

Lina Gjerdevik

# A comparison of growth and timing of outward autumn migration between a lake run and a sea run brown trout (*Salmo trutta*) population.

Master's thesis in Biology with Teacher Education

Supervisor: Jan Grimsrud Davidsen

Co-supervisor: Mikkel Emil Lange Friis

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## Abstract

This study investigated the growth and autumn migration patterns of brown trout (*Salmo trutta*) tagged and tracked by acoustic telemetry in two Norwegian rivers located at similar latitudes: one sea run population migrating to a marine fjord (total body length: 310 – 650 mm) and one lake run population migrating to a freshwater lake (total body length: 300 – 630 mm). The hypotheses tested were: (1) The two first years after first migration, the annual growth rates were higher in the population of sea run than lake run brown trout, (2) There was no difference in the timing of riverine exit between the sea run and lake run brown trout populations. Results indicated that during the first year after migration, the lake run population had a significantly higher estimated growth rate than the sea run population, a difference that was not observed the second year after migration. The lake run trout had a larger total body length at the time of first migration, though not significantly, potentially enabling earlier shift to piscivory diets, contributing to the higher growth the first year in the lake. Conversely, predation pressure and osmotic challenges likely constrained the growth of the sea run population the first year after migration to sea. Furthermore, the growth in both brown trout populations first year after migration, could have led to a higher number of piscivory fish, potentially leading to a more similar growth between the two populations second year after migration. The research also showed that the lake run population migrated later in the season than the sea run population, possibly due to a longer period with no precipitation, followed by a larger rainfall, triggering a general migratory response in the lake run brown trout. In both populations, outward migration occurred throughout the day, independent of light phases, suggesting that factors such as water discharge and predator pressure play a crucial role in influencing the timing of outward migration in autumn.

## Sammendrag

I denne studien er det undersøkt vekst- og migrasjonsmønster hos brunørret (*Salmo trutta*). Disse ble merket og sporet ved hjelp av akustisk telemetri i to norske elver, lokalisert på like breddegrader: én sjøvandrende bestand som migrerte til en marin fjord (total kroppslengde: 310 – 650 mm), og én innsjøvandrende bestand som migrerte til en ferskvannsinnsjø (total kroppslengde: 300 – 630 mm). Hypotesene som ble testet var: (1) De to første årene etter første migrasjon, var den årlige vekstraten høyere hos den sjøvandrende sammenlignet med den innsjøvandrende brunørretbestanden, og (2) Det var ingen forskjell i tidspunkt for utvandring fra elva mellom den sjøvandrende og innsjøvandrende brunørretbestanden. Resultatene indikerte at i løpet av det første året etter utvandring hadde den innsjøvandrende bestanden en signifikant høyere estimert vekstrate enn den sjøvandrende bestanden; en forskjell som ikke ble observert det andre året etter utvandring. Den innsjøvandrende ørreten hadde en større total kroppslengde ved første migrasjon, selv om den ikke var signifikant, noe som potensielt muliggjorde en tidligere overgang til fiskespising, og videre kunne bidratt til den høyere veksten det første året i innsjøen. Predasjonstrykk og osmotiske utfordringer kan i tillegg ha begrenset veksten til den sjøvandrende bestanden det første året etter migrasjon. Videre kunne tilvekst i begge populasjoner første år etter migrasjon ha ført til flere fiskespisere, som igjen kunne ført til en likere vekst mellom populasjonene det andre året etter migrasjon. Studien viser at den innsjøvandrende bestanden migrerte senere i sesongen enn den sjøvandrende bestanden. Dette kan muligens være på grunn av en lengre periode uten nedbør, etterfulgt av en periode med mye nedbør, som igjen medførte en generell migrasjonsrespons hos den innsjøvandrende brunørreten. Hos begge populasjonene skjedde utvandringen gjennom hele dagen, uavhengig av lysfase. Det antyder at faktorer som vannføring og predasjonstrykk spiller en avgjørende rolle for utvandringstidpunktet om høsten.

# Preface

Through working on the thesis, I have engaged myself in field work, data analysis, programming in R and academic writing. These are all important experiences to bring into the classroom to inspire and encourage pupils for their study. Programming and modelling are basic skills pupils are supposed to gain during mathematics and biology education (Kunnskapsdepartementet, 2019; 2021). The hand on experience I have from this project is valuable for a deeper understanding on how to apply real life data in statistical modelling. It is highly valuable for a teacher to have a deeper understanding what he/she is teaching the pupils.

This study is contributing to more information on a key stone and increasingly endangered species. Conservation on freshwater and marine biodiversity is directly linked to the UNs 2030 Agenda for Sustainable Development, goal number 6 "Clean waters and sanitation" and 14 "Conserve and sustainably use the oceans, seas and marine resources» (United Nations, 2015). To protect and conserve the resources on the planet is more important than ever. As values and attitudes starts forming at a young age, different perspectives and evidence must be presented and discussed in school.

I want to thank my supervisor Jan Grimsrud Davidsen and my co-supervisor Mikkel Emil Friis Lange for introducing me to the field of acoustic telemetry and excitingly teaching me about brown trout and the ecosystem it is inhabiting. My deepest gratitude for their kindness, support and help during this process, even during their hectic times.

The master's project was a part of "Mission Mjøsa". During field work Arne Julsrud Berg (Mjøsmuseet) and Lenaelvas Fiskeriforening contributed with valuable practical information and help, which I am very thankful for. I am grateful for Marie Nevoux teaching me about ultrasound on fish and interpreting the gender of the fishes in the field. A big thank you to the staff members at Ferskvannsgruppa at NTNU university museum for being welcoming and providing me help when needed, and for excitingly teaching me about freshwater fishes. Furthermore, thanks to Lars Rønning for contributing with practical work related to the receivers, to Aslak Darre Sjursen for teaching me scale reading and double-checking my interpretations, and to Marc Daverdin for providing me the maps in figure 1 and 2.

Finally, I would like to thank my family and friends for being encouraging and supportive.

*Lina Gjerdevik*

*Trondheim, June 2024*





# Table of contents

1 Introduction.....	1
2 Method .....	3
2.1 Study sites.....	3
2.1.1 Snillfjorden and Snilldalselva .....	3
2.1.2 Mjøsa and Lenaelva .....	5
2.2 Data collection with use of acoustic telemetry.....	7
2.2.1 Capture .....	7
2.2.2 Sampling.....	7
2.2.3 Tagging.....	7
2.3 Tracking of brown trout.....	8
2.4 Receiver performance .....	8
2.5 Scale sample analysis .....	8
2.6 Calculation of Fulton’s body condition factor .....	9
2.7 Data filtering .....	9
2.8 Timing of migration, precipitation, and light phase.....	10
2.9 Statistical analysis .....	10
3 Results.....	12
3.1 Biological characteristics of tagged fish .....	12
3.2 Comparing growth between the two brown trout populations .....	13
3.3 Migrated vs. non-migrated brown trout.....	14
3.4 Autumn estuary migration date .....	15
3.4.1 Two estuary migration groups in river Lenaelva .....	17
3.5 Light phase during riverine exit.....	18
4 Discussion.....	19
4.1 Growth, total body length and age at the first time of migration .....	19
4.2 Growth in lake versus fjord .....	20
4.3 Decision on autumn riverine exit or not .....	21
4.4 Date of riverine exit .....	21
4.5 Light phase during riverine exit.....	22
5 Conclusion.....	23
References.....	24

# 1 Introduction

Brown trout (*Salmo trutta*) is a valuable species for both social and economic reasons, especially considering recreational angling (Liu *et al.*, 2019). Mature brown trout migrate upstream rivers to areas where they can spawn during the autumn or winter (Pethon & Nyström, 2019). After spawning, most brown trout descend the river, either seaward or lakeward (Klemetsen *et al.*, 2003). Migration timing is influenced by temperature, river flow and life history traits among the brown trout (Klemetsen *et al.*, 2003; Dahl *et al.*, 2004).

Migrating involves gains and risks. Descending the river offers growth opportunities and reproductive outputs (Jonsson, 1985). Additionally, waterflow and predation on brown trout from other piscivorous fish, mammals and birds and river icing during the winter may solely or in combination be reasons to descend the river after spawning (Ruggles, 1980; Klemetsen *et al.*, 2003). In temperate areas, productivity is generally higher in the ocean than in freshwater environments, suggesting that migrating to sea gives greater growth abilities than being freshwater resident for brown trout (Gross *et al.*, 1988). Migrating to marine habitats and lakes incurs significant costs, primarily increased energy use and mortality (Jensen *et al.*, 2019). Consequently, brown trout descend the river when the conditions favor migration over river residence (Jonsson, 1985).

Light intensity determines the risk of predation by visual predators such as piscivorous birds, mammals and fish in the river (Bendall *et al.*, 2005; Ibbotson *et al.*, 2011). Hence, post-spawning riverine migration for brown trout is most often undertaken in darkness to avoid predation (Hayes, 1953; Hesthagen & Garnås, 1986; Bendall *et al.*, 2005; Ibbotson *et al.*, 2011). Additionally, it has been found that migration occurs both diurnal and nocturnal in periods with more turbid water (Hesthagen & Garnås, 1986).

Juvenile brown trout remain in their native rivers in 1-8 years before they migrate to sea or a lake (Klemetsen *et al.*, 2003). Body size at first migration varies from 6 to 32 cm (L'Abée-Lund *et al.*, 1989). However, year-class and body size at first migration vary greatly, mainly depending on temperature and the characteristics of the native river of the brown trout (Klemetsen *et al.*, 2003). Both sea run and lake run brown trout face an increased risk of predation during their first migration. Additionally, sea run brown trout must also deal with salinity regulation issues (Klemetsen *et al.*, 2003; Ibbotson *et al.*, 2011). Survival after migration improves with body size for salmonids, as larger fish are less vulnerable to predation, and have better osmoregulatory capacity (Finstad & Ugedal, 1998; Ibbotson *et al.*, 2011; Jonsson & Jonsson, 2011). Therefore, first time migration for salmonids depend on body size (Jonsson & Jonsson, 2011). The size at first migration is often higher for salmonids with a slow growth rate (Økland *et al.*, 1993), and hence, individuals that grow fast, generally are younger at first migration compared to slow growers (Jonsson, 1985).

Brown trout can exhibit a range of different life strategies (Klemetsen *et al.*, 2003). They can hatch and remain resident in either a river or a lake (Jonsson & Jonsson, 2011). Those that are not resident may migrate between rivers and freshwater lakes, or between rivers and the sea. Consequently, some individuals may undertake marine feeding migration, while others stay in freshwater throughout their lives (Pethon & Nyström, 2019). Brown trout that migrate to sea exhibit anadromous behavior. These brown trout undergo smoltification which involves complex changes in behavior and morphology, enabling them to develop hypoosmoregulatory ability (Finstad *et al.*, 1988).

This process is characterized by a period of lipid depletion and changes in lipid metabolism (Sheridan *et al.*, 1983), resulting in a higher tolerance to increased salinity conditions, a more streamlined body form and decreased body condition (Gorbman *et al.*, 1982). Mortality rates are high immediately after migration to sea, primarily due to osmotic challenges and predation (Sigholt & Finstad, 1990; Jørgensen & Johnsen, 2014; Jensen *et al.*, 2019). In contrast, freshwater resident brown trout do not need to undergo smoltification before traveling between rivers and lakes, unlike their anadromous counterparts migrating to the sea (Jonsson & Finstad, 1995; Thorstad *et al.*, 2016).

Many studies have compared growth, total body length, age and migration timing between anadromous and freshwater river, or smaller lake, resident brown trout (Jonsson, 1985; Jonsson & Finstad, 1995; Jensen *et al.*, 2019; Birnie-Gauvin *et al.*, 2021; Jonsson & Jonsson, 2021). However, fewer studies have focused on comparing sea run and lake run brown trout that migrate to larger lakes. The objective of the present study was hence to compare autumn outward migration between a sea run and lake run population, specifically examining potential difference in the biological characteristics age and size at first riverine exit, growth the two first years in the river and the two first years after migration, total body length and body condition factor at the time of the outward migration. Additionally, the study examined potential relationships between light phase throughout the day, day of the year and the time of the outward migration. The following hypothesis were tested using acoustic tagging of brown trout from the two populations: (1) The two first years after first migration, the annual growth rates were higher in the population of sea run than lake run brown trout, (2) There was no difference in the timing of riverine exit between the sea run and lake run brown trout populations.

## 2 Method

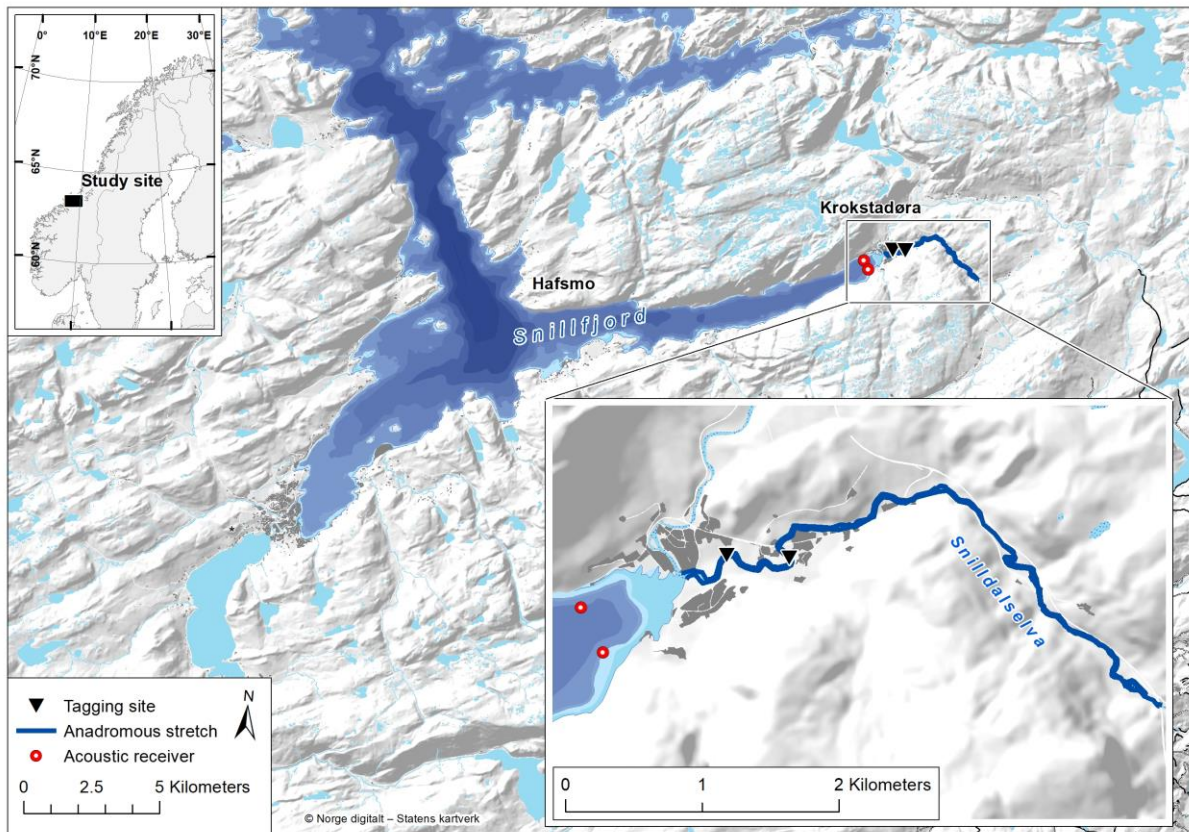
### 2.1 Study sites

This study compared brown trout from two study areas: one sea run population from river Snilldalselva, which drains into the Snillfjorden fjord in Trøndelag county (63°N), and one lake run population from river Lenaelva draining into lake Mjøsa, Innlandet county (61°N). The study in Snillfjorden was conducted in 2012, while the study in Mjøsa took place in 2023. In both areas, the study period was set to 20 September to 8 December.

#### 2.1.1 Snillfjorden and Snilldalselva

The fjord Snillfjorden is located in Trøndelag, central Norway. It has an area of 17.4 km<sup>2</sup> and stretches 14 km eastwards from the fjord Trondheimsfjorden toward the innermost part where the community center of Snillfjord is located (Figure 1) (Geonorge.no, 2024). Common fish species in the fjord system are cod (*Gadus morhua*), pollock (*Pollachius virens*), sprat (*Sprattus sprattus*), herring (*Clupea harengus*) and small sandeel (*Ammodytes tobianus*) (Solberg *et al.*, 2023). Goosander (*ergus merganser*), mink (*Mustela vison*) and otter (*Lutra lutra*) are also observed in the fjord (artskart.artsdatabanken.no, 2024c; b; d).

The river Snilldalselva is flowing into Snillfjorden. The river has a drainage basin of 42.7 km<sup>2</sup> and an average flow of 1.4 m<sup>3</sup>/s (Davidsen *et al.*, 2014). Anadromous stretch is 4.8 km, stopped by a physical migration barrier (Solem *et al.*, 2018), which also was situated at the highest point of the river, 50 meters height over mean sea level (Geonorge.no, 2024). Snilldalselva is covered or partly covered by ice during the winter. Periodically, the river floods and the ice will break up. Further, the river has only few deep pools (Davidsen *et al.*, 2014). Hence, the river is considered as a poor overwintering habitat for brown trout. Other fish species within the river are Atlantic salmon (*Salmo trutta*), stickleback (*Gasterosteidae*), flounder (*Platichthys flesus*) and European eel (*Anguilla anguilla*) (Davidsen *et al.*, 2014). Examples of potential brown trout predators living along the river is goosander, mink and otter (artskart.artsdatabanken.no, 2024d; b; c; a).

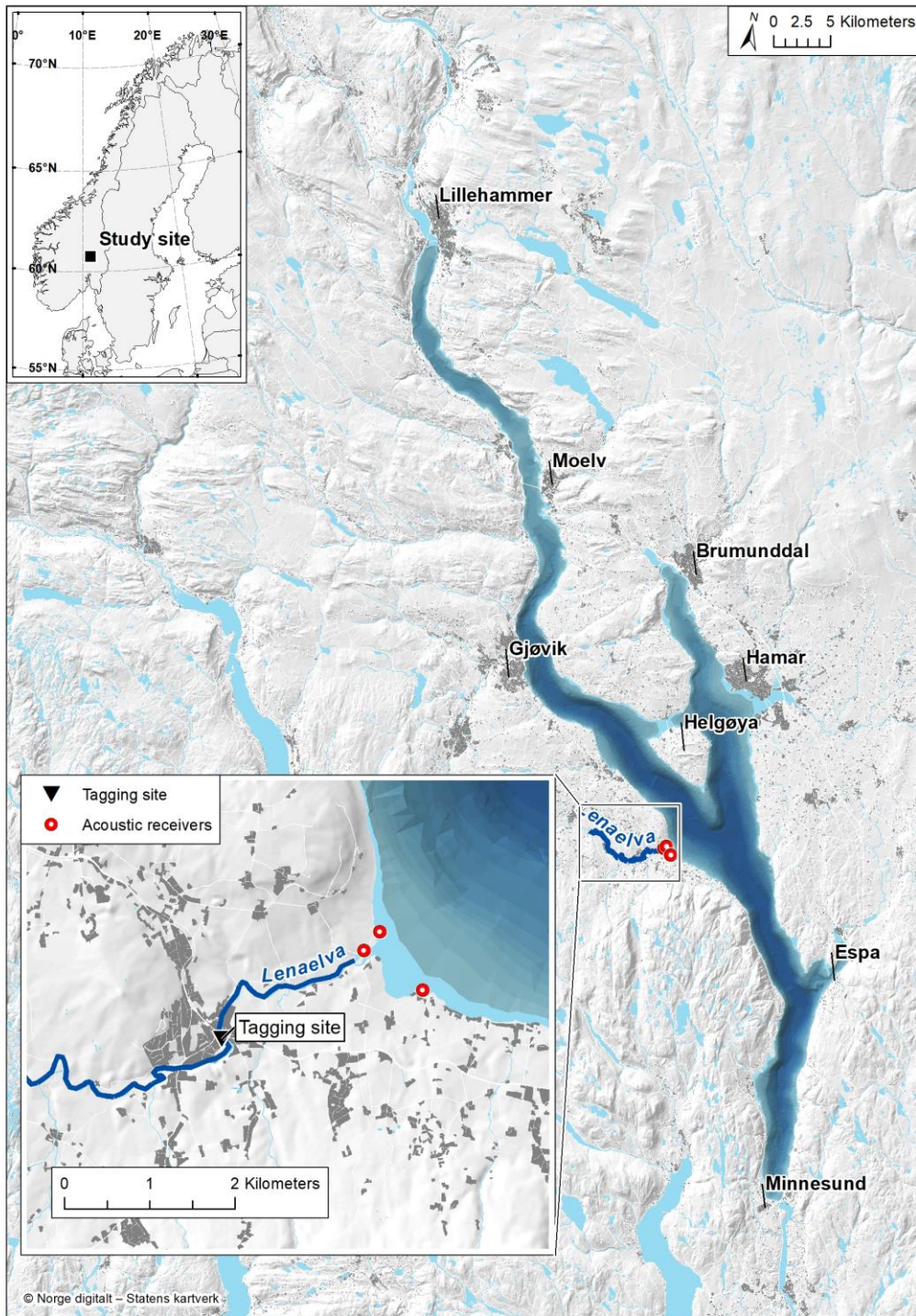


**Figure 1:** Map covering the fjord Snillfjord and the river Snilldalselva, showing the acoustic receivers (red dots), tagging sites (black triangle) and the anadromous stretch for the brown trout (blue line is the river).

### 2.1.2 Mjøsa and Lenaelva

Mjøsa is the largest lake in Norway, with an area of 362,9km<sup>2</sup> and a drainage area of 16 600km<sup>2</sup> (Bechmann *et al.*, 2021). The lake is located in southerneast part of Norway (Figure 2). Several larger cities are located nearby the lake. The lake inhabits 20 different fish species, including European vendace (*Coregonus albula*), European whitefish (*Coregonus lavaretus*), European smelt (*Osmerus eperlanus*), pike and burbot (Huitfeldt-Kaas, 1916; Selstad, 1991). Examples of potential brown trout predators at lake Mjøsa is great cormorant, goosander, mink and otter (artskart.artsdatabanken.no, 2024d; b; c; a).

Lenaelva is a river on the western side of Mjøsa with a drainage area of 292 km<sup>2</sup> and an estimated average flow of 4.5 m<sup>3</sup>/s (Kraabøl & Museth, 2009). Lenaelva is a spawning and nursing river for brown trout migrating to Mjøsa. The migration stretch for the brown trout from lake Mjøsa could potentially be 30 km, but is truly limited to 3 km due to an overgrown fish ladder (Kraabøl & Museth, 2009; Skoglund *et al.*, 2015). Due to this, the overgrown fish ladder could be the highest point in the migratory stretch, with a height of 165 meters over mean sea level (Geonorge.no, 2024). There are several smaller rivers draining into river Lenaelva (Kraabøl & Museth, 2009). Three intake dams for water supply for industry are located within the river, two of them are located within the migration stretch (Skoglund *et al.*, 2015) in addition to several deeper pools (Skoglund *et al.*, 2015). Fish species in the river are grayling (*Thymallus arcticus*), minnow (*Tanichthys albonubes*) and bullhead (*Ameiurus melas*) (Westly & Rustadbakken, 2006). In the downmost part of the river perch (*Perca fluviatilis*), pike (*Esox lucius*) and golden orfe (*Leuciscus idus*) has also been observed (Lenaelva Fiskeforening, n.d.). Potentially brown trout predators living along the river include mink and goosander (artskart.artsdatabanken.no, 2024d; c).



**Figure 2:** Map covering the lake Mjøsa and the river Lenaelva (blue line is the river), showing the acoustic receivers (red dots) and tagging sites (black triangle).

## 2.2 Data collection with use of acoustic telemetry

### 2.2.1 Capture

In river Snilldalselva, during the period 19 to 20 September 2012, 20 sea trout were captured in the river and the estuary. The fish were caught in gill nets which were checked continuously to reduce the time the sea trout were stuck in order to reduce stress and chances of injury on the fish. The fish was removed from the nets using scissors. The fish were kept in a keep net in a relatively calm part of the river prior to tagging.

In lake Mjøsa, during the period 11 to 21 September 2023, 25 freshwater brown trout, were captured in the tributary river Lenaelva. All fish were caught in a fish trap installed in a fish ladder. The fish trap was checked at least once a day, and captured fish were placed in a dark fish tank with continuous flow of freshwater and kept for up to three days prior to tagging.

### 2.2.2 Sampling

All brown trout were placed in tubs with a dark cover during sedation to avoid stress due to light exposure. The sea trout from Snilldalselva were anesthetized with 2-phenoxy-ethanol with a concentration of 0.5 mL/L until fully anesthetized. The freshwater brown trout in Lenaelva were exposed to a mixture consisting of 7 mL Benzoak Vet per 50 liters of water. During sedation, the first 16 measured brown trout in Lenaelva underwent ultrasound by a portable ultrasound scanner M-Turbo (Sonosite) with a 5-10 MHz linear transducer with default setting to determine sex by trained personnel. The sex of the remaining nine brown trout from Lenaelva and all brown trout from Snilldalselva were determined by their characteristic looks. Some of the mature male brown trout developed a more pronounced hooked lower jaw and did appear more slender and had a brighter color, such as vibrant red or orange spots along their side. Mature female brown trout could be mistaken for younger males. They did lack the hooked jaw, and their coloration tended to be less vibrant. Uncertainty between female and young male in some brown trout from Snilldalselva lead to lack of sex data for these individuals.

The brown trout were measured for mass and total body length during sedation. Further, 5-10 scales were removed for later age determination.

### 2.2.3 Tagging

Each individual brown trout had an acoustic transmitter operated into the abdominal cavity (Snilldalselva; n = 5 Thelmafiotel AS model MP-9-L, n = 6 Thelmafiotel AS model MP-13, n = 9 Vemoc Inc. model V13-1x, Lenaelva; n = 25 Thelmafiotel AS model MP-9-L). Battery life was estimated to be minimum 8 months. The transmitters send out unique identification code with duty time 30-90 second at frequency 69 Hz.

A 2 cm incision was made to the body cavity and a sterilized acoustic transmitter was inserted. At Lenaelva, the transmitter had a cylindrical shape with 30 mm length and a diameter of 9 mm. In Snilldalselva, tag size differed (See Davidsen et al., 2014 for further details). The incision was closed by two individual sutures and performed by trained personnel to ensure good animal welfare. The procedure was carried out within 3-



5 minutes. The gills were continuously irrigated. After the surgery, the brown trout were held in a recovery tank for 5-10 minutes, before they were returned to their respective rivers Snilldalselva and Lenaelva (upstream the fish ladder for the fish in Lenaelva).

## 2.3 Tracking of brown trout

The brown trout were tracked by automatic acoustic receivers. The receivers used in this study were placed in, or close to, the estuary of the rivers Snilldalselva and Lenaelva. Two acoustic receivers (Vemco, model VR2W) were placed in the fjord Snillfjorden, close to the river mouth of Snilldalselva (figure 1) while three receivers (Thelmahotel, model TBR700L) were located in the estuary of river Lenaelva (figure 2).

The study period spanned from 20 September to 8 December to ensure comparability, even though the fish were tracked beyond this timeframe. The study in Snillfjorden was conducted in 2012, and the study in Mjøsa was carried out in 2023.

## 2.4 Receiver performance

In acoustic telemetry, the ability to detect tagged fish varies based on where receivers are placed and their detection range at each location. The range at which tags can be detected fluctuates due to factors like transmitter features, background noise, and hydrological conditions affecting sound wave propagation, such as water flow, air bubbles, rain, and waves (Winter *et al.*, 2021). As a result, detection range varies significantly both spatially and temporally. The proportion of passing fish that were detected on different acoustic receivers, evaluated the receiver performance.

In Snillfjorden, all brown trout (16 out of 16) that passed the receivers in the estuary were later detected in the fjord, indicating a 100% receiver performance (Eldøy, 2014). In lake Mjøsa, 94% (17 out of 18) of the brown trout registered further out in the lake, were detected by the three acoustic receivers in the estuary of Lenaelva.

## 2.5 Scale sample analysis

The scales sampled during the tagging procedure were used to determine age and back calculate growth, or annual length increase, of each individual brown trout. At the NTNU University Museum Microscopy lab, three to eight fish scales were placed on 1 mm Lexan plates and imprinted by using a pressing iron. The imprints were further studied to measure length between seasonal growth and to count the number of seasonal growth cycles. Using Lea-Dahls' method (Dahl, 1910; Lea, 1910), distance between seasonal growth cycles were used to backward calculate an estimation of yearly growth, and the number of cycles were used for age estimation.

## 2.6 Calculation of Fulton's body condition factor

The condition of the fish was calculated using Fulton's body index formula (K) (Ricker, 1975). The condition factor was adjusted for the brown trout by the coefficient for the linear regression of the logarithm of mass and logarithm of total body length, at 2.925. The adjusted condition formula was further calculated for each individual brown trout by the formula:

$$K = \frac{\text{mass (g)} * 100}{\text{total body length (cm)}^{2.925}}$$

## 2.7 Data filtering

A total of 45 brown trout were included in this study: 20 individuals from river Snilldalselva and 25 from river Lenaelva.

During the scale sample analysis age and growth were back-calculated for the brown trout with clear growth rings, excluding fish with replacement scales or scales with imprints that introduced uncertainty. Total body length at first migration was back-calculated for 24 individuals from the Lenaelva river and 16 from the Snilldalselva river, and these individuals were included in the analysis for total body length at first migration. Age at first migration was back-calculated for 17 individuals from the Lenaelva river and 13 from the Snilldalselva river, and these individuals were included in the analysis for age at first migration.

The scale sample analysis excluded several brown trout from growth analysis: eight for the first living year (Snillfjord = 2, Mjøsa = 6), nine for the second living year (Snillfjord = 2, Mjøsa = 7), seven for the first year after migration (Snillfjord = 4, Mjøsa = 3), and nine for the second year after migration (Snillfjord = 6, Mjøsa = 3).

During the study period, 34 of the tagged brown trout migrated out of the two rivers while the remaining 11 did not. Possible reason for the lack of detections include non-functioning acoustic transmitters batteries, the fish moving out of the receiver's detection range or too rapidly for the acoustic receiver to detect the signal from the transmitter, overwintering in the river or mortality. Consequently, 16 sea run brown trout from Snilldalselva and 18 lake run brown trout from Lenaelva were included in the migration analysis.

Gender was not determined for nine (45 %) of the sea run individuals from the Snilldalselva river, so no analysis that included gender were conducted for the Snilldalselva population.

## 2.8 Timing of migration, precipitation, and light phase

Acoustic receivers in the estuary of river Snilldalselva and Lenaelva detected the transmitters identifying the brown trout. For the brown trout that were detected, the first registration in the estuary after leaving the river determined the date and time of downward migration. The date was converted into day of the year.

Precipitation during the period of riverine exit (21 September to 26 November) was checked for the weather station at Apesvoll in Østre Toten (2023) and Lenes in Hemne (2012) (seklima.met.no, 2024).

Light phase at the time of the outward migration was divided into 4 different categories, depending on the sunlight's intensity: nighttime (total dark), dawn (increasing sunlight), daylight and dusk (sun setting). To correlate light phase to the individual time of migration, the specific location's light phase for given time and date was determined and referenced according to the values provided in [<https://stjerneskin.com/soloppgang.htm>].

## 2.9 Statistical analysis

The statistical analysis was conducted in R Studio (Rstudio Team, 2023) with R version 4.3.3 (R Core Team, 2023). The chosen level of significance was set to  $p < 0.05$ .

Statistical tests were performed to compare the two brown trout populations for adjusted condition factor and total body length at tagging, total body length and age at first migration, annual growth first and second year in river, and first and second year after migration. Welch two-sample t-test was used if assumption of normality was met, if else, Wilcoxon rank sum test was used. Normality was tested on the different rivers of origin separately, visually by using the functions `qqnorm`, followed by `qqline` and histogram, and thereafter statistically by Shapiro-Wilk test. To check if there was a statistical difference in number of fish per light phase at migration between the two brown trout populations, Fisher's exact test for count data was applied due to the small sample size. To test for statistical difference between the number of migrations at the different light phases, Chi-squared test for goodness of fit was utilized. In addition, to test if rain influenced the migration timing in Lenaelva and Snilldalselva, Spearman's rank correlation rho test was applied.

To compare biological characteristic variables in generalized linear models (GLM), the continuous variables were standardized by R base function `scale`. To avoid collinearity between total body length and condition factor, Fulton's body condition index was adjusted as described in section 2.6. Furthermore, age was excluded as an explanatory variable for GLMs due to its high correlation to total body length.

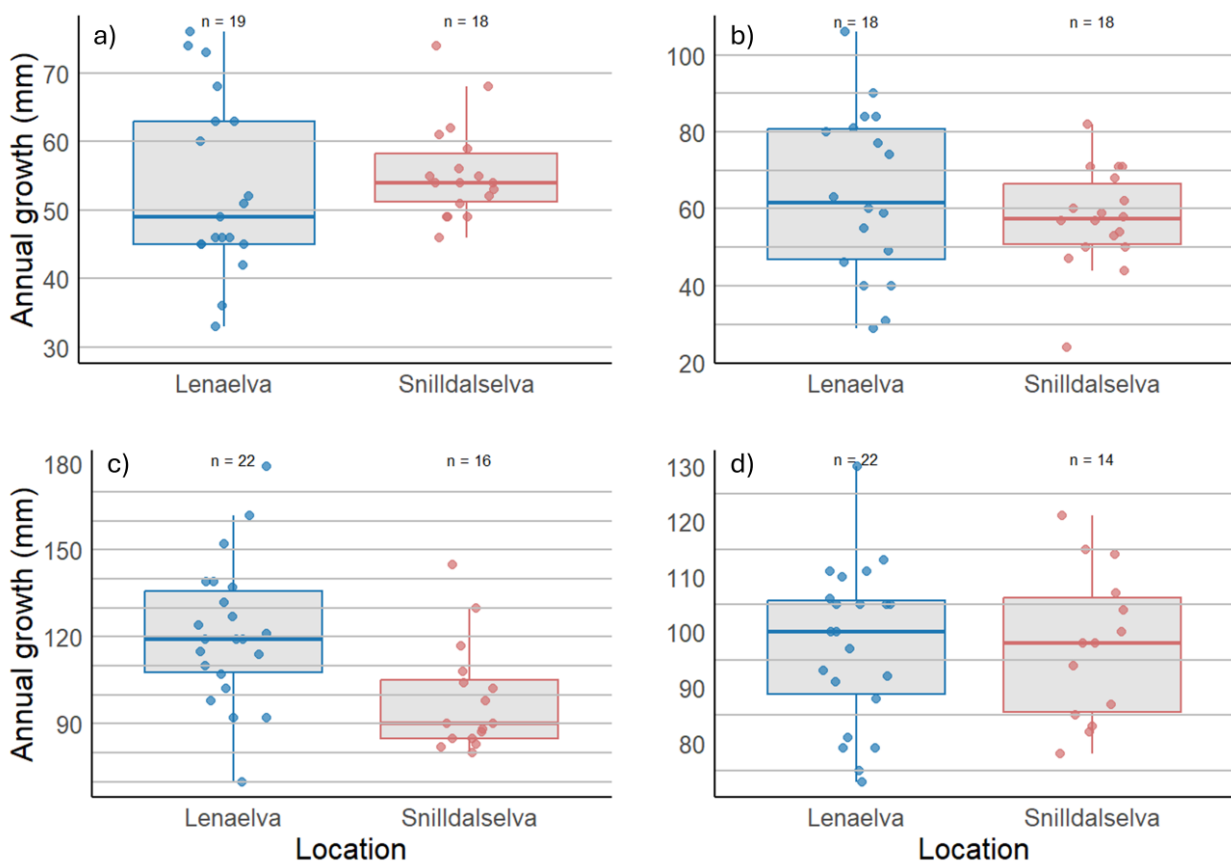
The collinearity within models was checked using the `check_collinearity` function in the `performance` R package (Lüdecke *et al.*, 2020), and collinearity was found to be low (variance inflation factor [VIF]  $\leq 1.59$ ). For creating the generalized linear models, function `glm` from R package `MASS` was used (Ripley, 2011). When testing the fit of the chosen variables to the generalized linear model and its conditional average, the `dredge` and the `model.avg` functions from `MuMIn` R package were utilized (Barton, 2009).

To test if total body length, adjusted condition factor or river of origin affected the riverine exit, a GLM with gamma distribution (link = "log") was used. For comparing detected brown trout *versus* those without any detections, a binomial distributed GLM with the same parameters was applied. The same parameters were tested, in addition to sex, to check if they did influence that there were two distinct migration groups in Lenaelva.



### 3.2 Comparing growth between the two brown trout populations

The age and growth were backward calculated using sampled fish scales. The lake run brown trout population had a higher growth rate the first year after migration (figure 4c) (Wilcox rank sum;  $W = 281$ ,  $p < 0.05$ ) compared to the sea run population. However, there was no significant difference in growth for the first year (figure 4a) (Welch two sample t-test;  $n = 37$ ,  $p = 0.51$ ) or the second year (figure 4b) (Welch two sample t-test;  $n = 36$ ,  $p = 0.32$ ) the brown trout lived in their native rivers. There was no difference in growth during the second year after the fish had migrated (figure 4d) (Welch two sample t-test;  $n = 36$ ,  $p = 0.98$ ).



**Figure 4:** Growth first (a) and second (b) living year, and first (c) and second (d) year after first migration for brown trout populations in Lenaelva (blue) and Snilldalselva (red). The box-and-whisker plots show the median values (bold lines), the interquartile ranges (boxes), the 5<sup>th</sup> and 95<sup>th</sup> percentiles (whiskers) and datapoint for each individual brown trout (dots), with number of individuals in each group denoted at the top of each box. Outliers are datapoints outside 5<sup>th</sup> and 95<sup>th</sup> percentiles.

### 3.3 Migrated vs. non-migrated brown trout

The effect of river, total body length and adjusted condition factor were used to test whether the fish had probability of detection in the river estuary. There were 34 detected brown trout in the estuary *versus* 11 brown trout that were never detected by estuary acoustic receivers. In Lenaelva, 4 out of 20 (20%) were not recorded and in Snilldalselva, 7 out of 25 (28%) were not recorded. From model selection based on GLMs with binomial distribution, three models had  $\Delta AICc < 2$ , including the null parameter (table 1). One model included only total body length, and another included only river of origin. None of the parameters had a significant influence on the probability of detection in the estuary according to conditional average (table 2).

**Table 1:** Model selection of GLM with binary distribution with the response variables: detected brown trout ( $n = 34$ ) and non-detected brown trout ( $n = 11$ ). All models with  $\Delta AICc < 4$  are included. Supported models ( $\Delta AICc < 2$ ) are shown in bold. Weight tells the strength of predictor-variable influence. DF indicates degrees of freedom.

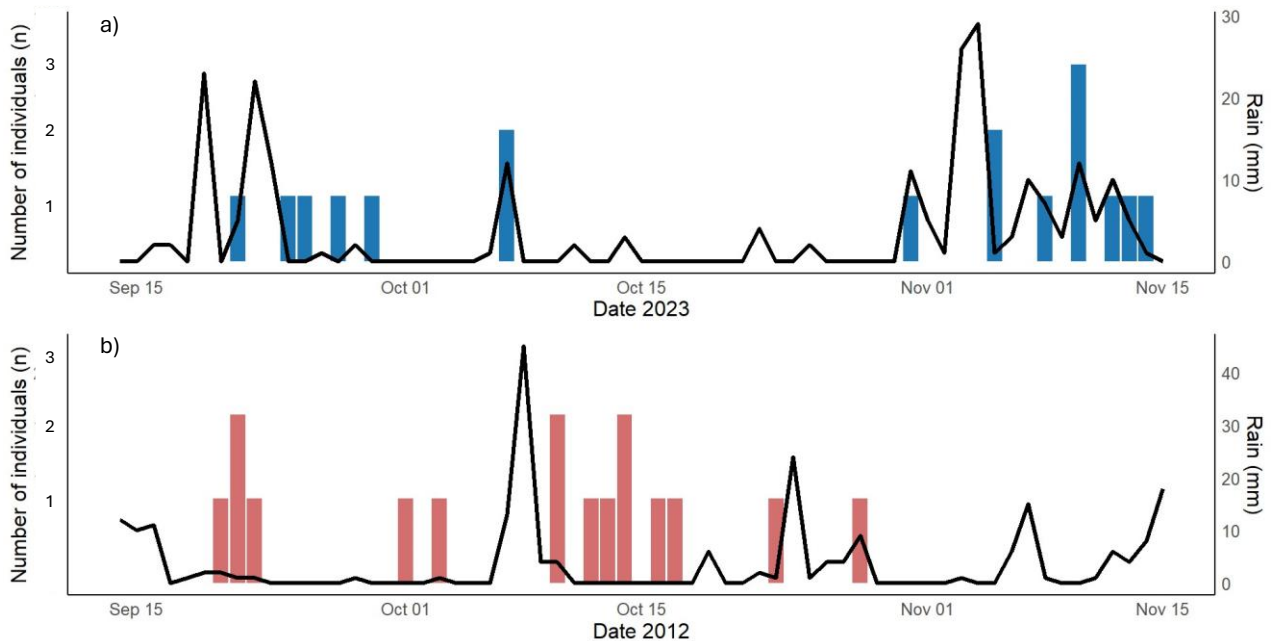
Model tested	AICc	$\Delta AICc$	Weight	DF
<b>&lt;NULL&gt;</b>	<b>52,15</b>	<b>0,00</b>	<b>0,43</b>	<b>1</b>
<b>[Total body length]</b>	<b>53,86</b>	<b>1,71</b>	<b>0,18</b>	<b>2</b>
<b>[River of origin]</b>	<b>53,95</b>	<b>1,80</b>	<b>0,18</b>	<b>2</b>
[Adjusted condition factor]	54,33	2,18	0,14	2
[Total body length], [River of origin]	56,06	3,92	0,06	3

**Table 2:** Parameter estimates, standard errors and P-values for the variables describing the detected brown trout ( $n = 34$ ) and non-detected brown trout ( $n = 11$ ). The conditional average table is based on GLM with gamma distribution ( $\Delta AICc < 4$ ).

Term	Estimate	Std.Error	P-value
Intercept	1,093	0,384	0,006
Total body length	-0,225	0,364	0,539
River of origin (Snilldalselva)	0,394	0,752	0,611
Adjusted condition factor	-0,016	0,350	0,914

### 3.4 Autumn estuary migration date

From the 25 tagged brown trout in river Lenaelva, 18 individuals were detected in the estuary of the river during the period 21 September to 26 November, while from the 20 tagged brown trout in river Snilldalselva, 16 were detected in the estuary between 20 September and 26 October (figure 5).



**Figure 5:** Bar plots show number of brown trout entering the estuaries with values denoted on the left side of the plot and black line show rainfall per day (mm) denoted on the right side of the plot in a) river Lenaelva ( $n = 18$ , blue) and b) river Snilldalselva ( $n = 16$ , red) in the period 15 September to 15 November in year 2023 and 2012, respectively.

The effect of river of origin, total body length and adjusted condition factor on the date of migration to the estuary downstream the river was further examined using GLMs. From the model selection of GLMs, two models had  $\Delta AICc < 2$ . One model included only river of origin as an explanatory variable, while the other included both river of origin and total body length (table 3). Conditional averaging confirmed that river of origin had a significant effect on the timing of riverine exit, as the population from river Snilldalselva migrated earlier than the population from river Lenaelva ( $p < 0.05$ , table 4). None of the other parameters had a significant effect on the timing of riverine exit.



**Table 3:** Model selection of GLM with gamma distribution on the response variable day of the year at estuary migration date downstream the river for brown trout ( $n = 31$ ). All models with  $\Delta AICc < 4$  are included. Supported model ( $\Delta AICc < 2$ ) is shown in bold. Weight tells the strength of predictor-variable influence. DF indicates degrees of freedom.

Model tested	AICc	$\Delta AICc$	Weight	DF
<b>[Location]</b>	<b>297,1</b>	<b>0,00</b>	<b>0,52</b>	<b>3</b>
<b>[River of origin], [Total body length]</b>	<b>298,5</b>	<b>1,47</b>	<b>0,25</b>	<b>4</b>
[River of origin], [Adjusted condition factor]	299,4	2,39	0,16	4
[Total body length]	300,8	3,77	0,08	3

**Table 4:** Parameter estimates, standard errors and P-values for the variables describing the timing of estuary autumn entry (day of the year) for brown trout ( $n=31$ ) downstream two rivers. The conditional average table is based on GLM with gamma distribution ( $\Delta AICc < 4$ ). Asterisk mark explanatory variable estimates significantly different from intercept.

Term	Estimate	Std.Error	P-value
(Intercept)	5,690	0,016	<2e-16
River of origin (Snilldalselva)	-0,058	0,023	0,012*
Total body length	0,014	0,012	0,26
Adjusted condition factor	-0,005	0,012	0,68

### 3.4.1 Two estuary migration groups in river Lenaelva

There were two distinct groups of brown trout that migrated to the estuary of river Lenaelva. One group entered the estuary during the period 21 September to 9 October ( $n = 7$ ; figure 5a) and one group entered the estuary between 31 October and 26 November ( $n = 10$ ). Based on model selection of GLMs and conditional averaging, none of the described models were able to explain the difference between two distinct migration groups (table 5 and 6). In Lenaelva, there was a strong positive correlation between the intensity of precipitation and the migration timing of the brown trout (Spearman's rank correlation  $\rho$ ;  $S=35419$ ,  $p < 0.05$ ), but not in Snilldalselva (Spearman's rank correlation  $\rho$ ;  $S=9282$ ,  $p = 0.715$ ).

**Table 5:** Model selection of GLM with binary distribution on the response variable early migration group (21 September to 9 October) and late migration group (31 October to 26 November) in river Lenaelva at autumn estuary migration for brown trout ( $n = 17$ ). All models with  $\Delta AICc < 4$  are included. Supported model ( $\Delta AICc < 2$ ) is shown in bold. Weight tells the strength of predictor-variable influence. DF indicates degrees of freedom.

Model tested	AICc	$\Delta AICc$	Weight	DF
<b>&lt;NONE&gt;</b>	<b>26,31</b>	<b>0,00</b>	<b>0,45</b>	<b>1</b>
[Sex]	28,33	2,03	0,16	2
[Adjusted condition factor]	28,70	2,39	0,13	2
[Total body length]	28,75	2,45	0,13	2
[Tagging date]	28,85	2,54	0,13	2

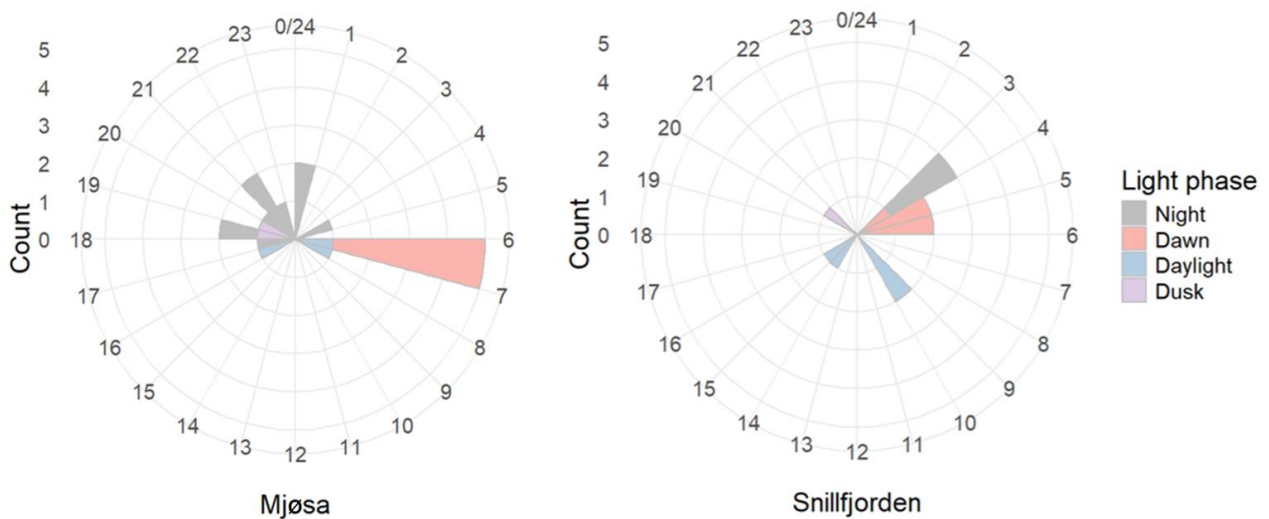
**Table 6:** Parameter estimates, standard errors and P-values for the variables describing the two groupings of estuary migration timing for Lenaelva brown trout ( $n=17$ ) downstream the river. The conditional average table is based on GLM with gamma distribution ( $\Delta AICc < 4$ ).

Term	Estimate	Std.Error	P-value
(Intercept)	0,530	0,592	0,40
Sex (female)	-0,734	1,033	0,51
Adjusted condtion factor	-0,215	0,547	0,72
Total body length	0,167	0,522	0,77
Tagging date	0,053	0,501	0,92

### 3.5 Light phase during riverine exit

The brown trout were assigned a light phase corresponding the time of migration (figure 6). There was no difference in the count data for brown trout migrating at the different light phases (night = 11, dawn = 9, daylight = 7, dusk = 3) (Chi-squared test;  $\chi^2 = 4.667$ ,  $p = 0.20$ ).

Even though there were several brown trout migrating at night time from the Lnaelva river population compared to the Snillfjorden population, there were no significant differences in lightphase during the riverine exit to lake Mjøsa ( $n = 18$ ) and to Snillfjorden ( $n = 12$ ) (Fishers exact test;  $p = 0.26$ ).



**Figure 6:** Number of brown trout entering the estuaries in Mjøsa (left) and Snillfjorden (right) by hour of the day, with estimated light phase of each individual (night = grey, dawn = red, daylight = blue, dusk = purple).

## 4 Discussion

Comparison of growth the first year after migration between a lake run and sea run population of brown trout, revealed that the higher growth first year after migration in the lake run population could be due to a higher total body length and age at first migration, though not significant, that may enabled an earlier shift to piscivory compared to the sea run population. Additionally, predation pressure and osmotic challenges likely constrained the growth of the sea run population the first year after migration to sea. That there was no significant difference in annual growth second year after migration could be attributed to piscivory diets in both populations, due to growth first year after migration. A significantly later autumn outward migration in the lake run brown trout population could be caused by water discharge or predation pressure.

### 4.1 Growth, total body length and age at the first time of migration

The presence of more slow growing brown trout in the Lenaelva population, than in the Snilldalselva population, may have contributed to a higher, though not significantly different, total body length and age at first migration. This is consistent with previous findings, that lower growth rates first years of life in brown trout is correlated with a higher age and larger body size at first migration (Jonsson & Finstad, 1995; Elliott *et al.*, 2000). Annual growth, in rivers are found to be positively correlated with latitude, where river temperature and length of growth season, determined by number of days with water temperature over 7 °C per year, is shorter at higher latitudes (Symons, 1979; Jonsson & L'Abée-Lund, 1993). Since the two rivers were situated at similar latitudes and altitudes, it is likely they provided comparable temperatures and growth seasons, which are critical factors for growth. However, temperature was not measured in this study.

The characteristics of the native rivers could also affect age and size at first migration (Klemetsen *et al.*, 2003). Streams with lower water velocity and deeper pools are vital for the growth and overwintering of larger brown trout, due to the risk of winter icing (Nikol'skiĭ, 1963). Therefore, the lower water flow and fewer deeper pools in the river Snilldalselva, may have selected for smaller size at first migration in the sea run population. In river Lenaelva, there were several deeper pools and weirs, in addition to several smaller rivers draining into the river, potentially providing multiple feeding grounds that could support larger brown trout (Kraabøl & Museth, 2009).

Predation risk in the lower part of the river and in the estuary could also select for older and larger first time migrating brown trout (L'Abée-Lund *et al.*, 1989). In the estuaries, there were probably presence of predators preying heavily on juvenile brown trout, such as cod and pollock in the river outlet of Snillfjoden, and pike in the river outlet of Lenaelva (Hvidsten & Lund, 1988; Fremstad, 2023). Additionally, pike tend to stay in the lower parts within the Lenaelva river, threatening brown trout before they reach the estuary. This could potentially have caused brown trout from Lenaelva to remain upstream longer to grow larger before migrating to the downmost part of the river and out to the lake.

## 4.2 Growth in lake versus fjord

The significantly higher estimated growth rate first year after migration in the lake run population, compared to the sea run population, could be attributed to local variation in food abundance and/or temperature, which are crucial for growth after the riverine exit (L'Abée-Lund *et al.*, 1989; Jonsson & Jonsson, 2021). Due to the lack of temperature measurements at the different location during the study period, the influence of temperature on growth remains unknown. However, the diet of the brown trout varies with fish size, habitat, season and age (Bridcut & Giller, 1995). During the first migration, smaller brown trout primarily feed on terrestrial insects in the estuary, but shift to fish feeding as they grow larger (Lyse *et al.*, 1998; Davidsen *et al.*, 2017). In the estuary of Snilldalselva, competition for food resources could be higher, particularly due to the presence of Atlantic salmon, but also other marine species such as flounder. In contrast, the Lenaelva population may have experienced less competition (Jenkins Jr *et al.*, 1999).

The larger although not significant, total body length at first migration in the lake run population (mean = 17.5 cm, SD = 5.80) compared to the sea run population (mean = 12.8 cm, SD = 2.72), potentially enabled earlier shift to piscivory diet, contributing to the higher growth the first year in the lake (Davidsen *et al.*, 2017; Hughes *et al.*, 2019). Since mouth size in brown trout correlates with the diet size, the larger individuals in the lake run population may have been able to consume larger food items when approaching the more productive lake habitat instead of the river (Jonsson, 1985; Bridcut & Giller, 1995). Previous studies suggest that salmonid typically start fish feeding at a body size between 22 and 25 cm (Jensen *et al.*, 2006; Davidsen *et al.*, 2017). Some of the lake run brown trout had already, or nearly, reached this size at their first migration.

Furthermore, smaller fish are more vulnerable to predation compared to larger individuals, and therefore often adapt behavior to avoid predation, such as moving to deeper waters or hiding in darker habitats during daylight (Ibbotson *et al.*, 2011; Jonsson & Jonsson, 2011). The slower growth observed in the first year after migration in the sea run population could be attributed to a higher need for hiding to avoid being eaten by predatory species such as mink, otter, goosander, cod or pollock in the estuary (Hvidsten & Lund, 1988; Vowles & Kemp, 2019). Especially cod, pollock and goosander prey heavily on small brown trout (Hvidsten & Lund, 1988). Additionally, the lake run population underwent smoltification first year after migration, where osmotic challenges and predation pressure make mortality rates high immediately after migration to sea (Sigholt & Finstad, 1990; Jørgensen & Johnsen, 2014; Jensen *et al.*, 2019). Thus, the energy demands and high predator pressure during sea entrance could potentially be a reason for the lower growth in the sea run population compared to the lake run population.

That lack of significant difference in estimated growth the second year after migration between the two populations could be due to a markable growth during the first year after migration, probably allowing both the sea run and lake run population to feed on fish during the second year after migration, thus exhibit higher annual growth. A previous study at lake Mjøsa found that stomach content of brown trout (ranging from 26 to 84 cm) consisted exclusively of European vendace, European whitefish and/or European smelt (Taugbøl *et al.*, 1989). Similarly, in a study in the fjord system of Snillfjorden, brown trout (ranging from 21 to 73 cm) fed on a variety of items, but that fish feeding on sprat, herring and small sandeel was the dominant feed (Davidsen *et al.*, 2017). Additionally, previous studies suggest that as brown trout grows larger, their resistance to saltwater increase and osmotic stress decreases due to a smaller body surface to body mass ratio (Hoar, 1988). This implies that the sea run population

experienced a lower stress during second year after migration, compared to the first year.

### 4.3 Decision on autumn riverine exit or not

The higher proportion of non-detected brown trout in the estuary of Lenaelva (28%) than in Snilldalselva (20%), though not significant, could be due to a more benign habitat, where several weirs and deeper pools in Lenaelva could make overwintering grounds available for brown trout, and less exposed for icing break-ups during winter (L'Abée-Lund *et al.*, 1989; Eriksson *et al.*, 2008). For brown trout migrating to marine waters, lower water temperatures combined with higher salinity levels reduce the capacity for osmoregulation, and hence cause stress for the individual fish (Finstad *et al.*, 1988; Larsen *et al.*, 2008). During winter, anadromous brown trout often remain in the native river, if suitable areas such as deeper pools or lakes are available, in estuaries or migrate to neighboring rivers to overwinter to avoid the stressful osmoregulatory conditions (L'Abée-Lund *et al.*, 1989; Östergren & Rivinoja, 2008). In this study, no lakes were located upstream in the native river systems. However, two of the tagged brown trout in Snilldalselva were observed in a lake upstream a neighboring river within the fjord system (J.G Davidsen per com). These observations suggest that the sea run brown trout migrated to find better overwintering conditions outside the Snilldalselva river. In lake Mjøsa, there was no salinity stressor for brown trout, potentially making the overwintering conditions within lake Mjøsa more suitable for brown trout compared to Snillfjorden.

Predation pressure on the Snilldalselva population from otters also may explain the higher, though not statistically, proportion of sea run migrating individuals compared to the lake run brown trout (Ruggles, 1980; Thorstad *et al.*, 2016). In Europe, the otter are the most notable river predator of larger brown trout (Carss *et al.*, 1990). Otter abundance is presumably higher in Snilldalselva compared to Lenaelva, as indicated by several recent observations (artskart.artsdatabanken.no, 2024b). Predation by otter is found to be highest during the autumn spawning season when the brown trout migrate, and particularly as they navigate shallow riffles (Carss *et al.*, 1990). This predation pressure could, hence, contribute to the higher proportion of brown trout exiting the Snilldalselva river. Conversely, the Lenaelva population may have fewer predators in the river compared to the lake, potentially leading more individuals to overwinter in the river.

### 4.4 Date of riverine exit

A longer, and significantly later, migration period for the lake run population (20 September to 15 November) than for the sea run population (20 September to 26 October), could be due to a period of low water flow, followed by a larger rainfall and an increase in flow. Previous studies have shown a relationship between water discharge in the river and migrating behavior down the river (Hvidsten & Johnsen, 1997; Jonsson & Jonsson, 2002). A reaction to periods of poor migratory conditions, such as low water flow, an increase in flow could lead to a general migratory response (Jonsson & Jonsson, 2002). This could have been the case in both population in this study. In Lenaelva, almost no rainfall occurred from 25 September to 30 October, and there were almost no migrating brown trout, except for one rainy day, where two brown trout exited the river

Lenaelva. After a larger rainfall in early November, a second group of brown trout exited the river. Even though there was no significant relationship between the day of rainfall and migrating brown trout in Snilldalselva, a group of eight brown trout migrating after a larger rainfall from 8 to 9 October. This supports the theory that increased water flow can induce migratory behavior.

#### 4.5 Light phase during riverine exit

That there was no difference in riverine exit between the four light phases or between the two populations could be due to high water flow and hence turbid waters in both of the two rivers. Previous studies have mainly found a nocturnal migration pattern in salmonids as a response to smaller predation risk from piscivore birds, mammals and fish predators (Hayes, 1953; Bendall *et al.*, 2005; Ibbotson *et al.*, 2011). Furthermore, studies have shown that salmonid migration occurs both diurnal and nocturnal in periods with more turbid water (Hesthagen & Garnås, 1986; Jonsson, 1991). Higher water discharge causing turbidity in the water, seemed to influence the migration timing in both population, and could possibly have been a larger affection on timing of migration than the light intensity (Jonsson, 1991; Hvidsten *et al.*, 1995; McCormick *et al.*, 1998). Additionally, it has been suggested that higher water flow and higher turbidity, could lead to surface ripples, and in combination with bright sunlight, which produces reflection, could end up in reduced predation success from birds and fish (Jacobsson & Järvi, 1977; Ruggles, 1980; Davidsen *et al.*, 2005).

## 5 Conclusion

In conclusion, the study highlights that the lake run population had more slow growing brown trout, which may have contributed to their higher mean age and total body length at first migration, potentially enabling an earlier shift to piscivory and higher growth the first year in the lake. In contrast, predation pressure and osmotic challenges likely constrained the growth of the sea run population in the first year after migrating to the sea, with local food abundance and competition also playing crucial roles. No significant difference in estimated growth the second year after migration between the two populations suggests that a markable growth during the first year after migration, that probably allowed both populations to prey on fish, thus exhibit higher annual growth during the second year after migration. These results indicate that growth patterns in the river are influenced by a complex interplay of environmental conditions, food availability, and predation pressure. Additionally, the later outward autumn migration in the lake run Leanelva population compared to the sea run Snilldalselva population could be due to water discharge in Lenaelva and higher predation pressure in Snilldalselva. Brown trout migrated throughout the day, independent on light phases, again, suggesting that water discharge play a crucial more role in migration timing. Although it is important to take into consideration the limitations of the study due to lack of water temperature data and the actual diet for the brown trout. These factors, which are important for growth, both in the river and after migration (Jonsson & L'Abée-Lund, 1993), were not compared for the two population, and could have influenced on the results in this study. Furthermore, the low sample size and restricted geographic and temporal scope of the study limit the generalizability of the findings. Hence, it would be interesting to repeat the study by including several years and multiple study areas. Additionally, investigating water temperature at different locations, as well as food availability and diet among populations of sea run and lake run brown trout migrating to larger lake environments, would provide valuable insight.



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