. 1999; Boel et al. 2014). The anadromous trout now commences a physiological and morphological adaption, preparing the fish for a marine life. This includes changes visual pigments, buoyancy, metabolism, behaviour and changes in the ionic regulation that improves salinity tolerance (Hoar 1988; Jonsson & Jonsson 2011). The regulating factor of the smolting process are known to be responsive to environmental changes such as temperature and water discharge (Jonsson 1991 ; Hembre et al. 2001), but even more important; Photoperiod. Increased day length advances the smolting processes, and works as a timer (Wedemeyer et al. 1980). Temperature on the other hand, affects the rate of developement. (McCormick et al. 2002). Both water discharge and temperature can work ass important environmental cues for the onset of seaward migration (Hembre et al. 2001; Urke et al. 2010). There are different

theories on why parr undergoes this habitat shift. Strong theories are based on the growth benefits to utilize the more productive marine environment, and to avoid adverse environmental conditions such as icing and drought (Borgstrøm & Heggenes 1988; Klemetsen et al. 2003). The most common smolt ages are 2 and 3 years over large parts of the distribution area (Jonsson & Gravem 1985), however the smolt age is strongly connected to water temperature (L´Abée-Lund et al. 1989). From 102 European rivers between 54 °N and 70 °N, mean smolt ages from anadromous brown trout ranged between 2.1 years to 5.6 years (Jonsson & L'Abée-Lund 1993). This study could not conduct any correlation between smolt size and latitude or temperature. The size of the smolt has on the other hand been proven larger and older in large brooks, compared to small (Jonsson et al. 2001). Most of the smolt migrates for feeding in the ocean within a short period in the spring or early summer (Jonsson & Jonsson 2002). Tagging experiments from 2009 in Lærdalselva has revealed the window of this migration to range within 29 April to 29 June. Changes in water flow tend to induce this up and downstream migration (Urke et al. 2010). Once in the sea, the general pattern is that the anadromous brown trout feed in the fjord and coastal waters during summers, often within a 100-kilometre range from the outlet (Klemetsen et al. 2003). Both the immature and the mature fish can return to fresh water for spawning and wintering the following summer or autumn, preferably to their river of origin (Jensen 1968; Jonsson 1985). Some individuals however tend to spend the winter in the sea, adjacent lakes or vary their winter residence between the river and the sea (Jonsson & Jonsson 2002; Rikardsen et al. 2007). A long-term study from the arctic region also has proven several anadromous brown trout to overwinter in other watersheds, nearby their river of origin (Jensen et al. 2015) The tagging experiments in 2008-2009 from Lærdalselva documents that the smolts exploit areas in the Sognefjord, especially inner parts in the northern adjacent fjords. Portions of the larger fish prove to reside in the outer parts of Sognefjorden. These are long migrations, and to some extent, much longer migrations than reported in other studies on anadromous brown trout (Kristensen et al. 2011).

2.2.3 Competition and density

Competition for fundamental recourses such as food and territories takes place between species, and can be an important population regulatory factor (Jonsson & Jonsson 2011). The anadromous brown trout in Lærdalselva is coexisting with Atlantic salmon, and these have due to ecological similarities a large spacious niche overlap (Heggenes et al. 1999).

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Dominance and social status is important factors in growth and survival in salmonids, as the dominant individuals can exploit the positions that give the most energetic yield. Inter and intraspesific competition takes place within cohorts and between cohorts. The intracohort competition is however known to be strongest, as aggressive behaviour is most common between individuals of the same size (Elliott 1990) Furthermore several studies have shown a negative relationship between individual growth and population density (Jenkins et al. 1999; Jonsson & Jonsson 2011).

2.3 Data collection

2.3.1 Fish sampling

All The scales in this study are sampled from anadromous brown trout captured in Lærdalselva. Fish has been sampled in Lærdalselva during the period 1950- 2014 by anglers, scientists and other stakeholders. The old material from the 50s and 60s are mainly related to the impact studies before the hydropower construction. Bjørn Olav Rosseland, who is one of my supervisors have provided the material, which I have access to. In relation to the first rotenone treatment in Lærdalselva in 1997 a huge amount of fish died. The veterinary institute in Trondheim collected scales from all these, in which I have analysed a small part of.

The material from recent years has been provided by NIVA (Norwegian Institute of Water Research). These are fish mainly captured using a portable electrofishing gear, which is an important sampling gear for fish in wadeable running waters (Forseth & Forsgren 2009). Experienced anglers have also captured some of the fish. During fieldwork, I was a part of the KUSTUS project and took part in many different operations. Among other electrofishing, scale sampling and surgical tagging of fish from Lærdalselva, Aurlandselva, Årdalselva and Fortunselva. The scales were collected from the area where the first scales are formed, above the lateral line between the dorsal fin and adipose fin (Borgstrøm & Hansen 2000), and then dried in envelopes holding information about each individual. The tagged fish are being registered by acoustic transmitters different places in Sognefjorden, to form an image of the migration patterns of the different populations of anadromous brown trout and Atlantic salmon in Sognefjorden (Urke et al. 2010).

Figure 4: Electrofishing

2.3.2 Age determination and back-calculation of growth

Age and growth of the fish were determined by scale reading. Approximately 200 scales from fish with growth before hydropower regulation (1954-1970), 94 scales from fish with growth after hydropower regulation (1974-1996), 120 scales from fish with growth after hydropower regulation, *G. salaris* infection and *G. salaris* treatments (1996-2011), and 50 scales from fish with growth from recent years (2012-2014) includes in this study. In addition 40 scales from three neighbour rivers (Aurlandselva, Fortunselva, Årdalselva) from 2013. This is to compare the growth in the marine environment between neighbouring rivers.

Table 1: Overview of scale samples from Lærdalselva

Sampling year	n.	Treatment	Source
1956	17	Before hydropower	Bjørn Olav Rosseland
1963	49	Before hydropower	Bjørn Olav Rosseland
1964	60	Before hydropower	Bjørn Olav Rosseland
1966	21	Before hydropower	Bjørn Olav Rosseland
1970	49	Before hydropower	Bjørn Olav Rosseland
1994	14	Hydropower	NIVA
1997	79	Hydropower	Vet. inst Trondheim
2008	29	Hydropower, *G. salaris* and *G. salaris* treatments	NIVA
2009	32	Hydropower, *G. salaris* and *G. salaris* treatments	NIVA
2012	62	Hydropower, *G. salaris* and *G. alaris* treatments	NIVA
2013	44	Present times	NIVA
2014	14	Present times	NIVA

Each scale has been carefully selected to satisfy essential requirements, and with prior knowledge of the fish length. Only scales with a small central plate has been used (Jonsson & Stenseth 1976). Most of the old scales were fragile, and have not been cleaned. The scales from recent years were cleaned with normal hand soap and thereafter dried before shooting. Each scale was placed between two microscope slides, and photographed with a camera (Leica DFC320. 0.63X magnification), connected to a stereoscopic microscope (Leica MS5, 16x magnification). Measurements on each scale were carried out in the program image pro express 6.3.0.531 for windows XP/vista (copyright Media Cybernetics, Inc.) The first scale readings, and all scales difficult to interpret, has been analysed in cooperation with with competently personnel. Thrond O. Haugen, Reidar Borgstrøm and Atle Rustadbakken have guided me in this work.

Anadromous brown trout are coexisting with stationary Brown Trout in Lærdalselva, and the scale samples sometimes only framed "Trout". In those cases I distinguished them by looking

at the recognizable pattern one can see from an anadromous brown trout scale – the clear contrast between the river and sea growth (Frost & Brown 1967).

To estimate the age of the fish, annual zones on a scale are characterized by a succession of bands of wide-spaced and narrow-spaced circuli. The circuli are formed close together in winter when the growth is poor and farther apart in summer when the growth is good (Jonsson 1976; Jonsson & Jonsson 2011). From the scales of the anadromous brown trout in Lærdalselva the freshwater winter annuli was identified by the short distances between the circuli, and sometimes forking of the circuli (Jonsson 1976). An even more wide-spaced circuli distance than seen in the freshwater summer growth due to the improved feeding opportunities, indicated the entering of the sea. Furthermore, the sea-winter bands were identified by shorter circuli distances and sometimes forking of the circuli (Dahl 1910). The forming of these annuli is determined by low water temperatures during winter season in temperate European climates (Elliott 1989). It's meaningful to mention that this scale reading theory sometimes collides with reality. The anadromous brown trout complex way of living make almost each scale unique and the pattern from one cohort can differ tremendously from another. For example can the period when entering seawater occur very diffuse on a scale, as the anadromous brown trout can exploit different habitats, for example brackish water. In addition, there is not unusual for the anadromous brown trout to return to their home river shortly after migration (Jonsson & Gravem 1985). The fish was aged using a standard notation following Dahl (1910), which involved counting winter annuli. Andromous fish species develop spawning marks, and these are identified by eroded circuli on the side edge of the scale (Dahl 1910). However, spawning marks are less common in anadromous brown trout than in Atlantic Salmon. Additionally they are also less destructive, hence the annuli in most cases are intact and recognizable (Jonsson et al. 1991). Regardless, illegible scales were rejected.
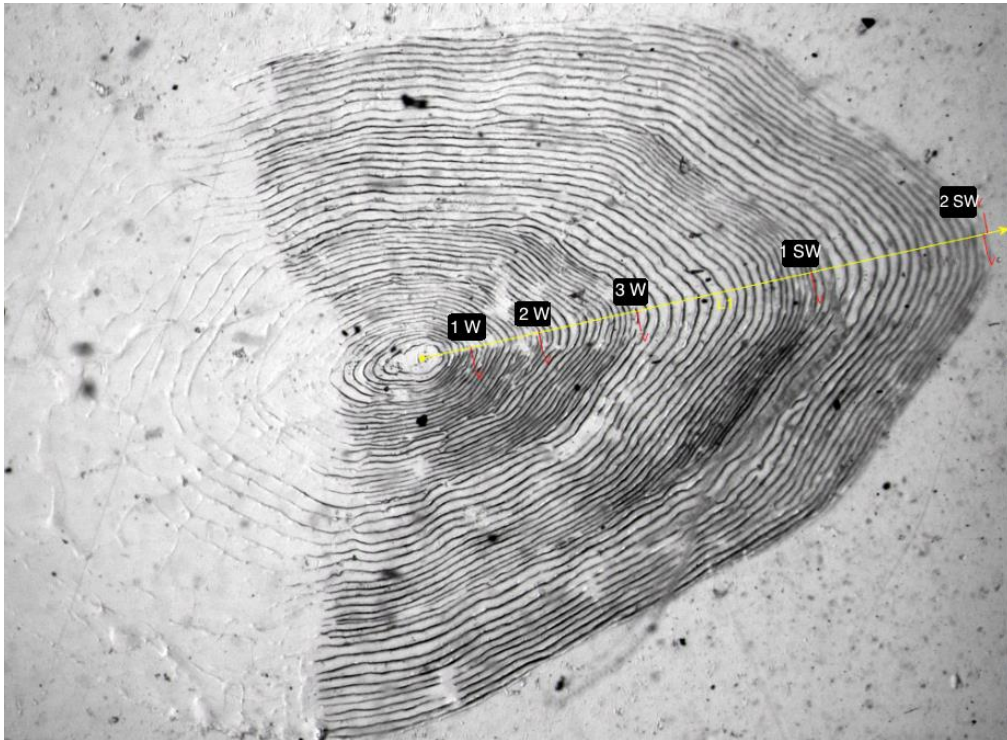
Figure 5. Scale from anadromous brown trout. The longest axes of the scale from the focus to the end of the scale (yellow line) and winter zones (red lines) are illustrated.
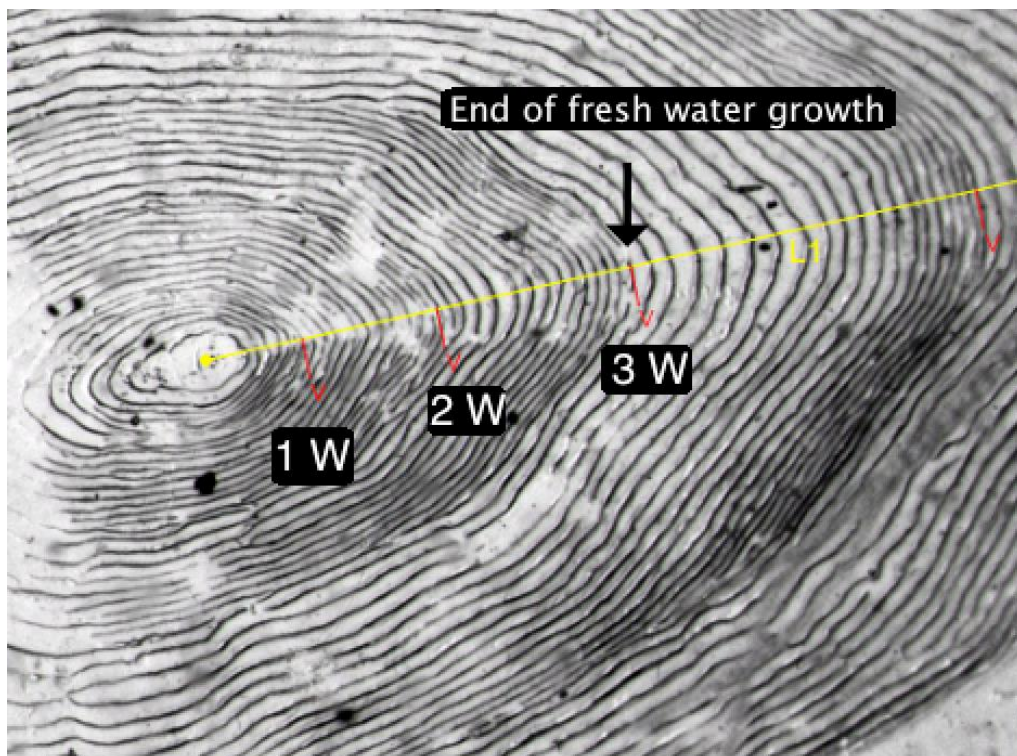

Figure 6. Section of scale from anadromous brown trout, illustrating the freshwater annuli (1-3W) and end of freshwater growth zone.

The scale size and annual increments were measured along the longest axes of the scale, from the focus to the end of the scale using the picture analysing software Image pro express 6.3. Growth was back calculated using the Lea-Dahl-equation: $L_n = (S_n/S) \cdot L$

L_n = Length of the fish at age n

L = Length of fish at capture

S_n = Length of the scale at age n

S = total length of scale

This linear-back-calculation assumes that there is a direct proportionality between the fish length and the size of the scale (Lea 1910; Jonsson et al. 1991).

2.3.3 Measurement errors

The material for measurement error consisted of ten randomly selected scales. All ten scales were measured 10 times in random order. This practise was conducted over 3 days, and with a fellow conspirator to make sure I did not recognize the scales. The analysis of measurement error comprised the standard error of the total scale radius and smoltradius. The scale measurement errors were 1.6% ±0.9% (SD) for the scale smoltradius, and 0.74% ±0.75% for the total scale radius. The measurement error declined as more readings were carried out.

2.3.4 Environmental data

Meteorological data was obtained from the Norwegian Meteorological Institute and the database "eKlima" (Meteorologisk institutt 2015). Water temperatures from 1964-2014 and water discharge from 1961-2014, have been registered from an observation station at Tønjum in Lærdalselva. The Norwegian Water Resources and Energy Directorate (NVE) provided these data. The water discharge is further on divided in three percentiles (i.e., 10%, 25%, 50%) indicating the per cent of a distribution. In some cases the water temperature is used as total degree-days from an appropriate starting date, above 4 °C. Air temperatures was obtained from weather stations in Lærdal municipality, at Tønjum (1964-1996) No. 54130),

Molde (1996-2008 No. 54120) and Lærdal IV (2008-2014 No. 54110). North Atlantic Oscillation (NAO) data was obtained from National oceanic and atmospheric administration, driven by the U.S department of commerce. This study uses only the NAO in Desember-March as an index of amount of snow in the catchment area. In order to fit models to be used for predicting water temperatures the 10 years of missing water temperatures (1954-1964), air temperatures, NAO, water discharge and day of year was used (DoY).

2.4 Statistical analysis

A key aim of this study is to explore whether anadromous brown trout traits expressed in both freshwater and the marine environment life stages have changed under different environmental regimes during the 1950s-to-present periods in Lærdalselva. This was done by discretizing this period into four regimes, which I from here onwards will refer to as "treatment periods". These were:

1) Before hydropower (Before HP): prior to 1974
2) Hydropower (After HP): 1974-1996
3) Hydropower, *G. salaris* and *G. salaris* treatments (HP&gyro): 1996-2011
4) Present times(Present): 2012-2014

2.4.1 Air-to-water temperature model

In order to supplement a non-complete water temperature data series from Tønjum (1964-1996) an air-to-water temperature model was fitted as a linear mixed effects model using the R package nlme (linear and nonlinear mixed effects models)(Pinheiro & Bates 2000). The daily mean water temperature data during May-October were fitted fixed effects of mean daily air temperatures, moving average water temperatures over 5 days, water discharge and annual winter NAO (December-March) along with day of year (DoY). The winter NAO was included as a proxy for snow-depth conditions in surrounding mountain areas embedded in the watercourse (fitted as an interaction with DoY as the influence of snow-melting will decrease over time). Alternative autocorrelation orders were also fitted the model, but tended to have convergence problems for autocorrelation structures beyond two days. In order to find the most parsimonious model structure that best balance bias and model precision, I used

Akaike's Information Criterion (AIC) to select among candidate model structures (Akaike 1974)

2.4.2 Growth analysis

Effects from various environmental variables such as water temperature, water discharge and treatment conditions (i.e., before HP, After HP, HP&gyro, Present) on back-calculated growth rates and various size responses were quantified by fitting linear models in R (MacCullagh & Nelder 1989). Anova effects tests were retrieved using the anova-procedure in R. Model selection among the fitted candidate models were performed using AIC.

2.4.3 Smolt reaction norms

In order to explore if smolt reaction norms (SRN), i.e., the probability of an individual being smolt as function of age and (back-calculated) length, I fitted three alternative generalized linear models to the binomial response "smolt" (MacCullagh & Nelder 1989). This smolt-variable was assigned '0' for age and the corresponding back-calculated length values at which an individual had not yet smoltified and '1' for ages and lengths at which the individual had smoltified. This assignment process was based on the individual's back-calculated growth trajectory assuming a marked increase in growth rate to accompany the post-smolt period (Jonsson & Jonsson 2011). The three candidate models were Pr(smolt)=:

1. Length*age
2. Length*age+treatment period
3. Length*age*treatment period

Again, AIC-based model selection was undertaken and outcomes in support of either model 2 or 3 will be interpreted in favour of adaptational changes in the SRN in the Lærdal anadromous brown trout population (Heino et al. 2002)

As mentioned, model selection for all the analysis was performed using AIC and models with AIC differences (□AIC, i.e., the difference between a given model's AIC-value and the model with the lowest AIC) below 2 were considered as having considerable support (Burnham & Anderson 1998).

3. Results

3.2. River water discharge

There was a significant change in water discharge during May-September between treatment periods (**Table 2**, p=<0.05). Lærdalselva has experienced reduced discharge during all periods following the river regulation, with the lowest discharge during the HP-period (13.6±1.0 m^3/sec lower discharge compared to the Before-period, **Table 2**) and slightly lower reduction for the two remainder periods (10.1±0.9 and 10.8±1.7 m^3/sec, respectively).

Table 2: parameter estimates on the effects of treatment periods on discharge m^3/sec

Parameter estimates				
	Estimate	SE	t value	p-value
Intercept(Before HP)	46.6963	0.7076	65.99	< 2e-16 ***
treatment(After HP)	-13.5748	1.0007	-13.565	< 2e-16 ***
treatment(Gyro&HP)	-10.0666	0.9226	-10.911	< 2e-16 ***
treatment(Present)	-10.7897	1.6845	-6.405	1.59e-10 ***

3.3 River temperatures

There were no significant differences in mean growth-season water temperatures before and after the HP regulation in 1974, nor between any of the other treatment periods (one way anova: F=0.0268, p=0.87). The same result applies to degree-days above 4°C.

The most supported LME air-to-water model for the whole period explained 97% of the variation in water temperature (**Figure 7**). The most supported model contained an interaction effect between mean air temperatures moving-averaged to 5 days, winter NAO, day of year and air temperature (**Table 3**). The selected model had a 1st-order autocorrelation structure.

Table 3. The most supported air-to-water LME temperature model parameter estimates for the whole 1954-2014 period. maX=moving average over x days. DoY= day of year. NAO=North Atlantic Oscillation. The 1st-order autocorrelation coefficient was estimated to be AR(1)=0.87.

| Terms	Estimate	SE	t	p
Intercept	-7.330738	1.716925	-4.269690	<0.0001
Air temperature(ma5)	-1.061345	0.137237	-7.733644	<0.0001
NAO	-2.034292	1.230015	-1.653875	0.098200
DoY	0.120922	0.017318	6.982381	<0.0001
DoY^2	-0.000298	0.000040	-7.504284	<0.0001
Air temperature	0.571223	0.119303	4.788000	<0.0001
Air temperature(ma5)*NAO	0.349806	0.116440	3.004179	0.002700
Air temperature(ma5)*DoY	0.010807	0.001321	8.181122	<0.0001
Air temperature(ma5)*DoY^2	-0.000022	0.000003	-7.579394	<0.0001
NAO*DoY	0.016484	0.012651	1.303007	0.192600
NAO *DoY^2	-0.000031	0.000029	-1.057849	0.290200
Air temperature(ma5)*Air temperature	-0.032485	0.009531	-3.408409	0.000700
NAO*Air temperature	0.107332	0.102196	1.050253	0.293600
DoY*Air temperature	-0.002920	0.001141	-2.559625	0.010500
DoY^2*Air temperature	0.000005	0.000003	1.904055	0.056900
Air temperature(ma5)*NAO*DoY	-0.003209	0.001118	-2.869626	0.004100
Air temperature(ma5)*NAO*DoY^2	0.000007	0.000003	2.671420	0.007600
Air temperature(ma5)*NAO*Air temperature	-0.013907	0.008276	-1.680462	0.092900
Air temperature(ma5)*DoY*Air temperature	0.000263	0.000088	2.991759	0.002800
Air temperature(ma5)*DoY^2*Air temperature	-0.000001	0.000002	-2.819845	0.004800
NAO*DoY*Air temperature	-0.001148	0.000987	-1.162557	0.245000
NAO*DoY^2*Air temperature	0.000003	0.000002	1.143114	0.253000
Air temperature(ma5)*NAO*DoY*Air temperature	0.000133	0.000077	1.730533	0.083600
Air temperature(ma5)*NAO*DoY^2*Air temperature	0.000000	0.000002	-1.678549	0.093300
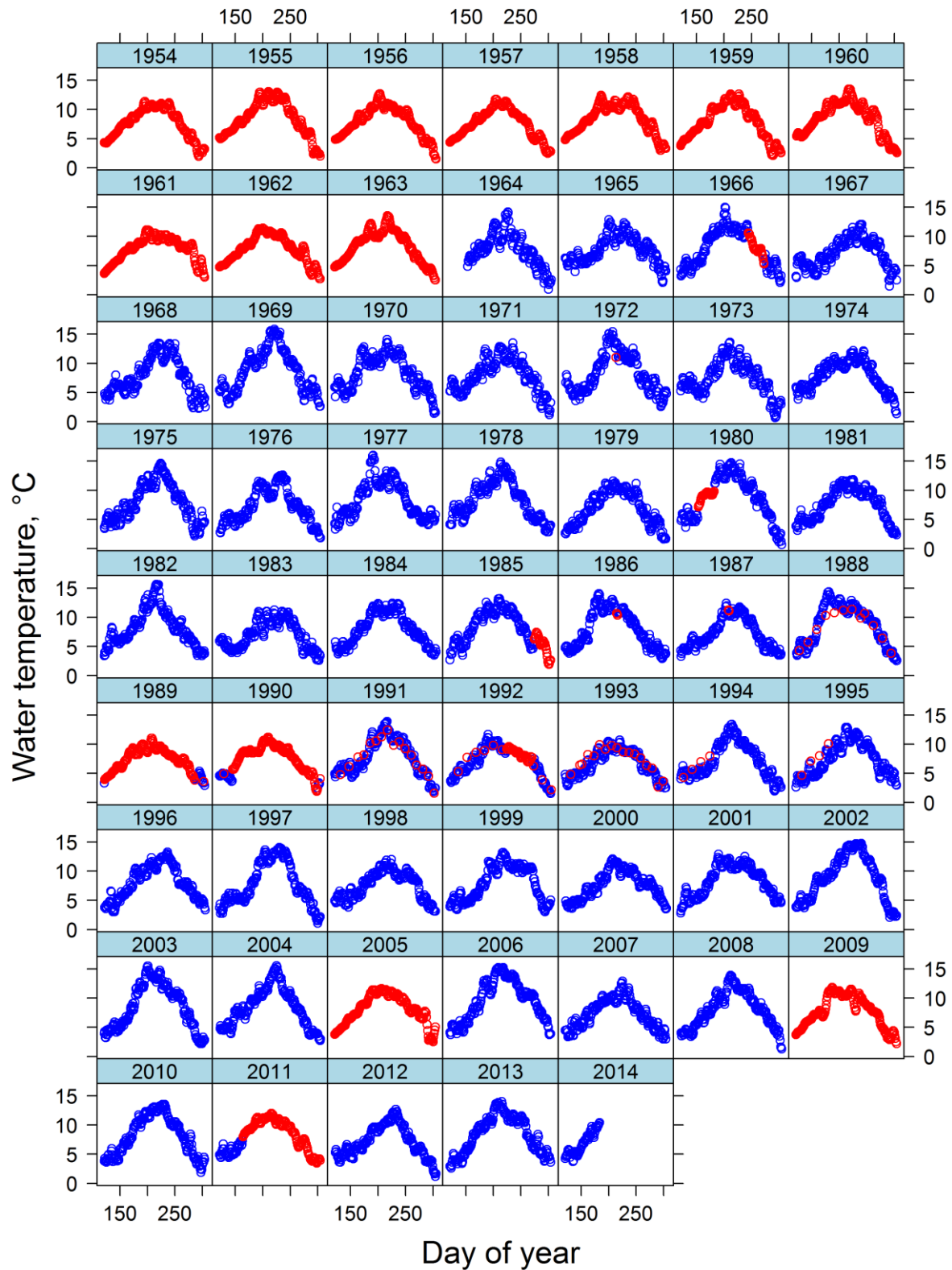
Figure 7: Water temperatures from Lærdalselva 1954-2014 in growth season May to September. Blue symbols indicates actual measurements, and red indicates air-to-water predicted values (**Table 3**)

3.2. Growth analysis

Freshwater

3.2.1. The 1st-year back-calculated length

A one-way anova did not reveal a significant treatment-period effect on back-calculated length at 1st-year (p=0.48). However, there was a weak, but significant difference on back-calculated length at 1st-year between the before HP and after HP treatment periods (p=0.042) after correcting for water temperature (**Table 5**)

The most supported model fitted data on back-calculated length at 1st-year in freshwater showed an additive effect between degree-days above 4°C and treatment periods (**Table 4**). This model was only marginally more supported than the 2nd and 3rd most supported models (ΔAIC = 0.29 and 0.51, respectively).

According to the most supported model degree-days above 4 °C has a positive, though no significant (p=0.13) effect on back-calculated length at 1st-year (**Figure 8**). All treatment coefficients (i.e., the difference between before HP and the respective treatment periods) were negative with significant values for the period after HP (p=0.042, **Table 5**).

Table 4. The most supported models, fitted to back-calculated length at1st-year. dd4 = degree-days above 4°C, Discharge 25% = the annual 25% percentile water discharge value during the growth season (May-October), NAO = mean NAO for December-March period.

Model structure	Df	AIC	ΔAIC
dd4+treatment	6	581.6	0.00
treatment	5	581.8937	0.29
dd4*treatment	8	582.1137	0.51
dd4+NAO+discharge 25%	5	583.4774	1.88
dd4+NAO+treatment	7	583.5556	1.96
dd4+discharge 25%+treatment	7	583.5844	1.98
dd4+NAO+Discharge 10%	5	583.7275	2.13
WaterTemp*treatment	8	583.8085	2.21
WaterTemp+NAO+Discharge 50%	5	584.2429	2.64
WaterTemp+NAO+discharge 25%	5	584.5026	2.90
WaterTemp+NAO+Discharge 10%	5	584.5554	2.96
WaterTemp+discharge 25%+treatment	7	584.7983	3.20
WaterTemp*discharge 25%+NAO	6	586.1757	4.58
WaterTemp+NAO+Discharge 10%+treatment	8	586.5947	4.99
WaterTemp+NAO+Discharge 50%+treatment	8	586.6375	5.04
WaterTemp+NAO+discharge 25%+treatment	8	586.6384	5.04
WaterTemp*NAO*discharge 25%	9	589.8127	8.21
WaterTemp*NAO*discharge 25%*treatment	24	603.4867	21.89
WaterTemp*NAO*discharge 25%*treatment	24	603.4867	21.89

Table 5. Parameter estimates for the most supported general linear model (**Table 4**), testing the effect of degree-days more than 4°C and treatment periods on 1st-year back-calculated length

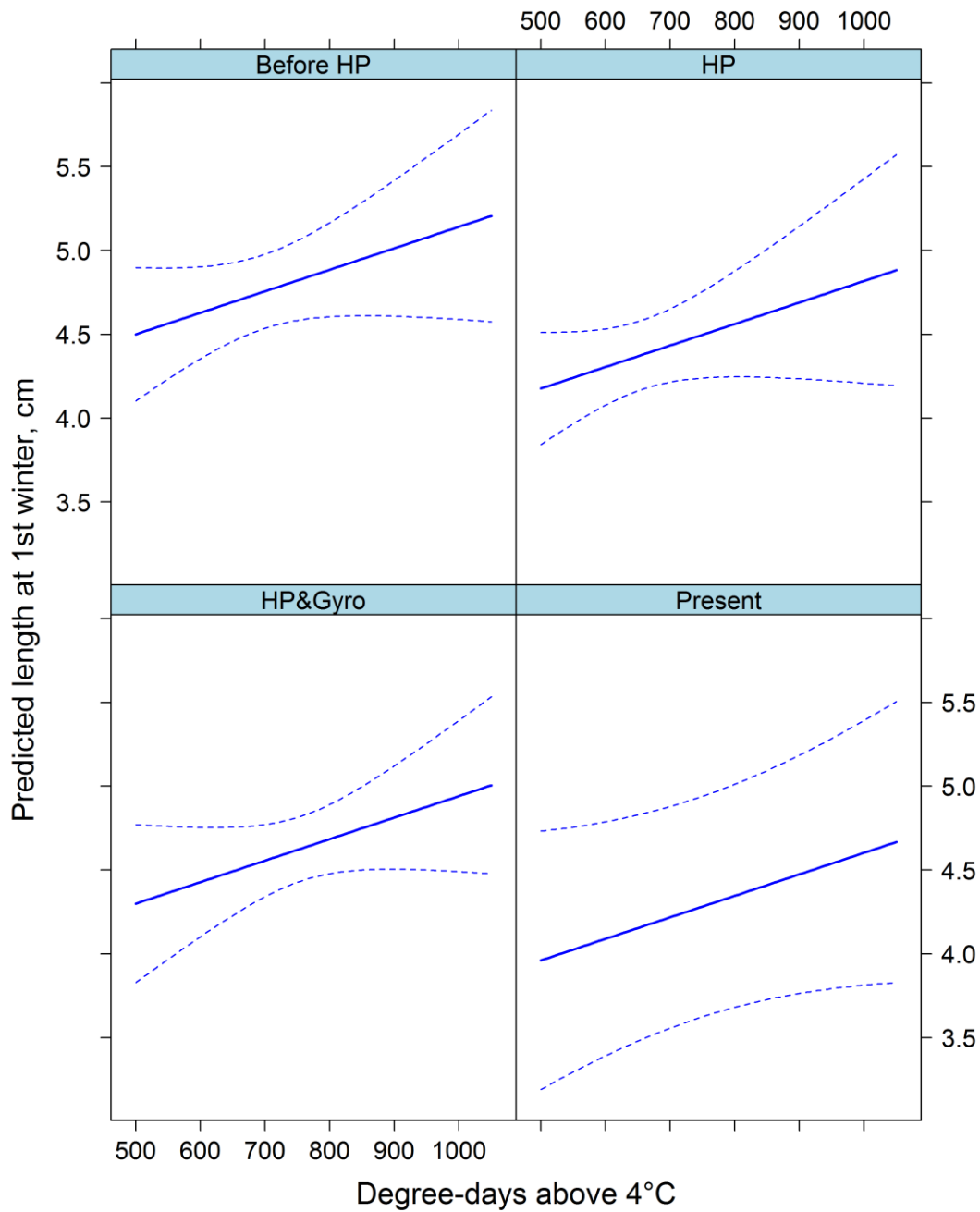| Parameter estimates				
	Estimate	SE	t value	p-value
Intercept(Before HP)	3.8589823	0.6063076	6.365	1.16E-09
dd4	0.0012829	0.0008546	1.501	0.1348
treatment(After HP)	-0.3234173	0.1580447	-2.046	0.0419*
treatment(HP&Gyro)	-0.2007926	0.1582282	-1.269	0.2058
treatment(Present)	-0.5389789	0.3559178	-1.514	0.1314

Figure 8. Predicted back-calculated length at 1st-year as function of degree-days above 4°C and treatment periods. Predicted size is plotted with bold line and corresponding 95% confidence interval as dashed lines. Predictions were derived from the most supported model provided in **Table 4**

3.2.2. The 2nd-year back-calculated growth rate

There was little evidence for an over-all difference in back-calculated 2nd-year growth rate among treatment periods (oneway anova: p = 0.17). The model selection procedure revealed that the 25% percentile growth-season water discharge (Discharge 25%) was a highly supported predictor variable for the 2nd-year back-calculated growth rate (**Table 6**) as it was included in all top-5 models. The most supported model included just this discharge effect. This effect was significantly positive (p=0.036, **Table 7** and **Figure 9**), meaning that back-calculated growth the 2nd-year is positively correlated with higher 25% percentile water discharge

Table 6. AIC table for the most supported models fitted to the data of back-calculated growth made the 2nd-year. Discharge25% = growth season, dd4=degree-days above 4°C, NAO = winter NAO

Model structure	df	AIC	ΔAIC
discharge 25%	3	-144.724	0.00
discharge 25%+dd4	4	-143.5427	1.18
discharge 25%+treatment	6	-143.0964	1.63
NAO+discharge 25	4	-142.8933	1.83
WaterTemp+NAO+discharge 25%	5	-142.7145	2.01
dd4+NAO+discharge 25%	5	-142.7	2.02
discharge 25%*treatment	9	-142.3732	2.35
WaterTemp+NAO*discharge 25%	6	-142.1768	2.55
dd4+NAO+Discharge 50%	5	-141.8706	2.85
WaterTemp+NAO+Discharge 50%	5	-141.8037	2.92
WaterTemp+NAO+Discharge 10%	5	-141.7851	2.94
dd4+NAO+discharge 10%	5	-141.7056	3.02
discharge 25%+dd4+treatment	7	-141.6595	3.06
discharge 10%	3	-141.4301	3.29
discharge 25%+dd4*NAO	6	-141.0752	3.65
WaterTemp*discharge 25%+NAO	6	-140.715	4.01
WaterTemp+treatment+NAO+discharge 25%	8	-139.7525	4.97
WaterTemp*Discharge 10%+treatment	8	-139.261	5.46
WaterTemp*NAO*discharge 25%	9	-139.0122	5.71
WaterTemp*NAO*discharge 25%	9	-139.0122	5.71
dd4*NAO*discharge 25%	9	-138.831	5.89
WaterTemp+discharge 10%*treatment	10	-137.1535	7.57
WaterTemp*NAO*discharge 25%+treatment	12	-136.4271	8.30
dd4*NAO*discharge 25%+treatment	12	-136.4164	8.31
WaterTemp*NAO*discharge 10%	9	-135.2194	9.50
WaterTemp*NAO*discharge 10%	12	-134.0961	10.63

Table 7. Parameter estimates for the most supported general linear model predicting the 25% percentile growth-season water discharge effect on back-calculated growth the 2nd-year.

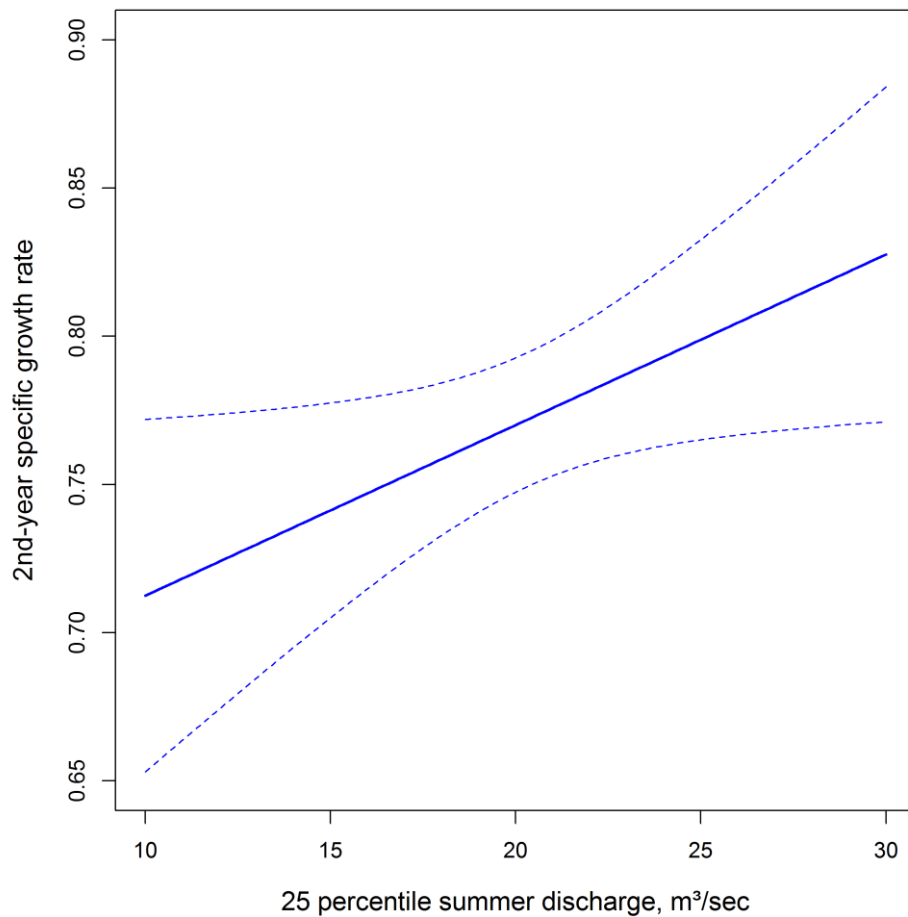| **Parameter estimates**				
	Estimate	SE	t-value	p-value
(Intercept)	0.654859	0.056518	11.587	<2e-16 ***
discharge 25%	0.005759	0.002725	2.113	0.0357 *

Figure 9: Predicted back-calculated specific growth during 2nd-year in fresh water. Growth is plotted with 95% confidence interval (dashed lines). Predicitons were derived from the most supported model provided in **Table 6**

Marine environment

3.2.3 1st-year in sea back-calculated growth rate

The back-calculated length the 1st-year in sea was significantly different among the treatment periods (one way anova: p=0.006, **Table 9**). The model selection procedure revealed that treatment periods was a highly supported predictor variable for the 1st-year in sea back-calculated growth rate, as it was included in all the top 3 models (**Table 8**). The most supported model included just the effect of treatment periods. The coefficient between before HP and the respective treatment periods were both positive and negative. The after HP treatment period shows significant negative values (**Table 9**)

Table 8. AIC table for candidate models fitted to the data of back-calculated growth made the 1st-year at sea.

Model structure	Df	AIC	ΔAIC
treatment	5	-282.4166	0
treatment+Air temperature	6	-280.6736	1.743
treatment+NAO	6	-280.5515	1.8651
Air temperature+NAO+treatment	7	-278.8201	3.5965
Air temperature*NAO+treatment	8	-277.1222	5.2944
treatment*Air temperature	9	-276.1576	6.259
Air temperature*NAO*treatment	16	-275.0692	7.3474
treatment*Air temperature+NAO	10	-274.2549	8.1617
Air temperature+NAO*treatment	10	-274.0447	8.3719
Air temperature+NAO*treatment	10	-274.0447	8.3719

Table 9. Parameter estimates for the most supported model predicting the effect of treatment periods on growth made the 1st-year at sea.

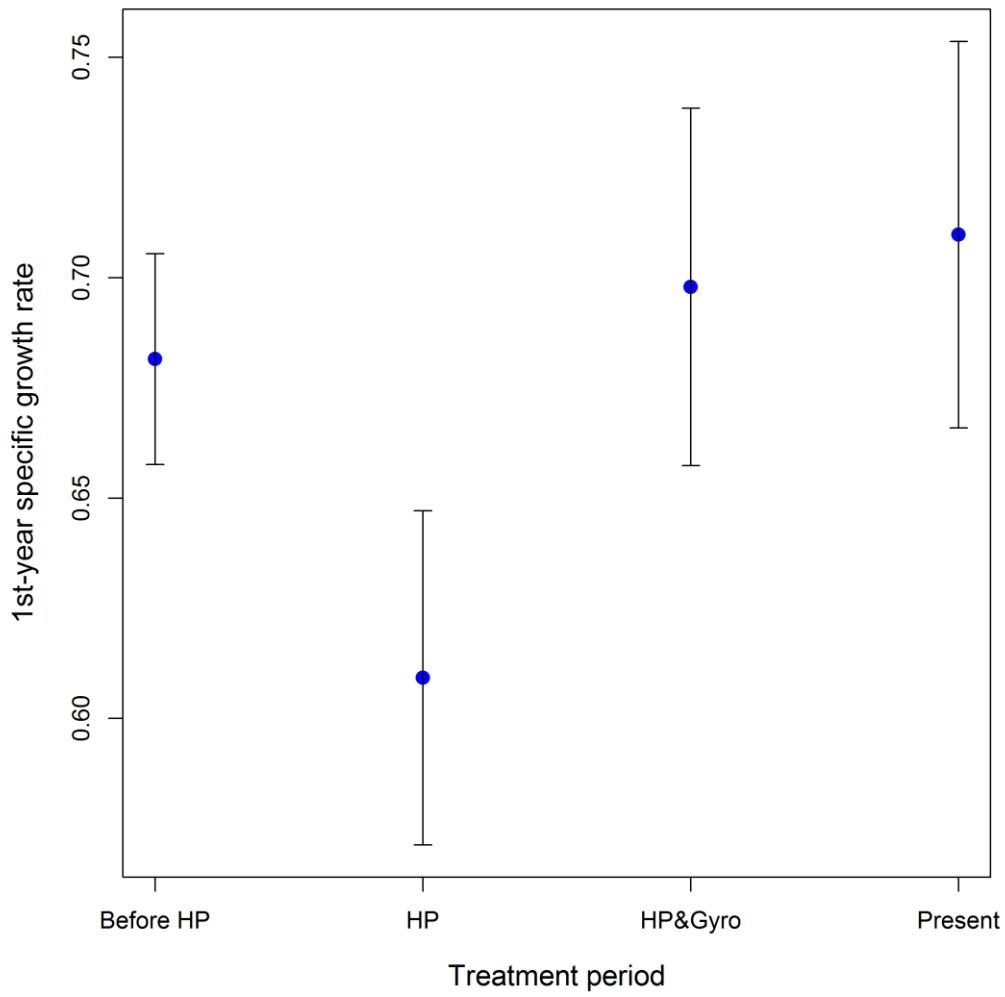| Parameter estimates	Estimate	SE	t-value	p-value
Intercept(Before HP)	0.68151	0.0122	55.842	< 0.05***
treatment(After HP)	-0.07229	0.02285	-3.163	0.00169 **
treatment(HP&Gyro)	0.01637	0.02401	0.682	0.49589
treatment(Present)	0.02821	0.02548	1.107	0.26893

Figure 10: Predicted back-calculated specific growth at 1st-year in sea. Predicted growth rate is plotted with 95% confidence interval (error bars). Predictions were derived from the most supported model provided in **Table 8**

3.2.4. 2nd-year in sea back-calculated growth rate

The 2nd-year back-calculated growth rate in sea was significantly different among treatment periods (one way anova: p=0.005). The most supported model showed an additive effect between treatment periods and air temperature (**Table 10**). The coefficient between before HP and the respective treatment periods were both significant positive (after HP) and significant negative (HP&gyro period).

Table 10. AIC table for the candidate models fitted to predict back-calculated growth made the 2nd-year at sea.

Model structure	df	AIC	ΔAIC
treatment+Air temperature	6	-437.8159	0
Air temperature+NAO+treatment	7	-436.3298	1.4861
treatment	5	-435.8316	1.9843
NAO+treatment	6	-434.7982	3.0177
Air temperature*NAO+treatment	8	-434.5005	3.3154
Air temperature+NAO*treatment	10	-431.3367	6.4792
treatment*Air temperature+NAO	10	-431.2104	6.6055
Air temperature	3	-428.907	8.9089
Air temperature*NAO*treatment	16	-428.1462	9.6697
mod.9(Air temperature*NAO)	5	-426.8622	10.9537

Table 11. Parameter estimates for the most supported GLM predicting the effect of air temperature and treatment periods on back-calculated growth made the second year at sea.

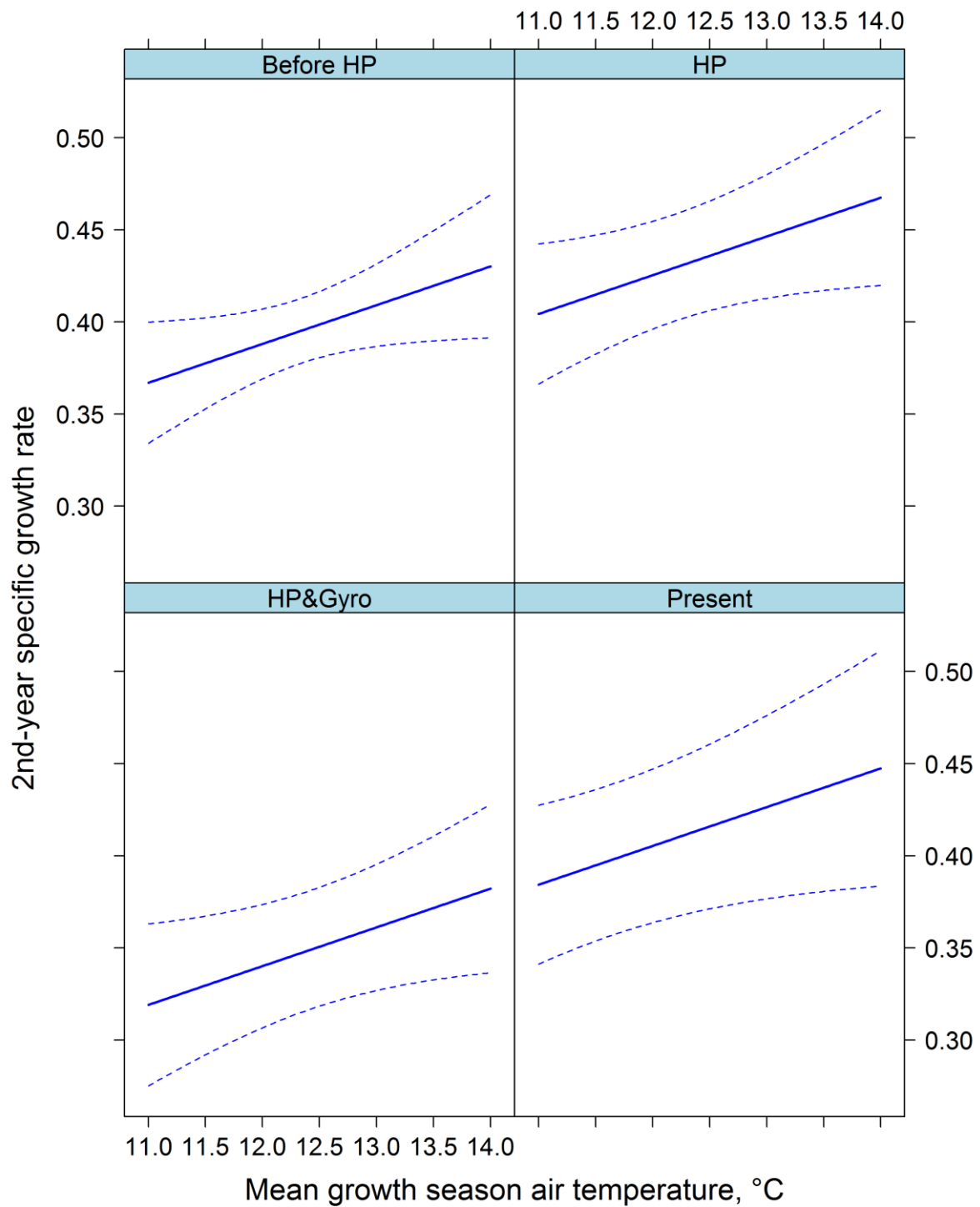| Parameter estimates	Estimate	SE	t-value	p-value
Intercept(Before HP)	0.13553	0.13105	1.034	0.3019
Treatment(After HP)	0.03729	0.01739	2.145	0.0328 *
Treatment(HP&Gyro)	-0.04798	0.01877	-2.556	0.0111 *
Treatment(Present)	0.01727	0.02392	0.722	0.4709
Air temperature	0.02105	0.0106	1.986	0.0480 *

Figure 11: Predicted back-calculated specific growth at second year in sea as function of air temperature and treatment periods. The predicted growth rate is plotted with 95% confidence interval (dashed lines). Predictions were derived from the most supported model provided in **Table 10**

3.2. Smolt reaction norms (SRN)

During the entire study period, the mean age and back-calculated smolt size from Lærdalselva were 2.85 years and 15.4 cm. There was strong evidence for shifts in the SRN over the study period as the most supported GLM included an additive effect of treatment period (**Table 12**). Predictions from this model revealed that the SRN shifted towards higher age and larger size at smolting during the after HP and HP&gyro periods compared to the period before HP (**Table 13, Figure 12**). For the present period, there was no evidence for a different reaction norm compared to the before period.

Table 12. AIC table for models fitted to the data of length and age at smolting

Model structure	df	AIC	ΔAIC
Age*Length+treatment	7	462.3138	0
Age*Length *treatment	16	473.3097	10.9959
Age*Length	4	488.7806	26.4668

Table 13. Parameter estimates and corresponding ANOVA test statistics for the most supported GLM fitted to predict smolt probability as function of age and length and treatment period.

Parameter estimates

	Estimate	SE	z-value	p-value
Intercept(Before HP)	-15.99201	1.7557	-9.109	< 2e-16 ***
Age	3.72917	0.66436	5.613	1.99e-08 ***
Length	1.14395	0.14869	7.694	1.43e-14 ***
Treatment(HP)	-1.73915	0.36529	-4.761	1.93e-06 ***
Treatment(Gyro&HP)	-1.16193	0.30951	-3.754	0.000174 ***
Treatment(Present)	-0.11552	0.47664	-0.242	0.808505
age*length	-0.1981	0.04687	-4.226	2.37e-05 ***

Test statistics

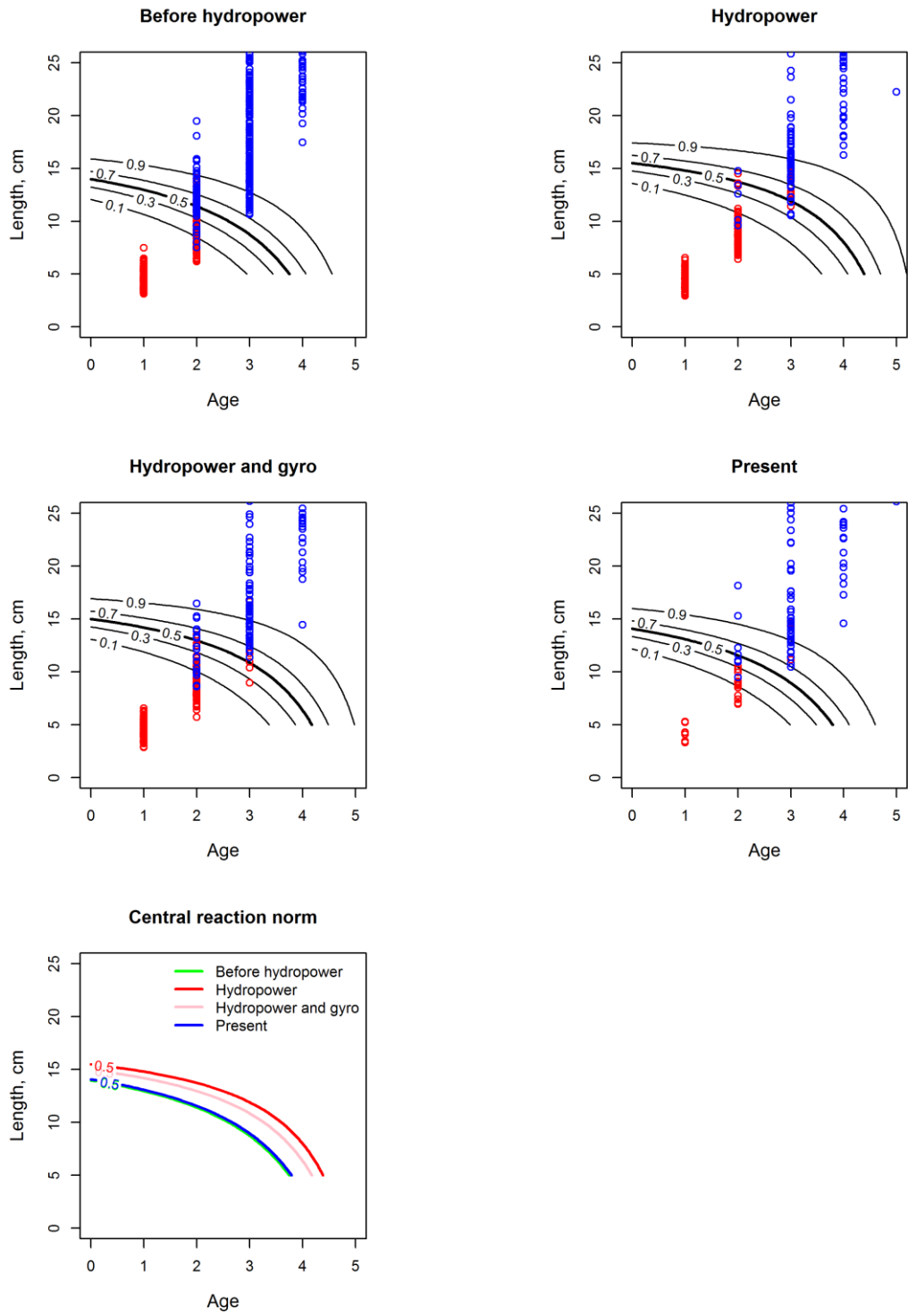|	Df	Deviance	Resid. Df	Resid. Dev	p-value
Age	1	1789.81	1832	675.85	< 2.2e-16 ***
Length	1	186.27	1831	489.59	< 2.2e-16 ***
treatment	3	34.53	1828	455.06	1.533e-07 ***
Age*Length	1	6.74	1827	448.31	0.009408 **

Figure 12: The probabilities of being a smolt at different lengths and fresh water ages in the different treatment periods. Red symbols indicate not smoltified brown trout, and blue symbols indicate smoltified trout

3.3. Between river variation

Back-calculated growth made in 2013, from post-smolts of anadromous brown in four
different rivers, demonstrated to be relatively equal between Lærdal, Fortun and Årdal, with
Aurland as an exeption showing lower growth rate during first year at sea compared to the
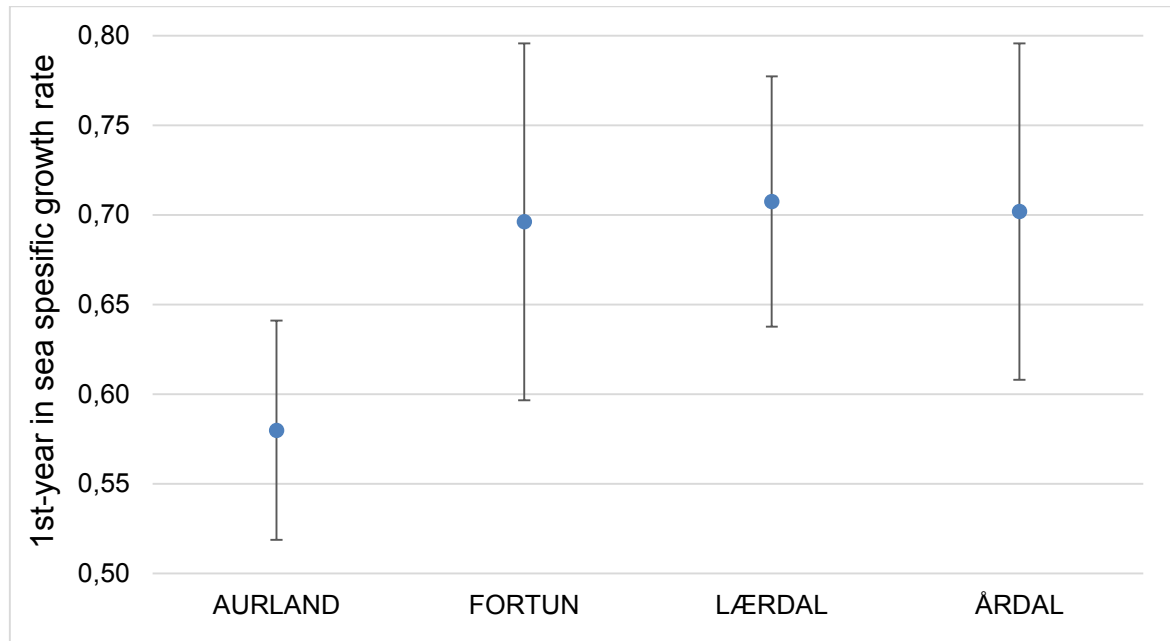other rivers ($p<0.05$, **Figure 13**).

Figure 13: First year in sea specific growth rate between rivers in Sognefjorden, shown with
95% confidence limits.

4. Discussion

4.1. Temperature and discharge variation

As the watercourse of Lærdalselva is regulated for hydropower purposes, one would on a general basis expect altered temperature conditions (Johnsen B.O. et al. 2011). In the river Surna, Northwestern Norway, river regulation caused a 6-8°C reduction in mean growth-season water temperature below the power plant (Brittain & Saltveit 1988). This seems however not to be the reality in Lærdalselva, despite altered flow conditions. Mean water temperatures from Tønjum, 12 km below Borlaug power plant only showed slight differences in temperature. There was no significant difference in mean growth-season measured water temperatures before and after HP regulation. The model for predicting water temperatures is only taking the influence by air temperature and NAO into account, yet explaining 97% of the variation in water temperature.

This study uses the construction of Borlaug powerplant in 1974 to distinguish between the period before and after HP regulation. Using the construction of Stuvane power plant in 1988 as reference would probably generate different temperature results. This powerplant depends on the need for electricity, and is affiliated magazines. Bottom draining of these magazine occur in both winter and summer, and this is known to cause altered temperature regimes (Johnsen B.O. et al. 2011).

Lærdalselva has experienced significantly reduced water discharge during all periods following the river regulation. Altered water discharge after hydropower development is a well-known consequence (Johnsen B.O. et al. 2011).

4.2. Variation in Growth

When discussing the likely effects of growth alternations from human induced environmental changes, one must keep in mind that it simultaneously has been going on an extensive climate change (Jonsson & Jonsson 2009b; IPCC 2014). This is especially valid in the marine environment where fjord dynamics, large natural variability and human encroachments make it difficult to pinpoint various effects on growth patterns. This study does not explore the

effects from experienced fish density. Nevertheless, this effect must not be undermined as individual growth has repeatedly been demonstrated to be density dependent (Jenkins et al. 1999; Jonsson & Jonsson 2011).

4.2.1. Fresh water environment

The anadromous brown trout population in Lærdalselva shows relatively slow growth their first two years of life. This is however the pattern from cold rivers in Norway, rarely obtaining temperatures close to the optimum temperature for growth (L´Abée-Lund et al. 1989) The best model predicting first year growth includes the cumulative temperature experience (degree-days) from water temperatures more than 4 °C and treatment periods. The relationship between brown trout growth and temperature is previously well documented (L´Abée-Lund et al. 1989; Jensen 1990; Elliott, J. A. et al. 1995; Forseth et al. 2009), whereupon growth seems to be net positive from temperatures above 4 ºC (Elliott, J. A. et al. 1995; Forseth et al. 2009). Back-cakculated First-year length is significant worse after HP regulation (**Figure 8**).

Many studies on hydropower development and ecological effects include effects on growth, thereby changed life histories in fishes from changed water temperatures (Johnsen B.O. et al. 2011). Regulation-induced growth reduction has been documented in both salmon and trout. As in the previously mentioned river Surna, where cold water resulting from the hydropower regulation during the growth season caused reduced growth, and delayed smolting (Saltveit 1990a). Although Lærdalselva water temperature has not changed after regulation, the changes in water discharge after hydropower regulation can contribute in the explanation of altered growth patterns. The growth of brown trout in a Norwegian regulated river has been demonstrated to be significantly lower in all age groups after a reduction in water discharge (Sandlund & Jonsson 2014). A study from an artificial environment in tanks, also show that juvenile brown trout exposed to fluctuating or stable low water levels had reduced growth rate when compared to brown trout exposed to a constant high water level, in the same temperature regime (Flodmark et al. 2004).

The growth of salmonids is a complex interaction between a wide range of factors – both biotic and abiotic (Baerum et al. 2013). In poikilothermic organisms such as anadromous

brown trout, water temperature, rate of water discharge, competition and food availability is extremely important factors controlling growth (Jonsson & Jonsson 2011).

Species in streams has evolved life-history strategies in response to the natural flow regime, and altered flow regimes can directly affect the breeding grounds of salmonids. There are studies documenting both increased and decreased densities in juvenile stages of salmonids from Norwegian rivers with reduced water discharge (Johnsen & Hvidsten 2004; Saltveit & Bremnes 2004). It is natural to think that less water discharge in Lærdalselva will lead to an increased inter-individual stress, as the juvenile salmonids will have to concentrate on smaller areas. Further, this may have been related to the significantly back-calculated worsened length at first year after HP. On the other hand, many studies have demonstrated impaired survival from altered flow regimes. Absence of or reduced floods, increased siltation, clogging of bottom substrate, reduced oxygen depletion and stranding of valuable spawning- and feeding grounds has been proven fatal for salmonid juveniles and resulted in lower egg survival in regulated rivers (Jensen et al. 2009; Johnsen B.O. et al. 2011). This should reduce the density-dependent competition, and, in turn, be reflected by improved growth from surviving individuals. (Jenkins et al. 1999) In 1986, Saltveit (1986) documented increased siltation and clogging of the bottom substrate from a landslide, to have negative impacts on both growth and density of salmonids in Lærdalselva.

It should be emphasized that energy costs in fish at a given temperature is constant, with the exception of direct physiological cost such as food intake. Physical disturbances such as floods, rate of water discharge, velocity, chemistry, temperature and bottom substrate are major determinants of the spatial- and temporal dynamics of aquatic organisms, and especially benthos (Resh et al. 1988). Several studies from regulated rivers have demonstrated a decline or changes in species diversity and abundance of macro invertebrates (Brittain & Saltveit 1988; Ugedal et al. 2002; Raddum & Fjellheim 2005; Johnsen B.O. et al. 2011). In addition, an increase in discharge or water velocity has been shown to lead to an increase in drifting invertebrates, which provides important food sources for brown trout (Brittain & Eikeland 1988). Consequently, given the decrease in flow, it can be derived that the benthic communities, and the invertebrate drift downstream the river has changed after hydropower development, thus reducing important nutrient resources for anadromous brown trout in Lærdalselva.

The best model predicting specific back-calculated growth rate the second year only took into account the minimum water discharge, which shows a positive correlation with back-calculated growth. The mechanisms controlling this are likely much the same as discussed for first-year-growth: Density-dependent interactions. Greater water discharge increases the water-covered area resulting in larger and more suitable growth areas for juveniles. The second most supported model from second year growth rate, only differing with 1 AIC, did take into account the temperature effect on growth rate.

4.2.2. Marine environment

I found a significant change in post-smolt back-calculated growth between the treatment periods. From the model predicting back-calculated growth rate at first year in sea, one can see a significant decrease in growth after HP, when corrected for air temperature (**Figure 10**). Anadromous brown trout populations declining from reduced survival and altered growth patterns in the marine environment has been documented the past four decades several places in Norway (Jonsson & Jonsson 2009a; Jonsson et al. 2009). Further, the post-smolt growth of anadromous brown trout can be related to hydropower developement, by influencing migration patterns, smolting processes and freshwater runoff towards the fjord systems (Jonsson & Jonsson 2009a; Johnsen B.O. et al. 2011). Natural and/or climatic changes can also influence growth directly, or indirectly by affecting changes in the marine ecosystem (Jonsson et al. 2009). The past decade the consequences on survival and growth from salmon lice and salmon farming has been a topic of research (Bjørn et al. 2009).

To arrive in a new habitat at the right time, the anadromous brown trout need timers to synchronise development and behaviour. The mechanisms behind reduced first year back-calculated growth rate in the sea from anadromous brown trout in Lærdalselva can be related to a miss-match between entering the marine environment and nutrient richness. Various populations of anadromous brown trout are demonstrated to react differently on factors stimulating seaward migration (Jonsson 1991 ; Hembre et al. 2001). Most studies from Norwegian rivers are however based on the importance of increased water temperature and water discharge (Hembre et al. 2001; Jonsson & Jonsson 2002). As earlier stated Urke et al. (2010) found the seaward migration of anadromous brown trout in Lærdalselva to take place between 29 April to 29 June in 2009, whereupon the migration responded positively to floods

and greater water discharge. We possess no information about the seaward migration from any of the other past treatment periods. It can however be discussed whether the seaward migration was affected by the regulation, due to the observed decrease in water discharge and absence of floods.

In general, individuals of anadromous brown trout populations all aim at reaching the sea at favourable water temperatures. Sea temperatures when Atlantic salmon smolt enters the sea from all rivers in Norway, is demonstrated to be 8 ºC or higher (Hvitsten et al. 1998). This pattern is also applicable for the anadromous brown trout population in Lærdalselva, all reaching the sea at temperatures higher than 8 ºC (Urke et al. 2010). The temperature rise in spring, like the rest of the nature in temperate regions entails a nutrient resurgence. Altered water discharge and absence of floods may have affected the smolt to descend to sea at sub optimal times after regulation. Smolts with to early seaward migration, can experience growth limitations from cold and nutrient-poor conditions in the sea (Jonsson & Jonsson 2009b). A long time series from the river Imsa has demonstrated early seaward migration and migration in the autumn to have fatal consequences on the survival of anadromous brown trout (Jonsson & Jonsson 2009a). In addition, it is demonstrated that salmonids are less able to osmoregulate in cold seawater (Sigholt & Finstad 1990).

The brackish layer in fjords works as an important feeding habitat and protection from salmon lice for migrating smolt (Heuch et al. 2005). Hydropower development, along with increased precipitation along the Norwegian coast may have changed the fresh water runoff towards fjord systems. From Sognefjorden we know several power plants draining bottom layers of lakes or magazines, and this may have led to colder temperatures during summers in Sognefjorden (Kristensen 2015). In addition a deeper brackish layer can lead to suboptimal exchanges in the water column, thus reducing nutrient richness and thereby primary production (Johnsen B.O. et al. 2011) The consequences of these factors throughout the food web, and how it can affect prey availability for salmonids is however poorly understood (Johnsen B.O. et al. 2011).

Second year back-calculated growth rate also shows to be significantly changed between treatment periods. The back-calculated growth rate second year at sea is however different from the first year back-calculated growth rate, upon which the second year growth rate seems to be significantly improved the period after HP. Second year back-calculated growth

rate is however significant worse in the HP&gyro period, when it is correlated for air temperature (**Figure 11**).

As previously stated, my results suggest an impaired back-calculated growth rate the first year in sea after HP. This may delay maturation and help to explain the improved back-calculated growth rate the second year in sea after HP, due to the negative correlation between growth and age at maturation (Alm 1959; Jonsson & Jonsson 2011). One can hypothesize that slow growth the first year in sea would lead to smaller proportions attaining maturity the 2nd-year in sea. Meaning that the anadromous brown trout does not need to allocate energy related to reproduction (Wootton 1998) the 2nd-year at sea, and instead maintain improved marine growth in this stage of life.

Sprat (*Sprattus sprattus*) is considered an important nutritional source for anadromous brown trout. At the same time the populations of sprat has experienced a serious decline in the fjords of Western Norway since 2001 (Jonsson et al. 2009). From the neighbouring river, Aurlandselva it is demonstrated a significant relationship between catches of sprat and anadromous brown trout (Sægrov et al. 2007). It may therefore not be excluded that reduced second year growth in the HP&gyro period is due to food availability and smaller sprat stocks in Sognefjorden.

The anadromous brown populations in Norway suffer from high infection rates from salmon lice, due to the major expansion of salmon farming (Bjørn et al. 2009). Studies have shown that high infection rates can result in an early return to rivers, and in turn lead to reduced growth and survival (Birkeland & Jakobsen 1997; Heuch et al. 2005). The reduced growth rate second year in sea from anadromous brown trout in Lærdalselva, in the HP&gyro-period coincides well with increased salmon farming in Sognefjorden (Holst et al. 2005). However, if the reduced growth were due to salmon lice this pattern should rather be discovered for the first year growth rate, as salmon lice-problems mainly are related to post-smolt growth (Bjørn et al. 2009). Elderly anadromous brown trout may however use the marine environment differently from younger anadromous brown trout. The acoustic telemetry studies in 2009 from Lærdalselva revealed just this, documenting some older individuals migrating towards outer parts of Sognefjorden (Urke et al. 2010). Studies have demonstrated the infection pressure to be more extensive in outer parts compared to inner parts of Sognefjorden (Holst et

al. 2005). This is most likely due to more comprehensive aquaculture activities in this part of Sognefjorden (Solbakken et al. 2012).

4.3. Smolt reaction norms

The probabilities to be a smolt at different ages and lengths have changed significantly during the treatment periods (**Figure 12**). The probabilities to be a smolt were at particularly younger ages, and at smaller sizes before HP, compared to the after HP and HP&gyro periods. From present times, the smolt ages and smolt sizes seem to become similar to values from the period before HP. Studies from Lærdalselva, exploring the human-induced bottleneck situations the past four decades could not document any changes in the genetic structure or diversity in the Atlantic salmon population (Johnsen et al. 2014). In addition, Brooks et al. (1989) found no differences in smolt age and size of Atlantic salmon in Lærdalselva before and after the hydropower regulation in 1974.

The mechanisms controlling niche and/or habitat shifts in brown trout is complicated and has been a topic for debates and discussions. Studies have however revealed standard metabolic rates, growth and nutritional status to be decisive for future migratory behaviour. Individuals with higher standard metabolic rates and growth undergo earlier migration because they can be energetically constrained in the future by limited food resources (Forseth et al. 1999; Boel et al. 2014). From Norway and the rest of Europe it has been demonstrated a significant increase in both smolt age and length with latitude. Further, age and size has been proven to decrease significantly with increasing sea temperature. Only smolt age has been demonstrated to decrease with increasing river temperatures (L´Abée-Lund et al. 1989; Jonsson & L'Abée-Lund 1993). The latter underlines that populations of anadromous brown trout can respond to climatic variables by phenotypic plasticity (L´Abée-Lund et al. 1989). From Lærdalselva, it seems to be a selection in favour of higher age and larger size in smolt from anadromous brown trout after hydropower regulation of the river. This is a strong indication of a genetic alteration of the population, or adaptational changes. The SRN express probabilities for smolting as a function of juvenile growth (size at age). Hence, a change in the SRN implies that the probability of smolting, for a given size-at-age, changes. As a consequence, one cannot infer that the change in SNR can be attributed to the observed change in 1st-year growth between before HP and after HP periods. The change in SRN rather suggests that

delaying the smolting process has been favoured by natural selection after hydropower regulation. In order to understand what factors have changed so as to favour staying longer in the river before migrating to sea, I believe this may be a result from the changed water-flow regime and the change in biotic interactions resulting from it. Reduced water discharge during the growth season may have altered the inter- and intra-specific interactions between salmon and brown trout fry. However, an increased interaction intensity in general will normally constrain individual growth and, in an ecological perspective, imply earlier smolting and smaller sizes at seaward migration (Boel et al. 2014). Atlantic salmon resides riffles and fast current velocities to a greater extent than trout. Less water discharge could have led to a greater degree of interspecific competition between these two species. The trout is considered to be a stronger competitor than Atlantic salmon (Kennedy & Strange 1986), and the victorious outcome of this competition might have made it advantageous for the trout to stay longer in the river after HP. As previously stated sea temperatures may have been changed after the regulation of rivers draining towards Sognefjorden. This may in turn have caused a phenotypic expression towards larger and older smolts (L´Abée-Lund et al. 1989). From Atlantic salmon it is demonstrated larger smolts as a local adaption to cold sea temperatures (Jensen & Johnsen 1986). In addition, ionic regulation in cold sea water is easier for large than for small smolts (Hoar 1988; Sigholt & Finstad 1990).

The interspecific competition with Atlantic salmon was most likely at a greater extent in the juvenile phase before the river was exposed to *G. salaris*. In addition, the rotenone treatment in 1997 resulted in massive mortality on the cohorts residing in the river at the time of treatment. Andersen (2002) documented significant growth improvements in juveniles of Atlantic salmon the year after rotenone treatment in Lærdalselva, which are circumstantial evidence on changed competitive relationships. Reduced stress from lessened competition may have impaired the benefits of early migration at smaller sizes, and can be a good ecological explanation to the selection towards larger and older smolts in the HP&gyro-period.

In the period after 2007, infection pressure of the parasite has been much lower, and functionally zero after 2011(Hindar 2014; kristensen 2015b) The SRN for present times suggest that fairly normal conditions are about to occur again in the river. The competitive relationship may have been re-established to the preceding periods, as the Atlantic salmon is rid of the *G. salaris* infections.

4.4. Between river variation

The post smolt back-calculated growth differences between Lærdalselva, Aurlandselva. Fortundselva and Årdal suggests different use of the marine environment. This hypothesis is supported by acoustic telemetry studies from Sognefjorden (Urke et al. 2010; Kristensen et al. 2011; Lunde 2014) showing different use of the fjord systems between Aurland and Lærdal.

4.5. Shortcomings

A typical mistake when interpreting scales, without having other biological texture with information about the age is to underestimate the age of the fish because of stunted growth (Borgstrøm & Hansen 2000). In addition there are measurement errors from my scale readings. Some of my findings from the effects on growth and smolting between the treatment periods are relatively small including few scale readings. Therefore, it may not be excluded that some of my findings are due to coincidences because of underestimations of age and/or measurement errors. However, I think the potential underestimations of the age, and measurement errors are relatively insignificant for my over-all findings and results. The point of my study has been to detect changes in the anadromous brown trout growth and smolting from Lærdalselva throughout more than 60 years, and I think the mistakes I have made during scale reading is equally distributed through all the periods. Having said this, including more scales for each fish would however made my scale analysis more accurate. Finally, this is a question about time spent, and the objectives of the study (Haraldstad 2011)

5. Concluding remarks and management implications

The key findings in this project were:

- No significant differences in growth season mean water temperatures among treatment periods.
- The water discharge has changed among the treatment periods, with less water after hydropower regulation.
- Length at first year in freshwater was significant reduced after hydropower compared to the period before hydropower.
- Second year growth rate during second year in freshwater, showed no evidence of treatment period effect. However, there was a positive correlation between summer low-water discharge and second-year specific growth rate.
- The marine growth has changed significantly among the treatment periods. First sea year growth rate has significantly declined during the period after hydropower compared to the preceding period.
- Second-sea year back-calculated specific growth rate has significantly improved after hydropower when compared to the before period. For the hydropower and *G. salaris* period, a decline in second-sea-year specific growth rate was found – after correcting for the positive effect of mean summer air temperature
- There has been a significant shift in smolt reaction norms (SRN) where the anadromous brown trout during the hydropower period shifted towards delayed smolting by almost a year and larger size compared to the preceding period. During the more recent periods the SRN has gradually shifted towards the original pattern.

To wrap up general findings, my study shows that the anadromous brown in Lærdalsleva is capable of rapid adaptions to anthropogenic-induced environmental change. Life-history traits, such as smolting seem to be a dynamic and flexible trait, highly adapted to the prevailing environment. Rapid evolution of adaptive traits in the family of salmonids is previously well known (Hendry et al. 2000). When making management decisions it is thus important to have a profound knowledge about such contemporary adaptive traits (Kinnison & Hairston 2007). Further, when protecting and making measures to improve the habitat, this should be done in conjunction with the EU Water Framework Directive. They propose a holistic management based on knowledge, with the goal of achieving good ecological status

in all inland water bodies within a given time. The anadromous brown trout of Lærdalselva is an important and highly valuable resource worth preserving, receiving a lot of management attention. In many respects, my study suggests various factors limiting growth in freshwater, which may complicate this holistic approach of management. However, my study shows on a general basis a greater need for more water to the anadromous stretch of the river, as the water discharge stands out to be a pervasive variable having great influence on freshwater growth. In addition, I believe the competitive relationships in the river has great influence on population viability (both Atlantic salmon and anadromous brown trout), which in some cases may constrain the growth of juveniles and thereby affect life history traits. This makes it temporarily hard to defend fish stocking and egg planting in Lærdalselva. Climate change, global warming, natural and/or human induced factors can have a major impact together and separately on growth, survival and life-history traits on anadromous brown trout in the sea. Long-term-oriented monitoring of the marine life should therefore be strengthened, with the goal of achieving a greater understanding of these complex systems.

6. References

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