

Hanne Risanger

# Temperature and salinity use of fjord migrating and estuarine resident veteran brown trout (*Salmo trutta*) in a fjord system in Northern Norway

May 2021





Norwegian University of  
Science and Technology

Temperature and salinity use of fjord  
migrating and estuarine resident veteran  
brown trout (*Salmo trutta*) in a fjord  
system in Northern Norway

**Hanne Risanger**

MSc Ocean Resources

Submission date: May 2021

Supervisor: Jan Grimsrud Davidsen

Norwegian University of Science and Technology  
Department of Biology



## ACKNOWLEDGEMENTS

Firstly, a huge thank you to my supervisor Jan Grimsrud Davidsen for giving great advice and support throughout this master thesis, and for giving me the occasional push when necessary. Thank you for being so inclusive and for also prioritizing the social aspects of writing a master thesis. I also want to thank Sindre Håvarstein Eldøy for helping me out with R and data analysis, but also for valuable feedback throughout the writing process.

A big thanks to all instances and people who made this project possible. This includes French National Institute for Agricultural Research (INRA) and Ocean Tracking Network (OTN, Halifax, Canada) for providing acoustic tags and receivers, Sinkaberg-Hansen, Plathes Eiendommer, Åbjøra Elveeierlag and the County Governor in Nordland for financing the project, as well as the Norwegian Environment Agency and the cooperation with the CHASES project financed by the Research Council of Norway for giving further finances and thus extending the research period.

An especial thanks to Signar Berg-Hansen and the employees of Sinkaberg-Hansen, Fritjof Plahte and Emil Jamtfall, Terje Hellstad, the crew on FF Gunnerus, Marc Daverdin, Stein-Hugo Hemmingsen, Phillippe Gaudin, Xavier Bordeleau and Javier Sanchez. Additionally, a huge thanks to locals helping out with practical challenges throughout the project.

Last but not least, I want to thank friends and family for being supportive and keeping my spirits uplifted through these unusual times.



## ABSTRACT

It is widely accepted that temperature and salinity are important abiotic factors affecting anadromous brown trout (*Salmo trutta*) throughout their lives. However, detailed knowledge on temperature and salinity use under their marine feeding migration is scarce. In this study, temperature and salinity use in Tosenfjorden and Flostrømmen estuary in northern Norway was investigated by externally tagging 55 anadromous brown trout (mean length =459 mm, SD  $\pm$  70) with temperature and salinity sensing acoustic tags and tracking them during their feeding migration period in 2015 and 2017. A large part of the tagged fish (2015: 54%, 2017: 72%) were observed to stay resident in the estuarine area where they were tagged. The experienced temperatures and salinities varied significantly between the fjord and the estuarine habitat, both generally being higher in the fjord. Fjord migrating fish in 2017 was observed to reside in the estuary for about a month during spring before entering the fjord, possibly waiting for fjord temperatures to reach the lower temperature for growth at  $\sim$ 4 °C. Some evidence indicated different salinity tolerance/preferences for fjord migrants due to them utilizing warmer and saltier waters in the estuary under the concurrent stay with the estuarine residents in 2017. A lower condition factor of the fjord migrants may also explain the observed differences, as these fish might have had a higher motivation to forage on nutrient rich marine prey in the deeper layers of the estuary. Experienced salinities were high ( $>$  30 ‰) for the fjord migrating fish in 2017 immediately after sea entry, indicating a good tolerance for the combination of high salinities and low water temperatures ( $\sim$ 4 °C). Estuarine fish experienced low salinities in June both years (2015: 2– 7 ‰; 2017: 1-10 ‰), possible due to increased water flow in the river and/or surface-oriented feeding. The majority of both fjord migrants and estuarine resident fish were found to dwell in brackish waters for most of their feeding migration period. Total body length, condition factor, sex and number of previous seaward migrations did not seem to be important predictors for the temperature and salinity use of the fish. Climate change and associated increasing temperatures in the marine phase of the study area may be advantageous for the sea trout in this region as the recorded temperatures from the tagged fish rarely reached the previously reported optimal temperature for growth of the species ( $\sim$ 16 °C). However, it is not known whether optimal temperature for growth varies with salinity, and how temperature and salinity preferences interact with prey availability and anti-predator behavior to shape the seaward feeding migrations of anadromous brown trout.





## SAMMENDRAG

Det er allment akseptert at temperatur og salinitet er viktige abiotiske faktorer som påvirker ulike aspekter av anadrom brunørret (*Salmo trutta*) sin livssyklus. Detaljert kunnskap om bruken av ulike temperaturer og saliniteter under den marine næringsvandringen er imidlertid begrenset. Temperatur- og salinitetsbruk under den marine næringsvandringen ble derfor undersøkt i Tosenfjorden og Flostrømmen i Nord-Norge, hvor 55 individer av anadrom brunørret (gjennomsnittlig lengde = 459 mm, SD  $\pm$  70) ble utvendig merket med temperatur- og salinitetsmålede akustiske sendere og deretter fulgt under næringsvandringene i 2015 og 2017. En stor del av de merkede fiskene (2015: 54%, 2017: 72%) ble igjen i estuariet hvor de ble merket. Omliggende temperaturer og saliniteter varierte i stor grad mellom habitatene, hvor begge generelt var høyere i fjorden. De fjordmigrerende fiskene in 2017 oppholdt seg i Flostrømmen i omtrent en måned før de vandret ut i fjorden, noe som kan forklares med at de ventet på at temperaturen i fjorden skulle nå nedre registrerte grense for vekst ( $\sim$ 4 °C). Resultater fra dette studiet tyder på at salinitetstoleransen/-preferansen var høyere hos de fjordmigrerende fiskene enn for de som ble værende i estuariet da fjordfiskene oppholdt seg i saltene og varmere vann i samme tidsperiode i estuariet i 2017. En lavere kondisjonsfaktor hos de fjordmigrerende fiskene kan også delvis forklare den observerte forskjellen mellom gruppene, da de fjordmigrerende fiskene kan ha hatt en større motivasjon til å jakte marine byttedyr i de dypere vannlagene av estuariet. De fjordmigrerende fiskene opplevde høye saliniteter (>30 ‰) tidlig i fjordmigrasjonen i 2017, noe som indikerer en god toleranse for kombinasjonen av høye saliniteter og lave temperaturer ( $\sim$ 4 °C). Estuariefisk opplevde konsekvent lave saliniteter i juni for begge årene (2015: 2– 7 ‰; 2017: 1-10 ‰), som kan ha vært et resultat av høy vannføring i elven og/eller overflateorientert jakt på byttedyr. Et flertall av fisk i dette studiet oppholdt seg i brakkvann størsteparten av næringsvandringen. Total lengde, kondisjonsfaktor, kjønn og antall tidligere næringsmigrasjoner hadde liten forklaringsverdi på bruken av temperatur og salinitet. Fremtidige klimaendringer og påfølgende økte temperaturer i den marine fasen av studieområdet kan være en fordel for sjøørreten i dette området da de registrerte temperaturene sjelden nådde den rapporterte optimaltemperaturen for vekst ( $\sim$ 16 °C). Foreløpig finnes det lite kunnskap om den optimale temperaturen for vekst hos brunørret endres ved ulike saliniteter, og hvordan temperatur- og salinitetspreferanser interagerer med tilgjengelighet på byttedyr og anti-predatorisk oppførsel som til slutt former den marine næringsvandringen til anadrom brunørret.

## Table of contents

<b>1</b>	<b>INTRODUCTION .....</b>	<b>1</b>
<b>2</b>	<b>MATERIALS AND METHODS .....</b>	<b>5</b>
2.1	STUDY AREA .....	5
2.1.1	<i>Tosenfjorden and Bindalsfjorden .....</i>	<i>5</i>
2.1.2	<i>River Åelva and Flostrømmen estuary .....</i>	<i>5</i>
2.2	TEMPERATURE AND SALINITY MEASUREMENTS ON DIFFERENT LOCATIONS .....	7
2.3	WATER FLOW IN RIVER ÅBJØRA .....	7
2.4	CAPTURE AND TAGGING OF SEA TROUT .....	8
2.4.1	<i>Tagging procedures.....</i>	<i>8</i>
2.4.2	<i>Total length and mass of tagged fish.....</i>	<i>9</i>
2.5	TRACKING OF FISH .....	10
2.6	SCALE ANALYSIS AND SEX DETERMINATION .....	11
2.7	DATA ANALYSIS .....	12
2.7.1	<i>Fulton's body condition (K).....</i>	<i>12</i>
2.7.2	<i>Data filtration .....</i>	<i>12</i>
2.7.3	<i>Statistical analyses.....</i>	<i>13</i>
<b>3</b>	<b>RESULTS .....</b>	<b>15</b>
3.1	STUDY GROUPS AND CONDITION FACTOR (K).....	15
3.2	COMPARISON OF TEMPERATURE AND SALINITY USE OF FJORD AND ESTUARINE FISH.....	16
3.2.1	<i>Temperatures of surrounding water masses .....</i>	<i>16</i>
3.2.2	<i>Salinities of surrounding water masses.....</i>	<i>18</i>
3.3	BETWEEN-YEAR COMPARISONS OF TEMPERATURE AND SALINITY USE .....	20
3.3.1	<i>Temperatures of surrounding water masses .....</i>	<i>20</i>
3.3.2	<i>Experienced levels of salinity.....</i>	<i>22</i>
3.4	TEMPERATURE AND SALINITY USE OF FJORD MIGRATING AND ESTUARINE RESIDENT TROUT UNDER THEIR CONCURRENT STAY IN AN ESTUARY.....	23
3.5	INFLUENCE OF INDIVIDUAL BIOLOGIC CHARACTERISTICS ON THE USE OF WATER MASSES WITH DIFFERENT LEVELS OF SALINITY AND TEMPERATURE .....	24
3.5.1	<i>Influence of biologic characteristics on temperature use for fjord migrating fish</i> <i>25</i>	
3.5.2	<i>Influence of biologic characteristics on salinity use of fjord migrating fish .....</i>	<i>25</i>
3.5.3	<i>Influence of biologic characteristics on temperature use for estuary residents..</i>	<i>26</i>
3.5.4	<i>Influence of biologic characteristics on salinity use for estuary residents.....</i>	<i>27</i>
<b>4</b>	<b>DISCUSSION.....</b>	<b>29</b>
<b>5</b>	<b>CONCLUSION .....</b>	<b>37</b>
	<b>LITERATURE .....</b>	<b>38</b>

# 1 INTRODUCTION

The brown trout (*Salmo trutta* L. 1758) is a cold-water salmonid species with a widespread distribution, demonstrated by its presence on all continents except Antarctica (MacCrimmon *et al.*, 1970). The life history of the brown trout is very plastic and varies between individuals and populations. All brown trout spawn in freshwater, and this is also where they spend the first stage of their lives. Later in the life cycle the fish may become anadromous and migrate into marine habitats to feed. At this stage the fish is often termed as sea trout (Thorstad *et al.*, 2016). Migrating to sea is energy demanding, both due to the movement itself and the physiological adjustment required for osmoregulation in saltwater (Bœuf & Payan, 2001). Predation risk is also higher when moving into marine waters, especially in the early stage (e.g. Dieperink *et al.*, 2002). Behavior and survival rate of anadromous fish in the marine phase are influenced by several factors, including temperature, physiological state and size of the fish (Drenner *et al.*, 2012). In the marine phase the anadromous brown trout generally reside in coastal areas close to shore (Berg & Berg, 1987; Davidsen *et al.*, 2014a; Jensen *et al.*, 2014), and mainly utilize the upper layers of the water column (Eldøy *et al.*, 2017; Kristensen *et al.*, 2018).

Migration strategies of anadromous brown trout are complex and may vary considerably between individuals and populations (Thorstad *et al.*, 2016). Partial migration, which historically has been viewed as one part of a population migrating and the other staying resident in their original habitat, is often observed in brown trout (Chapman *et al.*, 2012). However, previous research have suggested that migration strategies of anadromous brown trout should be considered as a continuum of strategies between freshwater residency and migration to sea (e.g. Cucherousset *et al.*, 2005; Davidsen *et al.*, 2014a; del Villar-Guerra *et al.*, 2014), due to the large variation in migratory timing, residence and migration distance. On one end of this continuum, some anadromous brown trout only perform short distance migrations to the estuaries of their natal watercourse (Davidsen *et al.*, 2014a; Bordeleau *et al.*, 2018; Eldøy *et al.*, 2021). Depending on the properties of the estuary (temperature, salinity, productivity etc.), the advantages of staying resident in this habitat throughout the feeding season may outweigh the rewarding, though high-risk action of migrating further out to sea (Bordeleau *et al.*, 2018). Migrating to an estuary may provide better foraging opportunities compared to remaining in the river, and being in a transition zone between freshwater and saltwater may allow the fish to adjust ambient salinities according to their physiological needs (Thorpe, 1994).

Temperature is known to be an important abiotic factor influencing many aspects of the brown trout's life cycle. Water temperatures limit the geographical distribution of brown trout and can affect life history traits such as time of spawning, egg hatching, timing of smolt migration etc. (Jonsson, 1991; Elliott, 1994; Jonsson & Jonsson, 2009). As an ectothermic fish, brown trout metabolism and, therefore also growth, is highly affected by water temperatures (Elliott, 1975a; b). Growth of brown trout have been observed between temperatures ranging from 4–19° C, with a growth optimum at approximately 16° C (Elliott, 1994; Forseth & Jonsson, 1994; Elliott & Elliott, 2010). Outside the temperature range, growth is believed to cease (Elliott, 1994). Kristensen *et al.* (2018) studied the depth and temperature preferences of brown trout in the marine phase and observed that the fish moved to deeper layers of the water column when surface temperatures exceeded 17 °C. In a study from a fjord system in northern Norway, Jensen *et al.* (2014) found that higher temperatures in the inner parts of the fjord increased the likelihood of finding anadromous brown trout at the outer parts of the fjord system. This trend, however, was not observed before the temperature in the inner areas exceeded 14°C. Rikardsen *et al.* (2007b) found that the fjord migrating brown trout in the Alta fjord generally resided in the warmer parts of the fjord throughout the study period. These studies indicate that sea trout may actively regulate its body temperature by seeking towards water masses of preferred temperatures.

One of the main challenges when moving from freshwater to seawater is the adaptation to a saline environment. Residing in full strength seawater is energy demanding due to increased metabolic activity related to osmoregulation (Bœuf & Payan, 2001), and growth in salmonid fish has been found to be affected by the salinity of the ambient waters (McKay & Gjerde, 1985; Ytrestøyl *et al.*, 2020). As an anadromous fish, the migrating brown trout is expected to tolerate a wide range of salinities. Tolerance for salinity in brown trout is tightly linked to fish size, and larger fish can tolerate higher salinities than smaller fish (Parry, 1960; Finstad & Ugedal, 1998). Salinity tolerance has been shown to change with temperatures, and the combination of low water temperatures and high salinities may be challenging for brown trout due to poor osmoregulatory capacity in cold water (Finstad *et al.*, 1988; Larsen *et al.*, 2008). Low water temperatures in combination with high salinities have been hypothesized to affect the timing of marine migration in salmonids. In Norway, populations at higher latitudes generally enter the sea later in the year than fish at lower latitudes, which is thought to be caused by differences in optimal conditions at sea in relation to temperature and salinity (Klemetsen *et*

*al.*, 2003; Thomsen *et al.*, 2007). Larsen *et al.* (2008) conducted a study on anadromous brown trout which indicated that the combination of low water temperatures and high salinities might be an important motivator for moving into freshwater in the winter. Despite the potential challenges caused by low temperatures and high salinities, anadromous brown trout in northern Norway have been observed to overwinter at sea (Knutsen *et al.*, 2004; Jensen & Rikardsen, 2008; Eldøy *et al.*, 2017). The study by Larsen *et al.* (2008) also observed intraspecific differences in salinity tolerance between the two populations under study, which indicate local adaptations resulting from exposure to different marine environments. Although several studies have investigated the effects of low temperatures and high salinities, fewer studies have focused on whether anadromous brown trout gravitate towards certain salinities under their marine migrations.

In Norway, many brown trout populations are under pressure. In a review of 430 Norwegian brown trout populations with anadromous individuals, almost half (48%) of the populations were classified as in bad or very bad shape. Only 20% were regarded as in good or very good shape (Anon., 2019). A future challenge for the species may be a changing global climate. The UN Intergovernmental Panel on Climate Change (IPCC, 2013) predicts that sea temperatures will increase, with the largest changes close to surface level. The sea surface is known to be an important habitat to anadromous brown trout (Eldøy *et al.*, 2017; Kristensen *et al.*, 2018), and a change in temperature here may have consequences for the species in the marine phase. This will especially be evident if increasing temperatures exceed the range for optimal growth of the species. It is also predicted that Europe will experience warmer and wetter winters in the future, with more precipitation and thus a higher freshwater runoff into marine waters. In areas with high precipitation rates, this may result in less saline environments in shallower marine habitats like estuaries and fjords (IPCC, 2013). The consequences of this are currently unknown and the outcome is difficult to predict since anadromous individuals will face impacts in both the marine and freshwater habitat.

Considering the scarce knowledge on temperature and salinity use under the marine feeding migration in combination with a changing global climate, a greater understanding of how temperature and salinity affect the behavior and migration strategies of anadromous brown trout is important in order to effectively predict future challenges for the species. Hence, the main aim of this study was to reveal temperature and salinity use of fjord migrating and estuarine resident brown trout in a fjord system in northern Norway. By tracking the movements and the

ambient temperatures and salinities of individual fish with acoustic telemetry, the following objectives were investigated: (1) experienced temperatures and salinities in their respective habitats for fish with two different migratory strategies, being either fjord migrants or estuarine residents (2) potential differences in temperature and salinity use between fjord migrating fish and estuarine residents under their concurrent stay in Flostrømmen estuary, and (3) potential influences of total length, condition factor, sex and number of previous marine migrations on temperature and salinity use.

## 2 MATERIALS AND METHODS

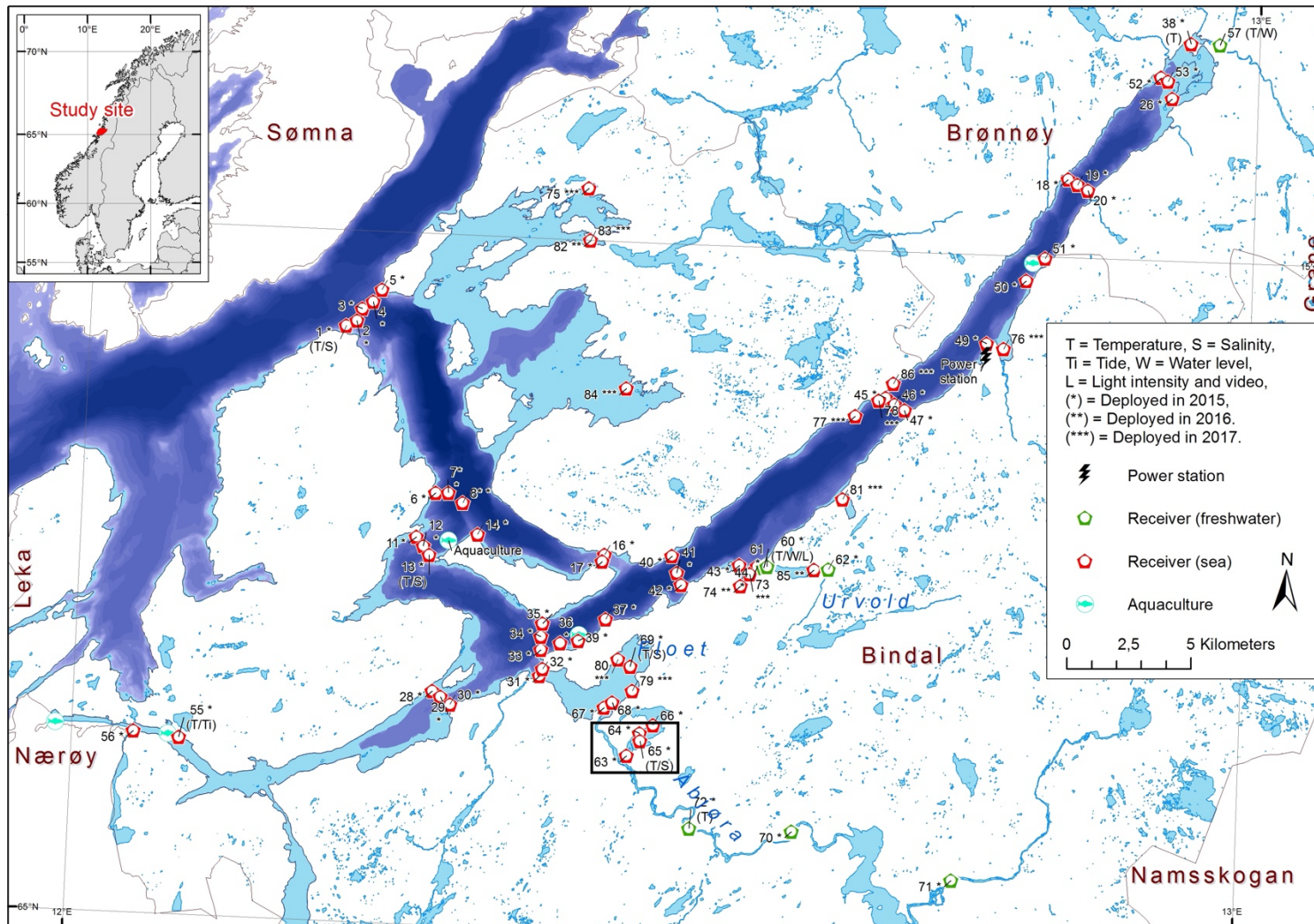
### 2.1 Study area

#### 2.1.1 Tosenfjorden and Bindalsfjorden

Tosenfjorden is a fjord system located in Brønnøy and Bindal municipalities in Nordland county, northern Norway (Figure 1). The fjord is 37 kilometers long (maximum depth of ~550 m) and is connected to Bindalsfjorden on its south-western end. Bindalsfjorden (maximum depth of ~700 m) is located in Bindal and Sømna municipalities and stretches 17 kilometers before it connects to the Norwegian Sea. This area is habitat for both anadromous brown trout, Atlantic salmon (*Salmo salar* L. 1758) and Arctic char (*Salvelinus alpinus* L. 1758).

#### 2.1.2 River Åelva and Flostrømmen estuary

Åbjøra watercourse (Figure 1) drains into the eastern side of Tosenfjorden. The lowermost part of the watercourse is known as River Åelva, which has a stretch of 24 km accessible to the anadromous fish. The lower part of the river includes a large estuary of about 1.6 km<sup>2</sup> of surface area affected by the tides, including shoreline areas covered in water at high tide and the estuarine pool Flostrømmen. The influence from both tidal saltwater and freshwater from the river creates a stratified water column with freshwater in the upper layers and gradually saltier waters towards the bottom. Further upstream is Lake Åbjørvatnet (surface area of 4.8 km<sup>2</sup>, 81 meters above sea level). Åbjøra watercourse is regulated for hydropower production and has a minimum discharge of 7 m<sup>3</sup>/s. The watercourse houses populations of anadromous Atlantic salmon and brown trout, as well as resident brown trout and Arctic char in Lake Åbjørvatn.

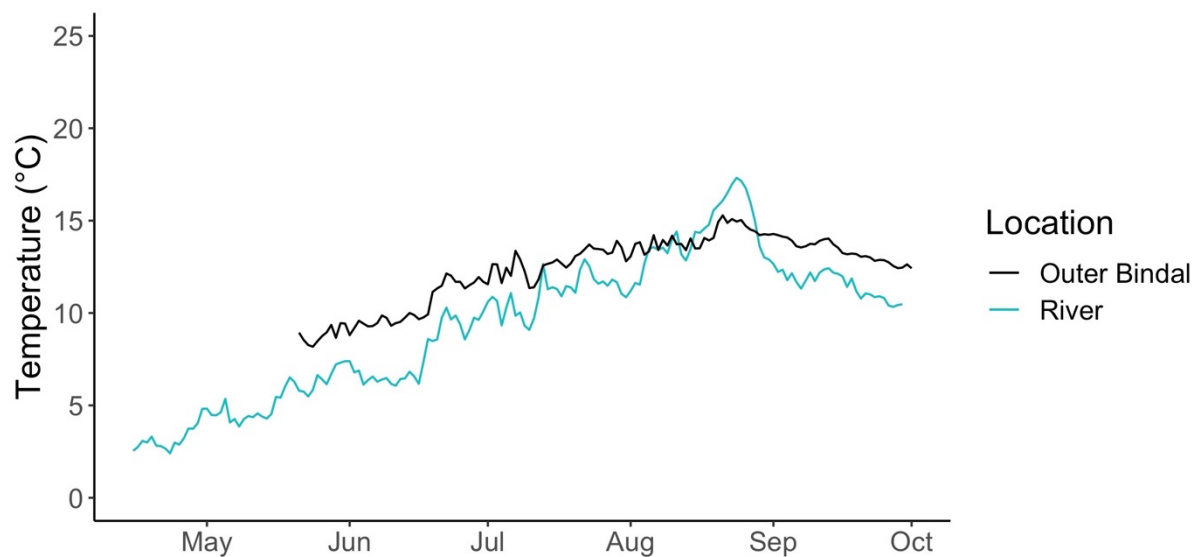


**Figure 1:** Bindalsfjorden and Tosenfjorden in northern Norway, with Åbjøra watercourse draining into Tosenfjorden. Pentagonal symbols represent deployed acoustic receivers in saline (red) and freshwater (green) habitats. Listening stations marked with T/S measured temperature (T) and salinity (S) at 1 meter at the given location. Flostrømmen estuary is highlighted by the black square (station 63 and 65).



## 2.2 Temperature and salinity measurements on different locations

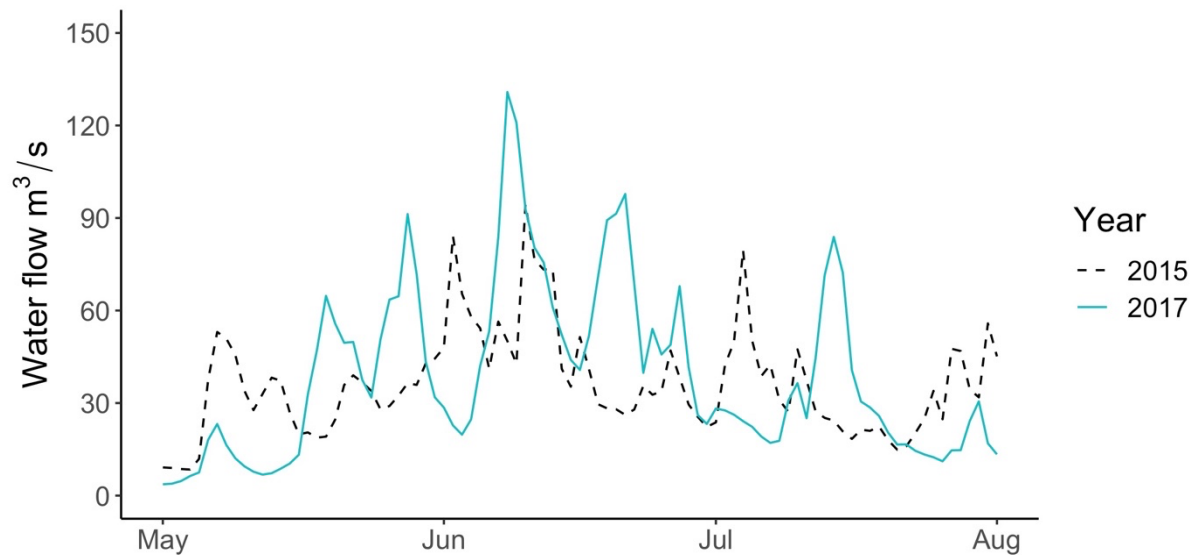
Temperatures and salinities were measured at certain locations in the fjord system and in the river Åbjøra. These abiotic factors were measured using data loggers (Star Oddi, Reykjavik, Iceland; Model DST milli-CT) which were placed beneath a buoy 1 meter below the surface. Temperatures measured in River Åbjøra and in outer Bindalsfjord (station 1) in 2015 are displayed in Figure 2. Measured salinities were either defined as freshwater (< 5 ‰), brackish water (5-30 ‰) or saltwater (> 30 ‰).



**Figure 2:** Temperature measurements (°C) from River Åbjøra and the outer part of Bindalsfjorden (Station 1) in 2015.

## 2.3 Water flow in River Åbjøra

Data on water flow ( $\text{m}^3/\text{s}$ ) from 2015 and 2017 in River Åbjøra was collected from The Norwegian Water Resources and Energy Directorate (NVE, 2021). Water flow varied between the two years, although similar trends were observed with waterflow peaking in mid-June for both years (Figure 3).



**Figure 3:** Registered water flow ( $\text{m}^3/\text{s}$ ) in River Åbjøra for 2015 and 2017 measured by the Norwegian Water Resources and Energy Directorate (NVE, 2021).

## 2.4 Capture and tagging of anadromous brown trout

### 2.4.1 Tagging procedures

A total of 55 fish were captured and externally tagged with individually coded temperature and salinity sensing acoustic tags (Thelma Biotel AS, Trondheim, Norway; model CT-MP9L, 9,0 x 42.5 mm, mass in water 4.2 g, power output 146 re 1  $\mu\text{Pa}$  at 1m, estimated minimum tag duration 300 days) in Flostrømmen in 2015 and 2017 (2015:  $n=13$ , 2017:  $n=42$ ). The tagging of the 2015 group was done 5–6 May, while the 2017 group was tagged 27–29 March. The fish were captured by angling and were held in keep nets for up to four hours before they had a transmitter attached.

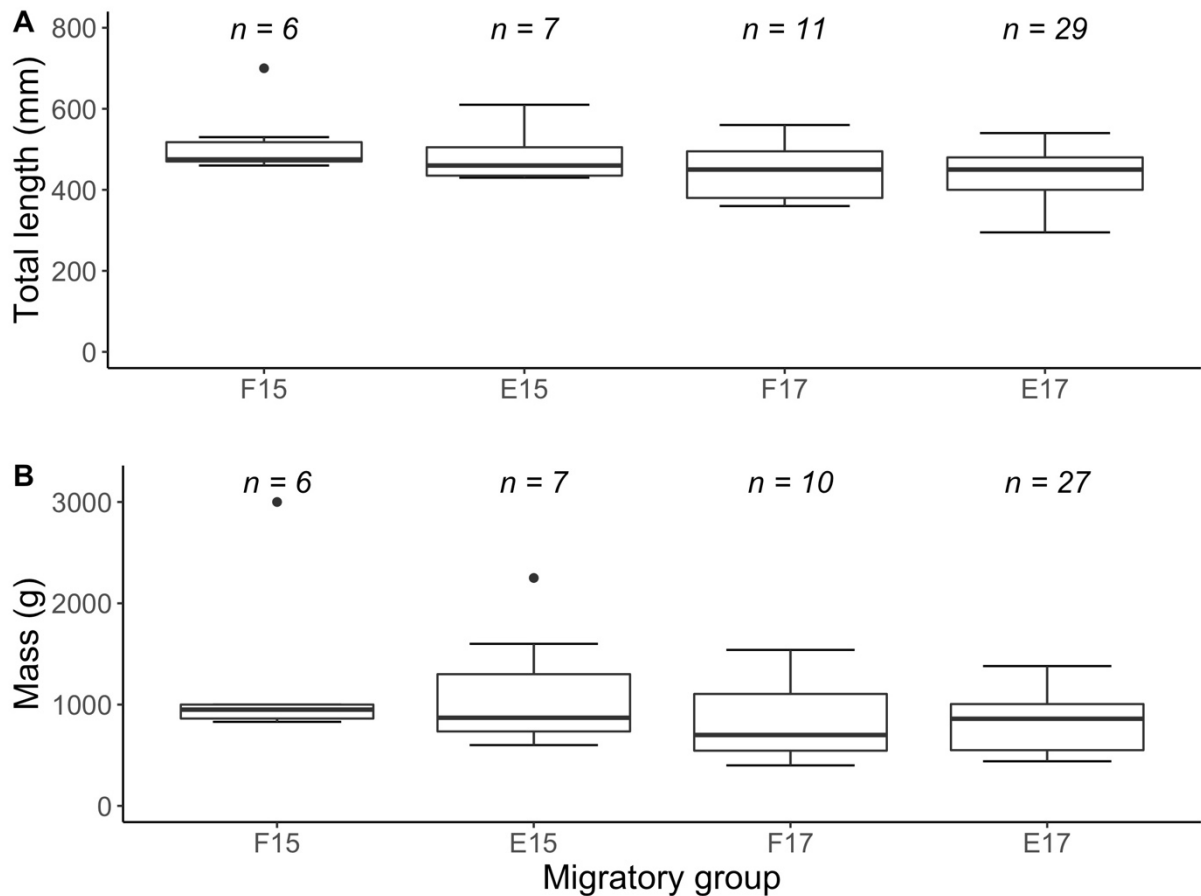
For tagging, the fish were anaesthetized with 2-phenoxyethanol (EC No. 204-589-7; SIGMA Chemical Co., St. Louis, USA;  $0.5 \text{ mL}\cdot\text{L}^{-1}$  water). An acoustic transmitter was externally attached to the fish below the dorsal fin with 0.5 mm steel wires inserted horizontally through the upper part of the dorsal musculature. The wires were threaded by using two hollow needles (1.25 mm in diameter), sharpened at one end. The needles were pushed through the musculature approximately 20 mm below the dorsal fin, and the spacing between the needles matched the length of the tag. To avoid erosion of the flesh by the tag or attachment wire, a silicone plate was attached between the tag and the skin, and a plastic plate was attached between the skin

and the wire on the opposing dorsal side following the procedures described in Davidsen *et al.* (2013). After tagging, the total body length ( $L_T$ ) and mass of each fish were measured. Five to ten scales were taken from the fish for later scale analysis. For further genetic sex determination a part of the adipose fin was cut off and stored in a cryo vial with alcohol. Throughout the tagging process, the gills were irrigated with fresh, ambient river water. After tagging, the fish were released in a calm part of Flostrømmen estuary.

To measure levels of salinity and water temperature encountered by the individual fish, each acoustic tag was equipped with a sensor for conductivity (range 0-34 ‰, resolution 2 ‰) and temperature (range 0-15 °C, resolution 1 °C). The tags were programmed to sample every 45 seconds and the most recent values, along with the individual fish ID, were transmitted with a random 30-90 s interval delay. The experimental procedures were approved by the Norwegian National Animal Research Authority (permission number 2015/8518 and 2018/67706).

#### 2.4.2 Total length and mass of tagged fish

Total length ( $L_T$ ) of the captured fish ranged from 295 mm to 700 mm (mean=459 mm, SD  $\pm$  70;  $n=53$ ), and mass varied from 400 g to 3000 g (mean=925, SD  $\pm$  470;  $n=50$ ). The mass (g) was missing for three fish. The two tagging groups were divided into four migratory groups according to tagging year and migration strategy (Figure 4). These groups consisted of fjord migrating individuals from 2015 and 2017 (group F15 and F17, respectively) and estuarine residents from 2015 and 2017 (group E15 and E17, respectively).  $L_T$  differed between the E17 and the F15 group (Wilcoxon rank sum test,  $p$ -value  $< 0.05$ ;  $n=35$ ), while no difference in total length was found between the other groups ( $p$ -value  $> 0.05$ ). There were no differences in body mass between the four groups ( $p$ -value  $> 0.05$ ;  $n=50$ ). Two of the tagged fish were never registered on any of the listening stations and were therefore not included in the study.



**Figure 4:** (A) Total body length (mm) and (B) mass (g) of anadromous brown trout from four groups based on migration strategy (F=fjord migrants, E=estuary residents) and tagging year (2015 and 2017). Each box represents the interquartile range (IQR), from the 25<sup>th</sup> percentile ( $Q_1$ ) to the 75<sup>th</sup> percentile. The lower whiskers represent  $Q_1 - IQR \cdot 1.5$ , and the upper whiskers represent  $Q_3 + IQR \cdot 1.5$ , respectively. The bold line represents the median of the tagging group, and the dots represent outliers.  $n$  equals the number of fish per group.

## 2.5 Tracking of fish

To be able to track the movements of the fish, 69 kHz acoustic listening stations were placed into the fjord and river systems prior to tagging (see Figure 1). Overall, 50 stations (Vemco, Halifax, Canada; models VR2W or VR2-AR) were used for this study. The listening stations were either anchored to stationary feeding stations at aquaculture facilities, attached to a 14 mm rope with a C3 buoy at the surface and a 140 kg anchor at the bottom, or submerged with acoustic release systems with two trawling balls with 14 mm rope and 40-80 kg anchor. Receivers attached to feeding stations and C3 boys were deployed at 5 m depth, while receivers attached to release systems were deployed at 15-30 m depths.

The acoustic fish tags sent out a unique sound signal (69 kHz) that was picked up by the listening stations when the fish was within the detection range, at approximately 200-400 meters depending on the water conditions (Bordeleau *et al.*, 2018; Eldøy *et al.*, 2021). The 2015 fish were tracked for a year after tagging date (5 May – 6 May). First detection in the fjord was 23 May, and last detection was 16 July. The 2017 fish were tracked from the day of tagging (27 March – 29 March) until the acoustic receivers were recovered in late September. For the 2017 group, first detection in the fjord was 14 April and last was 14 July.

Registered temperatures and salinities of the anadromous fish in their respective habitats were restricted to specific listening stations, limiting the area in which these variables were measured. The registered measurements from the fjord group only included registrations from the fjord system, and the registered measurements for the estuarine group only included registrations from the two listening stations in the estuary (63 and 65).

## 2.6 Scale analysis and sex determination

Scales were collected during the tagging of the fish. The scales were taken from behind the dorsal fin and above the lateral line, and by scale readings these were used to determine the age and number of previous seaward migrations for each individual fish. Five fish did not get their age nor previous seaward migrations determined due to missing scales of good quality. Age varied from 4-10 years (mean = 6, SD  $\pm$  1.2). The highest mean age was observed for the fjord group in 2015 (mean=8, SD  $\pm$  2.1). No significant differences in age were found between the groups (Wilcoxon rank sum test,  $p$ -value  $>$  0.05;  $n=48$ ). Number of previous seaward migrations varied from 2-7 (mean = 3, SD  $\pm$  1.2), however, no differences were found between any of the groups (Wilcoxon rank sum test,  $p$ -value  $>$  0.05;  $n=48$ ). The mean number of previous seaward migrations was highest for the fjord migrating group in 2015 (mean=4, SD  $\pm$  1.6), corresponding to their greater age. Sex was determined genetically by DNA analysis using the piece from the adipose fin that was collected from the fish under the tagging procedure. The DNA-analyses followed the method described by (Eldøy *et al.*, 2021).

## 2.7 Data Analysis

### 2.7.1 Fulton's body condition (K)

Fulton's body condition (K) for all fish with valid measurements of body length and mass ( $n=50$ ) was calculated using the formula

$$K = \frac{100 * W}{L^3}$$

where  $W$  is the mass (g) of the fish and  $L$  is the total length (cm) of the fish (Fulton, 1904). Fulton's body condition will further be referred to as condition factor.

### 2.7.2 Data filtration

A known problem in acoustic telemetry is false registrations (e.g. Simpfendorfer *et al.*, 2015). False registrations can happen when signals from different acoustic transmitters collide due to them transmitting at the same time, which may lead to the receivers interpreting this as a new signal (Pincock, 2011). Keeping these registrations in the data set may give misleading results. By filtering the data many of the false registrations can be eliminated and the data will represent reality more closely.

The initial number of registrations in the full tracking period, including fish from multiple rivers in Tosenfjorden, were 9 582 157. Pings that were not assigned to ID's which belonged to tagged fish in the system were removed. To minimize the risk of false data from data collisions in areas with many fish residing at the same time, the dataset was subsequently filtered on selected receivers (18, 37, 38, 44, 55, 61, 62, 63, 64, 65, 66, 67, 68, 69, 73 and 85). For a specific transmitter-ID the fish had to be registered at the same listening station at least twice within a time span of ten minutes to be accepted as true. Of the filtered registrations, 21 % (1 902 222) had transmitter IDs from fish tagged in Flostrømmen in 2015 and 2017. To minimize problems with false sensor data transmitted from the acoustic tags, registrations of data with 0 °C in May-July 2017 were removed. This resulted in a dataset of 1 589 948 registrations which were used for further analyses.

### 2.7.3 Statistical analyses

The fish were either defined as fjord migrants or estuarine residents. These migratory groups were defined according to which listening stations the individual fish had been registered by. If a fish was never registered on any listening stations past station 31 and 32 in the river mouth (Figure 1), they were regarded as estuarine residents. It is important to emphasize that even though these fish were defined as residents, they were also migrants because they migrated from the river to the estuary prior to the study. Fish detected further out in the fjord than station 31 and 32 were defined as fjord migrants. When calculating daily averages for the fish in Flostrømmen estuary, only registrations from the listening stations 63 and 65 were used. Anadromous brown trout from an earlier study was observed to use a considerable amount of time in this specific area (Davidsen *et al.*, 2018), which is why the habitat was restricted to these two listening stations. Forty-eight listening stations were classified as the fjord habitat (1-8, 11-14, 16-20, 26, 28-35, 37-42, 45-47, 49-53, 55, 56, 76-78, 81, 84 and 86).

All data analyses were performed using RStudio Version 1.2.5033 (RStudio Team, 2020) and R version 3.6.2 (R Core Team, 2020). Wilcoxon rank sum tests were used to test for differences in variance between total length ( $L_T$ ), mass, age and previous seaward migrations as the data did not meet the assumption of normality. The null hypotheses for the tests assumed no differences in the mean of the groups tested. Each migratory group (F15, E15, F17, E17) was compared to each other pairwise and all  $p$ -values  $< 0.05$  were considered significant. Mean water temperatures and salinity levels were also compared using Wilcoxon rank sum tests (e.g., Table 1 in results). When comparing means, these were only calculated for the time period when both groups were registered in the given habitat. For instance, when comparing mean temperature for fjord and estuarine fish in their respective habitats in May 2015, only detections from 23-31 May were used because no fish were recorded in the fjord before 23 May.

Mixed effects models were used to investigate the relationship between the use of water masses with different levels of temperature and salinity and individual biological characteristics. Due to a low number of fish in the 2015 groups ( $< 10$ ), no models were run for the 2015 groups. Models were conducted separately for the fjord and estuarine fish tagged in 2017 to test whether the most important explanatory variables differed between the two migration strategies. For both groups some fish were removed from the models due to missing values in the explanatory variables, resulting in  $n = 10$  for the fjord group and  $n = 23$  for the estuarine group. The function

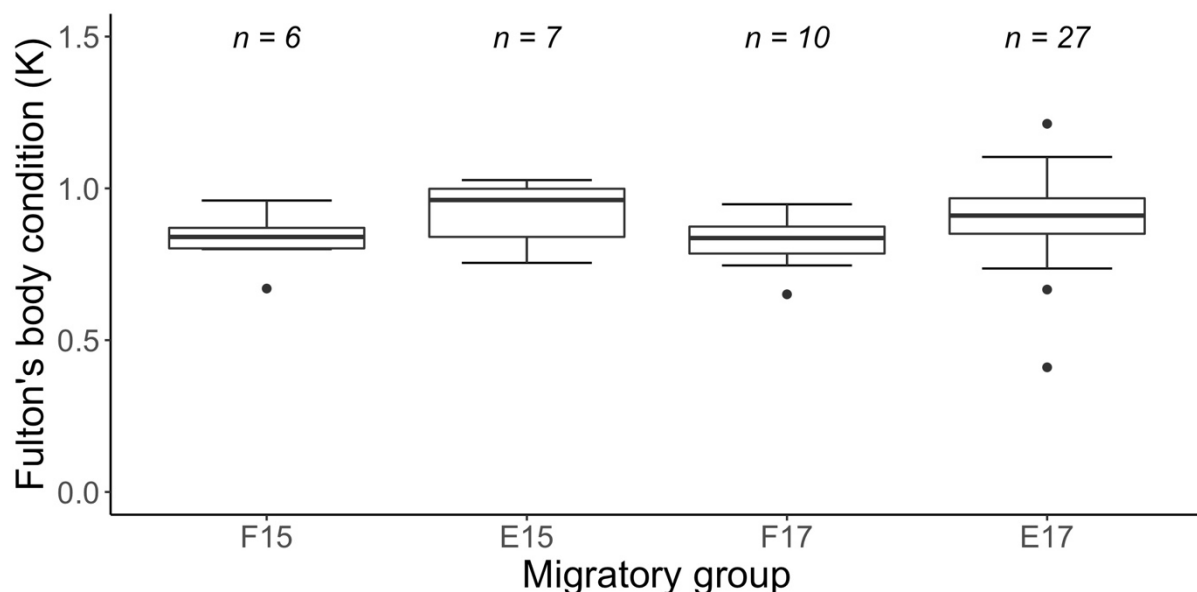
'lme' in the package nlme (Pinheiro *et al.*, 2020) was used to run the models, and a conditional model selection using the 'dredge' function in the MuMIn package (Bartoń, 2020) was used to find the best models ( $\Delta AIC < 2$ , Anderson *et al.*, 2001). Variance inflation factors (VIF) of the explanatory variables were investigated to test for multicollinearity between the explanatory variables. For the fjord group, number of previous seaward migrations and condition factor were included as explanatory variables in the final model. The same variables were included in the final model for the estuarine group, as well as sex. Sex was not included as an explanatory variable in the fjord model due to a skewed distribution (1 male, 9 females). Total length ( $L_T$ ) was originally included in all models, but this explanatory variable was not important according to the model selection and was therefore removed.  $L_T$  also showed a high multicollinearity with previous seaward migrations. Age and number of previous seaward migrations showed high multicollinearity, and for this reason age was not included in any of the models. Mass was not included to avoid interference with the condition factor variable, as condition factor is calculated from mass. Transmitter-ID was added as a random variable for all models.



### 3 RESULTS

#### 3.1 Study groups and condition factor (K)

A total of 53 fish (96%) were registered at some point during the study period. From the group of fish tagged in 2015, 54% remained in Flostrømmen estuary ( $n=7$ ; 6 males, 1 female), while the rest of the fish ( $n=6$ ; 4 males, 2 females) migrated to the fjord. From the 2017 tagging group, 72% ( $n=29$ ; 16 males, 13 females) of the sea trout remained in Flostrømmen estuary, while 28% ( $n=11$ ; 1 male, 10 females) migrated to the fjord. Fulton's condition factor of the fish ranged from 0.4-1.2, with a mean of 0.9 (SD  $\pm$  0.1, Figure 5). The estuarine residents in 2017 (E17) had a significantly higher body condition than the fjord migrants, F17 (Wilcoxon rank sum test,  $p$ -value  $<$  0.05;  $n=37$ ). There were no differences in condition factor between the other groups ( $p$ -value  $>$  0.05). The body mass of two fish from the estuary 2017 group and one fish from the fjord 2017 group were missing, and hence body condition could not be calculated for these fish.

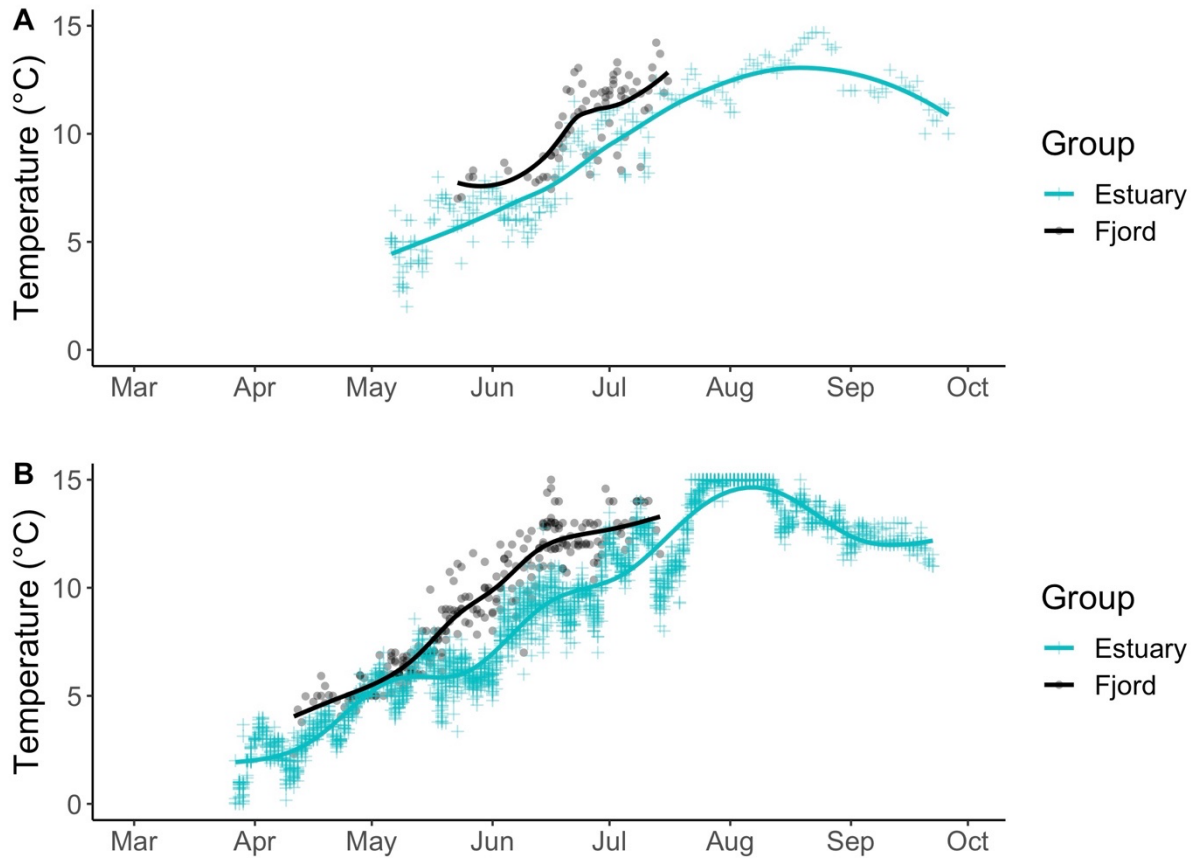


**Figure 5:** Fulton's body condition (K) for four groups of anadromous brown trout, named after migration strategy (F=fjord migrants, E=estuarine residents) and tagging year (2015 and 2017). Each box represents the interquartile range (IQR), from the 25<sup>th</sup> percentile ( $Q_1$ ) to the 75<sup>th</sup> percentile. The lower whiskers represent  $Q_1 - IQR \cdot 1.5$ , and the upper whisker represent  $Q_3 + IQR \cdot 1.5$ , respectively. The bold line represents the median of the tagging group, and the dots represent outliers.  $n$  equals the number of fish per group.

## 3.2 Comparison of temperature and salinity use of fjord and estuarine fish

### 3.2.1 Temperatures of surrounding water masses

Differences in registered temperature were prominent between the estuarine and fjord habitats for both 2015 and 2017 (Figure 6). The anadromous brown trout that migrated to the fjord in 2015 (F15) registered higher temperatures for all months compared to the estuarine group in 2015 (E15; Wilcoxon rank sum test,  $p$ -value  $< 0.05$ ,  $n=13$ ; table 1). Both groups experienced a relatively large range of temperatures (F15; 5-15 °C, E15; 2-15 °C) for the entire tracking period. Similar tendencies were observed for the 2017 groups, with fjord migrating brown trout (F17) experiencing higher temperatures for all months compared to the estuarine residents (E17;  $p$ -value  $< 0.05$ ,  $n=38$ ; table 1). Experienced temperature ranges were similar to the 2015 groups (F17; 1-15 °C, E17; 0-15°C).



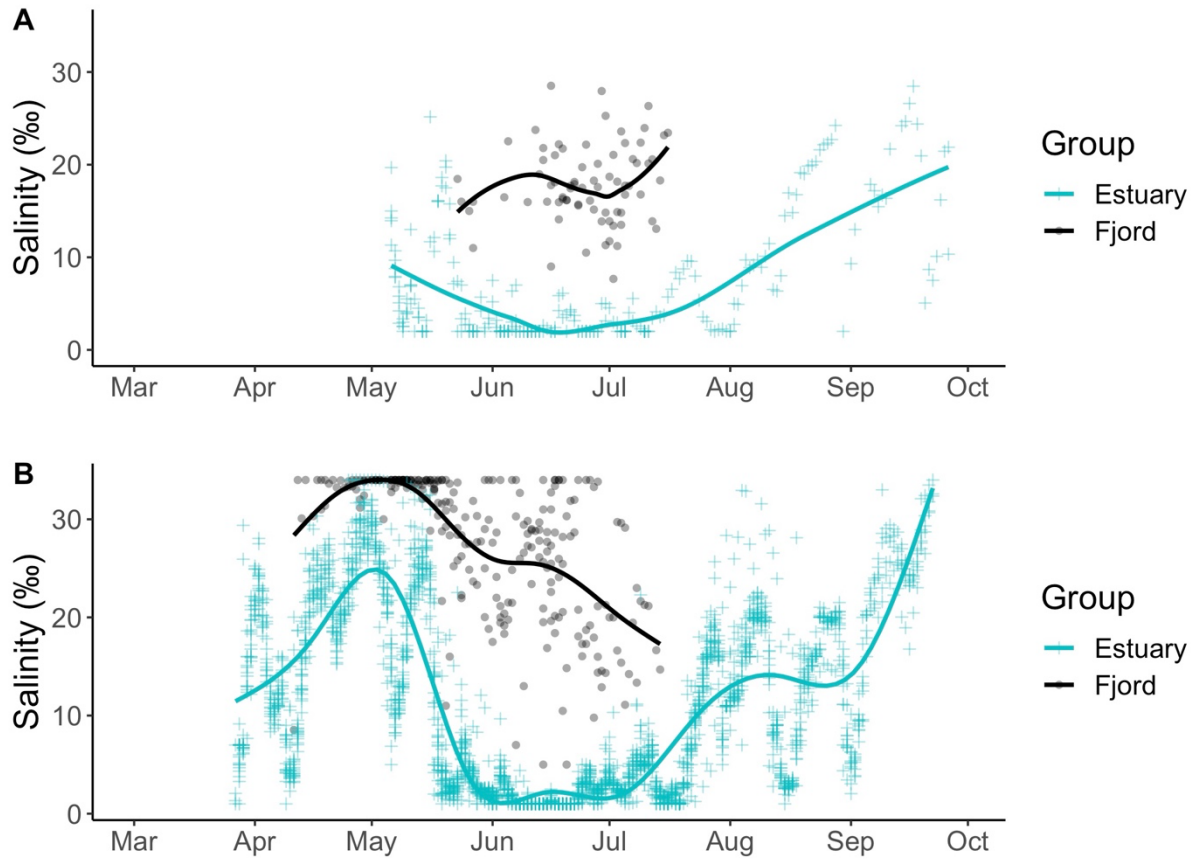
**Figure 6:** Registered temperatures (°C) for two groups of anadromous brown trout in two habitats. Fish were acoustically tagged and tracked in (A) 2015, and (B) 2017. For both years some fish migrated to the fjord (2015;  $n=6$ , 2017;  $n=11$ ) and some remained in Flostrømmen estuary (2015;  $n=7$ , 2017;  $n=29$ ). Registered temperatures for fjord fish were recorded by listening stations in the fjord (48 stations), while the corresponding registrations for the estuarine fish were recorded by two listening stations (63 and 65). Each mark represents the daily average calculated from individual fish (+ = estuarine residents, • = fjord migrants).

**Table 1:** Registered monthly mean temperatures (°C) for two groups (2015 and 2017) of anadromous brown trout with standard deviation (SD) in parentheses. Both years some fish migrated to the fjord (2015;  $n=6$ , 2017;  $n=11$ ) and some remained in Flostrømmen estuary (2015;  $n=7$ , 2017;  $n=29$ ). Registered temperatures for fjord fish were recorded by listening stations in the fjord (48 stations), while the corresponding registrations for the estuarine fish were recorded by two listening stations (63 and 65).

Month	2015			2017		
	Fjord (°C)	Estuary (°C)	$p$ -value	Fjord (°C)	Estuary (°C)	$p$ -value
April	-	-	-	5.0 (0.5)	3.2 (1.1)	$p < 0.05$
May	7.8 (0.5)	5.4 (1.5)	$p < 0.05$	7.5 (1.5)	5.9 (0.8)	$p < 0.05$
June	9.8 (1.6)	7.4 (1.7)	$p < 0.05$	11.7 (1.3)	9.0 (1.0)	$p < 0.05$
July	11.8 (1.5)	10.7 (1.5)	$p < 0.05$	13.2 (0.8)	12.4 (1.8)	$p < 0.05$
August	-	13.5 (0.9)	-	-	14.0 (0.9)	-
September	-	11.7 (0.8)	-	-	12.2 (0.4)	-

### 3.2.2 Salinities of surrounding water masses

For both years, the levels of salinities in the water masses used by the anadromous brown trout differed largely between the habitats (Figure 7). Overall, the fjord migrating fish in 2015 (F15) registered higher salinities for all months compared to the estuarine residents (E15) the same year (Wilcoxon rank sum test,  $p$ -value  $< 0.05$ ,  $n=13$ ; table 2). Although mean salinities differed between habitats, both groups were exposed to a range of salinities from almost complete freshwater to sea water (2-31 ‰). The patterns observed in the fjord migrants and estuarine residents in 2017 were similar to the 2015 groups. The fjord migrating fish in 2017 (F17) also registered consistently higher salinities for all months ( $p$ -value  $< 0.05$ ,  $n=38$ ) compared to the estuarine residents (E17). Similar to the 2015 groups, both the fjord migrants and estuarine residents in 2017 experienced salinities ranging from almost complete freshwater to seawater (F17; 5-34 ‰, E17; 1-34 ‰). Although experienced salinities differed for all months, the difference was especially prominent in June for both years. In this period the estuarine residents experienced almost complete freshwater for approximately a month.



**Figure 7:** Experienced salinities for two groups of anadromous brown trout acoustically tagged and tracked in **(A)** 2015, and **(B)** 2017. For both years, some fish migrated to the fjord (2015;  $n=6$ , 2017;  $n=11$ ) and some remained resident in Flostrømmen estuary (2015;  $n=7$ , 2017;  $n=29$ ). Registered salinities for fjord fish were recorded by listening stations in the fjord (48 stations), while the corresponding registrations for estuarine fish were recorded by two listening stations (63 and 65). Each mark represents the daily average calculated from individual fish (+ = estuarine residents, • = fjord migrants).

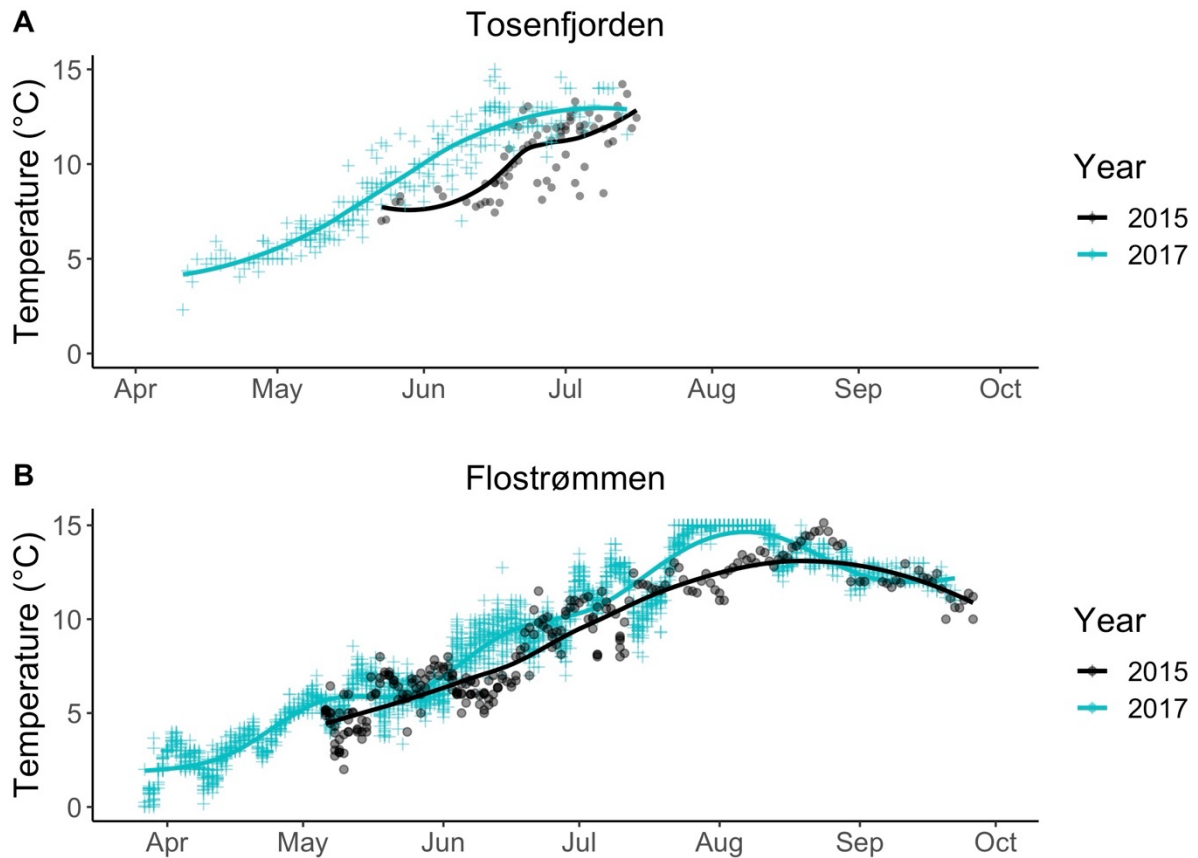
**Table 2:** Monthly mean salinities (‰) for two groups (2015 and 2017) of anadromous brown trout with standard deviation (SD) in parentheses. For both years some fish migrated to the fjord (2015;  $n=6$ , 2017;  $n=11$ ) and some remained resident in Flostrømmen estuary (2015;  $n=7$ , 2017;  $n=29$ ). Registered salinities for fjord fish were recorded by listening stations in the fjord (48 stations), while the corresponding registrations for the estuarine fish were recorded by two listening stations (63 and 65).

Month	2015			2017		
	Fjord (‰)	Estuary (‰)	p-value	Fjord (‰)	Estuary (‰)	p-value
April	-	-	-	33 (1.5)	18 (7.7)	$p < 0.05$
May	15 (2.4)	5 (1.5)	$p < 0.05$	31 (4.3)	13 (9.7)	$p < 0.05$
June	18 (3.9)	7 (1.7)	$p < 0.05$	25 (7.2)	2 (1.1)	$p < 0.05$
July	18 (4.5)	11 (1.5)	$p < 0.05$	20 (5.9)	6 (5.5)	$p < 0.05$
August	-	14 (0.9)	-	-	14 (6.5)	-
September	-	12 (0.8)	-	-	22 (7.5)	-

### 3.3 Between-year comparisons of temperature and salinity use

#### 3.3.1 Temperatures of surrounding water masses

For both the fjord and estuarine habitat, the two groups tagged in 2017 experienced higher temperatures compared to the fish tagged in 2015 (Figure 8). When comparing the corresponding time periods when both groups were feeding in the fjord it was found that the fjord migrants in 2017 experienced higher temperatures in May, June and July (Wilcoxon rank sum test;  $p$ -value  $< 0.05$ ,  $n = 17$ ) compared to the 2015 fjord migrants (Table 3). Both groups experienced a relatively large range of temperatures (F15; 5-15 °C, F17; 1-15 °C) for the entire period. Higher experienced temperatures for the estuarine fish in 2017 compared to 2015 were prominent for all months except September ( $p$ -value  $< 0.05$ ,  $n = 36$ ). The two groups experienced a similar temperature range for the entire period (E15; 2-15 °C, E17; 0-15 °C). Different timing of seaward migration between the groups was reflected by the experienced temperatures at sea entry. Fjord migrators in 2015 experienced a mean of approximately 7 °C when moving to sea, compared to the fjord migrators in 2017 who experienced a mean of approximately 4 °C.



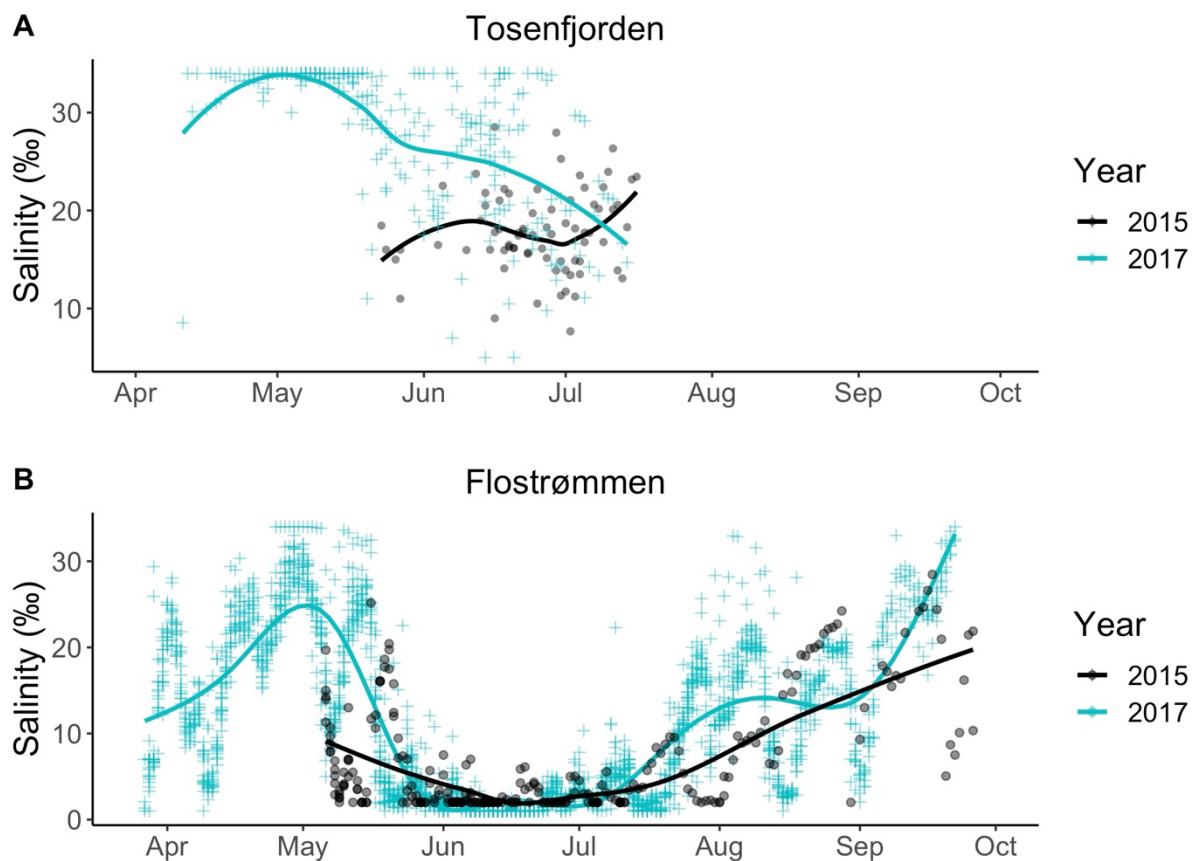
**Figure 8:** Individual daily averaged temperature (°C) recordings of (A) fjord migrating fish when registered on fjord receivers and (B) estuary resident brown trout when recorded on receiver 63 and 65 in Flostrømmen estuary. The fish were tagged in 2015 (•) and 2017 (+) and tracked the same year.

**Table 3:** Monthly mean temperatures (°C) for two groups (estuarine residents and fjord migrating) of anadromous trout with standard deviation (SD) in parentheses. For both years some fish migrated to the fjord (2015;  $n=6$ , 2017;  $n=11$ ) and some remained resident in the estuary (2015;  $n=7$ , 2017;  $n=29$ ). Registered temperatures for fjord fish were recorded by listening stations in the fjord (48 stations), while the corresponding registrations for the estuarine fish were recorded by two listening stations (63 and 65). The number marked with \* had a lower overall mean for the whole month, but a higher mean when comparing only the time period when both groups were registered in their respective habitats.

Month	Fjord			Estuary		
	2015 (°C)	2017 (°C)	p-value	2015 (°C)	2017 (°C)	p-value
April	-	5.0 (0.5)	-	-	3.2 (1.1)	-
May	7.8 (0.5)	7.5* (1.5)	$p < 0.05$	5.4 (1.5)	5.9 (0.8)	$p < 0.05$
June	9.8 (1.6)	11.7 (1.3)	$p < 0.05$	7.4 (1.7)	9.0 (1.0)	$p < 0.05$
July	11.8 (1.5)	13.2 (0.8)	$p < 0.05$	10.7 (1.5)	12.4 (1.8)	$p < 0.05$
August	-	-	-	13.5 (0.9)	14.0 (0.9)	$p < 0.05$
September	-	-	-	11.7 (0.8)	12.2 (0.4)	$p > 0.05$

### 3.3.2 Experienced levels of salinity

Registered salinities for the fjord migrating fish differed between 2015 and 2017 (Figure 9A), with higher salinities for the 2017 group in May and June, but not in July (Wilcoxon rank sum test;  $p < 0.05$ ,  $n=17$ ; Table 4). Salinity levels were more stable for the fjord migrating trout in 2015, while for the 2017 trout the salinity levels started out high and gradually decreased throughout the summer. The pattern was different for the estuarine residents (Figure 9B), who mostly experienced brackish to freshwater for both years. Mean registered salinities differed between the years for May, June and July ( $p$ -value  $< 0.05$ ,  $n = 36$ ), but not for August and September. Both estuarine resident groups followed a similar pattern and experienced almost complete freshwater in June.



**Figure 9:** Individual daily averaged salinity (‰) recordings of (A) fjord migrating and (B) estuary resident brown trout when recorded on (A) fjord receivers and (B) receiver 63 and 65 in Flostrømmen estuary. The fish were tagged in 2015 (•) and 2017 (+) and tracked the same year.



**Table 4:** Monthly mean salinities (‰) for two groups (estuarine residents and fjord migrating) of anadromous trout with standard deviation (SD) in parentheses. For both years some fish migrated to the fjord (2015;  $n=6$ , 2017;  $n=11$ ) and some remained resident in the estuary (2015;  $n=7$ , 2017;  $n=29$ ). Registered salinities for fjord fish were recorded by listening stations in the fjord (48 stations), while the corresponding registrations for the estuarine fish were recorded by two listening stations (63 and 65).

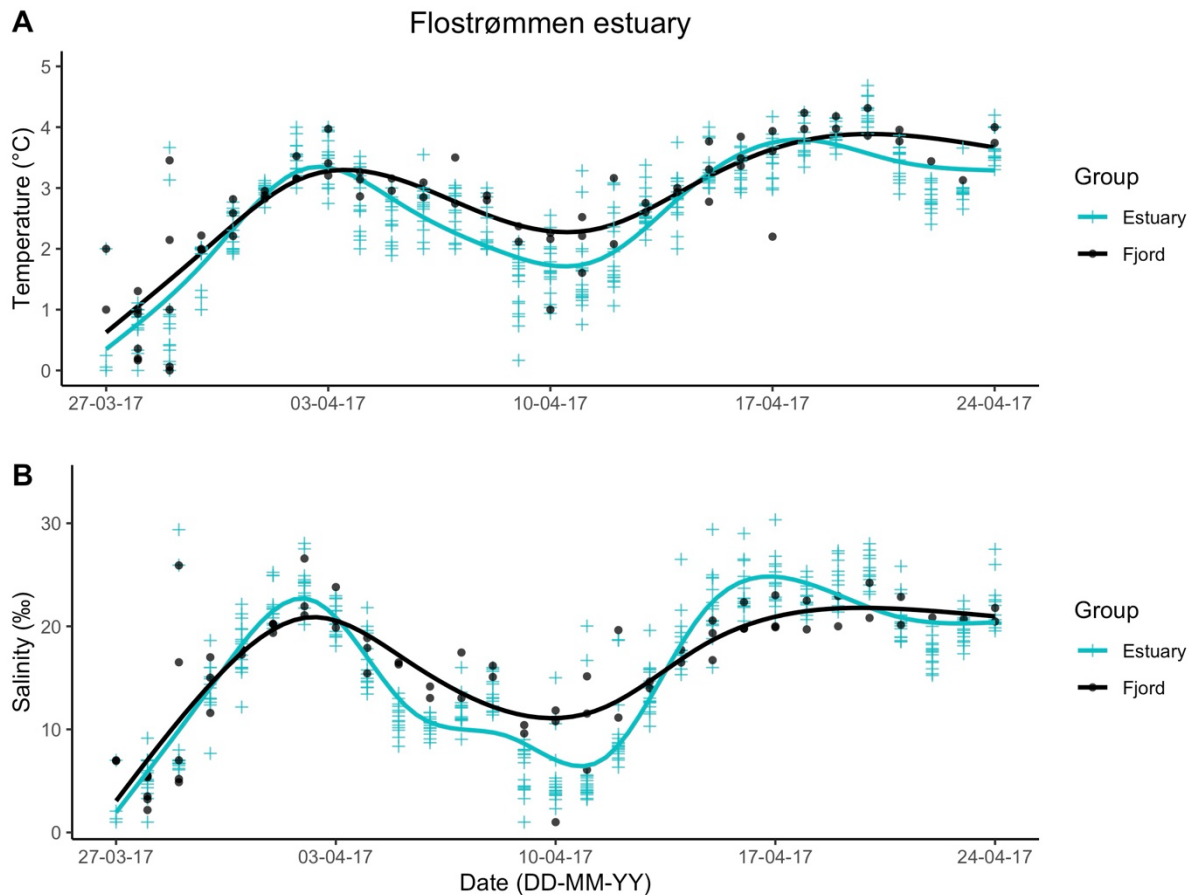
Month	Fjord			Estuary		
	2015 (‰)	2017 (‰)	p-value	2015 (‰)	2017 (‰)	p-value
April	-	33 (1.5)	-	-	18 (7.7)	-
May	15 (2.4)	31 (4.3)	$p < 0.05$	7 (5.6)	13 (9.7)	$p < 0.05$
June	18 (3.9)	25 (7.2)	$p < 0.05$	3 (1.1)	2 (1.1)	$p < 0.05$
July	18 (4.5)	20 (5.9)	$p > 0.05$	4 (2.4)	6 (5.5)	$p < 0.05$
August	-	-	-	13 (6.8)	14 (6.5)	$p > 0.05$
September	-	-	-	19 (6.6)	22 (7.5)	$p > 0.05$

### 3.4 Temperature and salinity use of fjord migrating and estuarine resident trout under their concurrent stay in an estuary

All fish were caught and tagged in Flostrømmen estuary. Before the fjord migrating fish left the estuary in 2017, both fish groups resided in the this habitat for approximately a month (20 March - 24 April). During their concurrent stay in the estuary, both groups experienced a narrow range of temperatures, never exceeding 5 °C (F17; 0 – 4.3 °C, E17; 0 – 4.7 °C; Figure 3A). Until the 3 April both groups utilized water layers with similar water temperatures, but from this date and until the fjord migrating fish left the two groups mainly used water layers with different temperatures (Figure 10). The largest difference was from 3 April to 14 April where the fjord migrating group (mean temperature 2.6 °C, SD  $\pm$  0.6 ) was found to experience a mean of 0.4 °C higher temperatures (Wilcoxon rank sum test,  $p$ -value  $<$  0.05,  $n=40$ ) than the estuary group (mean temperature 2.2 °C, SD  $\pm$  0.7). The fjord migrators also experienced 0.5 °C higher mean temperatures from 20-24 April compared to the estuary residents (F17; 3.6 °C, SD  $\pm$  0.4, E17; 3.1 °C, SD  $\pm$  0.3,  $p$ -value  $<$  0.05).

Mean level of salinity during the entire period of the concurrent stay in the estuary was 16 ‰ for both groups and ranged from complete freshwater to brackish water (F17; 1-26 ‰, E17; 1-30 ‰; Figure 3B). Following a similar but more distinct pattern as temperature, experienced salinities were higher for the fjord migrants from the 3 April until approximately 14 April. During this period, mean salinity for the fjord migrating group (mean 14 ‰, SD  $\pm$  4.2) was 4 ‰ higher than for the estuary residing group (mean 10 ‰, SD  $\pm$  4.5;  $p$ -value  $<$  0.05). From

14 – 21 April, the estuary residents experienced 3 ‰ higher levels of salinity compared to the fjord migrating group ( $p$ -value < 0.05). However, no corresponding divergence between the groups was observed for temperature for the same time period. No differences in salinities were found for the rest of the concurrent stay in the estuary.



**Figure 10:** Mean experienced (A) temperature (°C) and (B) salinity (‰) of two groups of anadromous brown trout with different migration strategies (+ = estuarine residents, • = fjord migrants) under their concurrent stay in Flostrømmen estuary. Each mark represents the daily average calculated from individual fish.

### 3.5 Influence of individual biologic characteristics on the use of water masses with different levels of salinity and temperature

For the fjord migrating and estuary resident fish tagged in 2017, possible relationships between use of water masses with different levels of temperature and salinity and individual biological characteristics was tested. Total length ( $L_T$ ) was initially thought to have an impact on

temperature and salinity use of the fish groups.  $L_T$  was therefore included in all the initial models, but model selection suggested low importance of this variable and it was therefore not included in any of the models.

### 3.5.1 Influence of biologic characteristics on temperature use for fjord migrating fish

The model selection showed that two models were satisfactory ( $\Delta AIC < 2$ ) for explaining temperature use of fjord migrating fish in 2017 (Table 5). Two explanatory variables from the initial model were included by the model selection, with condition factor included in both models and thus regarded as the most important factor.

**Table 5:** The two best models ( $\Delta AIC < 2$ ) explaining temperature use of fjord migrating brown trout based on the explanatory variables condition factor (CF) and previous number of sea migrations (SM).

(Int)	CF	SM	df	AIC	$\Delta AIC$
25.08	-20.48	-0.57	5	498586	0.00
23.25	-20.22		4	498586	0.09

The conditional model average of the two best models showed a strong negative relationship between condition factor and experienced temperature ( $p$ -value  $< 0.05$ ; Table 6), indicating that fish with higher condition factor generally resided in colder waters compared to fish with lower condition factor. However, the standard error was relatively high indicating that the results not necessarily are representative for the population. The model also indicated a negative relationship between number of previous seaward migrations and temperature; however, this relationship was not significant.

**Table 6:** Conditional model average estimating the effect of the explanatory variables condition factor (CF) and previous number of sea migrations (SM) on temperature use of fjord migrating anadromous brown trout. \* =  $p$ -value  $< 0.05$ , \*\* =  $p$ -value below 0.01.

	Estimate	Std. error	Z value	Pr( $> z $ )
(Int)	24.19	7.58	3.19	0.00 **
CF	-20.36	8.70	1.96	0.05 *
SM	-0.57	0.96	0.49	0.62

### 3.5.2 Influence of biologic characteristics on salinity use of fjord migrating fish

Two of the models were equally good ( $\Delta AIC < 2$ ) for explaining salinity use of fjord migrating fish. The most important factors for explaining salinity use of fjord migrators were condition factor and previous number of seaward migrations (Table 7).

**Table 7:** The two best models ( $\Delta AIC < 2$ ) explaining salinity use of fjord migrating brown trout based on the explanatory variables condition factor (CF) and previous seaward migrations (SM).

(Int)	CF	SM	df	AIC	$\Delta AIC$
9.72	12.10	1.21	5	787462	0.00
13.56	11.53		4	787464	1.78

As opposed to temperature, the conditional model averaging showed a positive relationship between experienced salinities and condition factor for fjord migrating fish in 2017 (Table 8), indicating that fish with higher condition factor resided in more saline waters. The conditional model averaging also suggested that fish with a higher number of previous seaward migrations resided in water masses with higher salinities. However, none of the estimates were significant ( $p$ -value  $> 0.05$ ) and standard errors were high.

**Table 8:** Conditional model average estimating the effect of the explanatory variables condition factor (CF) and previous number of sea migrations (SM) on salinity use of fjord migrating anadromous brown trout

	Estimate	Std. error	Z value	Pr(> z )
(Int)	10.84	18.97	0.57	0.57
CF	11.93	21.49	0.46	0.64
SM	1.21	2.37	0.42	0.67

### 3.5.3 Influence of biologic characteristics on temperature use for estuarine residents

The three best variables explaining temperature use of estuarine resident fish were condition factor (CF), number of previous seaward migrations (SM) and sex (S). Two models were considered as equally good ( $\Delta AIC < 2$ , Table 9). SM was included in both suggested models, indicating that this variable was of special importance when explaining temperature use.

**Table 9:** The two best models ( $\Delta AIC < 2$ ) explaining temperature use of estuarine resident anadromous brown trout based on the explanatory variables condition factor (CF), number of previous seaward migrations (SM) and sex (S).

(Int)	CF	SM	S	df	AIC	$\Delta AIC$
11.43	0.16	-1.15	0.86	6	2988859	0.00
9.70	2.31	-1.05		5	2988860	0.64

A conditional model average was conducted on the two equally good models (Table 10). A positive estimate of condition factor indicated that fish with higher condition factors reside in warmer waters in the estuary. The standard error was large, however, indicating that the estimate may not be representative for the population. Number of previous seaward migrations had a negative effect on temperature, and the estimate indicated that estuarine resident fish with a higher number of previous seaward migrations in general utilize water masses with lower temperatures. Male fish seemed to have experienced higher temperatures than the females in the estuary, however this variable was not significant ( $p$ -value > 0.05).

**Table 10:** Conditional model average estimating the effect of the explanatory variables condition factor (CF), previous number of sea migrations (SM) and sex (S) on temperature use of estuarine anadromous brown trout. \* =  $p$ -value < 0.05, \*\* =  $p$ -value below 0.01.

	Estimate	Std. error	Z value	Pr(> z )
(Int)	10.70	4.48	2.39	0.02 *
CF	1.06	4.54	0.22	0.83
SM	-1.11	0.39	2.68	0.01 **
S	0.86	1.12	0.72	0.47

#### 3.5.4 Influence of biologic characteristics on salinity use for estuarine residents

Condition factor (CF), previous seaward migrations (SM) and sex (S) were regarded as the most important variables explaining salinity use for the estuarine resident fish in 2017. Three models were regarded as equally good ( $\Delta$ AIC < 2), and condition factor was included in all three models which indicated special importance of this variable in explaining the salinity use of estuarine fish (Table 11).

**Table 11:** The three best models ( $\Delta$ AIC < 2) explaining salinity use of estuary resident anadromous brown trout based on the explanatory variables condition factor (CF), previous seaward migrations (SM) and sex (S).

(Int)	CF	SM	S	df	AIC	$\Delta$ AIC
6.69	10.17	-1.06	-0.56	6	3918078	0.00
7.80	8.78	-1.12		5	3918079	1.07
-0.48	15.09			5	3918080	1.64

Conditional model averaging showed a positive relationship between the condition factor and salinity experienced by the estuarine residents (Table 12). The model averaging also indicated that estuarine resident fish with a higher number of previous seaward migrations in general

utilized water masses with lower salinities, and that males experienced lower salinities than females. However, none of the estimates were significant ( $p$ -value  $> 0.05$ ).

**Table 12:** Conditional model average estimating the effect of the explanatory variables condition factor (CF), previous number of sea migrations (SM) and sex (S) on salinity use of estuarine anadromous brown trout.

	Estimate	Std. error	Z value	Pr(> z )
(Int)	5.45	7.57	0.72	0.47
CF	10.84	7.51	1.36	0.17
SM	-1.08	0.61	1.65	0.10
S	-0.86	1.83	0.44	0.66

## 4 Discussion

The fish in River Åbjøra in Tosenfjorden experienced a broad range of both temperatures and salinities during their seaward migration, either as fjord migrants or as estuarine residents. A distinct difference in temperatures and salinities was observed between the fjord habitat and Flostrømmen estuary indicating that the fjord migrants and estuarine residents experienced significantly different environments. Experienced temperatures and salinities were observed to differ between the fjord migrants and estuarine residents under their concurrent stay in Flostrømmen, implying a difference in preferred or tolerated temperatures/salinities.

The large amount of estuarine resident fish observed in this study support the view of a continuum of migration strategies as suggested by previous studies (e.g. Cucherousset *et al.*, 2005; Davidsen *et al.*, 2014a; del Villar-Guerra *et al.*, 2014)., as there is no doubt that these fish migrated from the river although they never entered the fjord. Assuming that prey availability was sufficient in the estuarine habitat, staying resident during the feeding migration in this area may have given the advantage of better foraging opportunities compared to the river without the risks of being exposed to marine predators and parasites at sea (Thorpe, 1994; Thorstad *et al.*, 2016). Another possible explanation for the estuarine fish staying resident may be that they had a lower tolerance for higher salinities, or a preference for lower salinities compared to the fjord migrants. Under the concurrent stay of the two groups in Flostrømmen in 2017, the fjord migrating group experienced a 0.4 °C higher mean temperature and 3 ‰ higher level of salinity compared to the estuarine residing group for a period of approximately two weeks. Considering the stratified waters of Flostrømmen estuary, higher experienced temperatures and salinities indicate that the fjord migrating fish moved deeper into the water column where the water was saltier and also warmer. As growth is tightly linked to temperature in ectothermic fish (Elliott, 1975b; a), residing in the warmest accessible water layers is likely to be advantageous up to a certain temperature. Although the experienced temperatures rarely exceeded the lower temperature for growth of the species at 4 °C, at such low temperatures a difference of only 0.4 °C might have made a significant biological difference for the fish. One possibility is therefore that the fjord migrating fish had a better tolerance for higher salinities, and therefore had the opportunity of moving down into warmer waters which may have increased activity patterns such as feeding (Jonsson & Jonsson, 2009). The estuarine residents were later observed to reside in waters with salinities ranging from freshwater to almost complete seawater throughout

the season, which indicates that they may also have tolerated higher salinities. However, as most of their residency was spent in fresh- or brackish water it is possible that these fish had a preference for lower salinities. The fjord migrants were found to have a lower condition factor compared to the estuarine residents in 2017. Thus, another possible explanation for the higher experienced temperatures and salinities for the fjord fish under their stay in Flostrømmen may therefore be that these fish were more energy depleted than the estuarine residents and therefore had a higher motivation to forage on nutrient rich marine prey in the lower water layers of the estuary. Other studies have illustrated that a reduced condition factor is an important motivator for seaward migration (Davidsen *et al.*, 2014b; Bordeleau *et al.*, 2018; Eldøy *et al.*, 2021). Hence, the lower condition factor for the fjord migrators may also explain why these fish adopted a marine migration strategy.

Brown trout in freshwater have been found to prefer temperatures closely related to their optimal temperature for growth at approximately 16 °C (Larsson, 2005), and thus the expectations for this study was that the brown trout would gravitate towards water masses as close to this temperature as possible. In the present study, mean temperatures experienced by the brown trout in both the fjord and estuary rarely approached the upper temperature limit for the tags at 15 °C. Considering the northern latitude of the study area (65 °N), water temperatures close to the optimal temperature for growth may not have been available to the fish. It is therefore possible that the fish resided in the warmest water masses accessible in the given habitat. Experienced temperatures were higher for the fjord migrating fish in both 2015 and 2017 compared to the estuarine residents. A possible explanation for the temperature differences is that the estuary was highly affected by cold freshwater runoff from the River Åbjøra in the spring and early summer months. The same pattern was observed by Rikardsen *et al.* (2007b) in the Alta fjord in northern Norway, where the water masses surrounding the River Alta outlet were colder than the rest of the fjord until the middle of June due to cold freshwater runoff from the river. In River Åbjøra, the temperatures of the river water surpassed the fjord temperatures mid-August in 2015, coinciding with the highest observed temperatures experienced by the trout in the estuary for this year. In August, the estuary residing fish were observed to experience gradually increasing salinities, which might be an indicator of the fish moving to deeper water layers as a thermal refuge as the surface freshwater layers approached 15 °C. Kristensen *et al.* (2018) found that fjord migrating brown trout actively moved deeper into the water layers when surface temperatures reached 17 °C. The same pattern was observed by Eldøy *et al.* (2017) in a fjord system in central Norway, where fish tended to move down in



the water column with increasing surface temperatures throughout the season. Although no thermal data from data loggers was obtained from the river and fjord in 2017, there is reason to believe that the similar patterns in experienced temperatures and salinities for the estuarine residents might be caused by the same mechanisms as in 2015.

Migration patterns of the fjord fish may have been partly motivated by temperatures. This was observed in the Alta fjord in northern Norway where fjord migrating brown trout resided in the warmer areas of the fjord during their summer feeding migration (Rikardsen *et al.*, 2007b; Jensen *et al.*, 2014). In both studies the authors suggested that anadromous brown trout might regulate their ambient temperatures actively by seeking water masses with preferred conditions. The fjord migrating brown trout in Tosenfjorden entered the marine habitat when sea temperatures reached approximately 4 °C in 2017, which is known to be the lower limit for growth for the species (Elliott, 1994). Marine migrations are ultimately thought to be motivated by increased overall fitness (Thorstad *et al.*, 2016), and to be able to start growing as soon as the fish enters the marine phase is likely of high importance which may explain the timing of fjord entrance. This was also proposed by Jonsson and Jonsson (2002), who observed that both smolt and post-spawners started moving downstream towards marine habitats when sea temperatures approached 4 °C. Waiting for sufficient growth conditions in the fjord may also explain why the fish stayed resident in Flostrømmen estuary for a prolonged period before they entered the marine phase. It is possible that the anadromous brown trout prefers colder and fresher waters if the marine habitat only offers temperatures outside the of growth range.

As salinity tolerance in brown trout have been shown to decrease at lower water temperatures (Finstad *et al.*, 1988; Larsen *et al.*, 2008), interactions between the two factors do occur. The experiments done by Larsson (2005) stated optimal temperature for growth in freshwater. How temperatures and salinities may affect growth in fish is complex and no comprehensive studies have been done on brown trout and their optimal temperature for growth in the marine environment. Handeland *et al.* (2003) found that optimal temperature for growth in saltwater for Atlantic salmon was approximately 13 °C, which is lower compared to registered optimal temperatures for growth for parr in freshwater at 16-20 °C (Jonsson & Jonsson, 2009). It is therefore possible that optimal temperature for growth of adult brown trout may also be lower in saltwater compared to juveniles in freshwater. The fjord migrating fish in 2017 registered a mean temperature of 12.5 °C for June and July which is similar to the findings of Rikardsen *et al.* (2007b). They found that fjord migrating brown trout in the Alta fjord experienced a mean

of 12.1 °C in the marine phase for the same time period. Jensen *et al.* (2014) found that fjord migrating brown trout started moving towards the outer parts of the fjord as temperatures reached 14 °C in the inner fjord, 2 °C below the optimal temperature for growth. Size has also been linked to optimal temperature for growth in salmonids, with a lower growth optimum in larger fish (Jonsson & Jonsson, 2009). Considering that the fish in this study were veterans, the combination of a potential lower growth optimum in the marine environment and large sized fish may partly explain why the registered temperatures rarely approached 16 °C.

Seaward migration in brown trout is largely motivated by the increased feeding opportunities in the marine environment (Gross *et al.*, 1988) and thus also a larger potential for growth. It is possible that experienced temperatures and salinities in the present study were highly influenced by the availability and location of prey in different water layers and/or areas within the fjord system. Brown trout are opportunistic feeders, and what they eat in the marine environment is affected by season, habitat and individual fish size (Knutzen *et al.*, 2001). In a study done on fjord migrating brown trout in the Altafjord in northern Norway prey availability was thought to be the most important factor for marine growth, while no correlation between the annual growth rate or survival and sea water temperatures was found (Jensen *et al.*, 2018). Similarly, Pemberton (1976) found that food availability was the most important factor influencing the presence or absence of anadromous brown trout in a specific area. Although studies indicate an optimal temperature for growth at 16 °C (Forseth & Jonsson, 1994; Larsson, 2005), Elliott and Hurley (2000) found an increase in optimal growth temperature with increasing energy intake. Changing to a more energy rich piscivorous diet in the marine environment may therefore increase the optimal temperature for growth. The fact that the growth optimum can change with energy intake implies complex interactions between optimal growth conditions and external factors. Temperature use of the anadromous brown trout may also reflect the preferred temperatures of the prey, and thus temperature may have an indirect effect on habitat use.

The fjord migrating fish in 2017 experienced high salinities at first sea entry, followed by a decrease in salinities in June and July. It is possible that the salinity levels decreased in the marine environment throughout the season as freshwater runoff from the rivers increased. However, this would mostly have affected the surface layers and the fish probably had the opportunity to seek towards higher levels of salinity in the deeper water layers for the entire feeding season. One possible explanation is that these fish initially fed on pelagic prey in more

saline waters, followed by a habitat shift towards more brackish areas as the prey availability changed. A study conducted in the Ranafjord (66 °N) in northern Norway found highest feeding rates of fjord migrating fish in spring and early summer, coinciding with high abundances of fish larvae and especially herring (Rikardsen *et al.*, 2006). This may support the idea that the fjord migrating fish in 2017 initially fed on pelagic fish, followed by a niche shift towards more brackish areas as prey availability changed. The fjord migrators in 2015 experienced brackish waters for their entire marine residency. The time period for the lower salinities coincides with the decreasing salinities for the fjord migrants in 2017, which may reinforce the argument of a niche shift during the summer months due to changing prey availability. Larger fish have been shown to feed on a more piscivorous diet (Garman & Nielsen, 1982; Knutsen *et al.*, 2001; Rikardsen *et al.*, 2007a), however the fjord fish in 2017 were not found to be larger than fish in 2015. A number of studies argue that the energy status of the fish when entering the marine phase may influence dietary choice (Eldøy *et al.*, 2015; Bordeleau *et al.*, 2018; Eldøy *et al.*, 2021), but no differences in condition factor were found between the fjord migrants in 2015 and 2017. Of all the migrating fish in 2017, 91 % were female (33% in 2015). Females have been found to migrate more often than males (Jonsson, 1985), and as female fecundity increases with size they might take higher risks when it comes to migrating into more marine habitats to feed (Jonsson & Jonsson, 1993). It is therefore possible that these fish migrated into more pelagic areas and consequently were exposed to higher salinities.

Considering the stratified water column of Flostrømmen estuary with freshwater in the upper layers and gradually more saline waters towards the bottom, the brown trout in the estuary had the possibility of residing in the layers with the most optimal conditions in relation to temperature and salinity. Experienced salinities in Flostrømmen estuary were similar for the two years. In both years, estuarine resident fish experienced salinities close to freshwater in June. Water flow in the river was high in this period for both 2015 and 2017, which might explain the low salinities experienced during this period. Another possible explanation is the feeding patterns of the fish in the estuary. Surface oriented insects were found to be an important food source for post-smolt brown trout in the marine environment in the summer (Pemberton, 1976), and it is possible that this also is the case for the estuarine residents in Flostrømmen. Surface insects might be abundant in the surface layers in June, and thus explaining the surface-oriented behavior for this period. High water flow in the river may also have caused increased turbidity in the estuary, and as salmonids are visual feeders (e.g. Henderson & Northcote, 1985;

Fraser & Metcalfe, 1997) they might have remained in the upper layers to be able to locate the prey (Langeland *et al.*, 1991).

Several studies have shown that different species of teleost fishes grow better at intermediate salinities (Bœuf & Payan, 2001). This effect has been shown on salmonid species such as Atlantic salmon (Ytrestøyl *et al.*, 2020) and rainbow trout, *Oncorhynchus mykiss* (McKay & Gjerde, 1985). The fjord migrating fish in 2015 stayed mainly in brackish waters (mean=18‰) whilst at sea. As the fish had the possibility of migrating further out or deeper down in the water masses to access higher salinities, it is possible that the fjord migrants in 2015 minimized stress related to osmoregulation by staying in brackish waters for most of their marine residency. McKay and Gjerde (1985) found that high salinities influence the growth of rainbow trout negatively, especially after exceeding 20 ‰. Their study, however, looked at fish in the weight range 51-153 g which are significantly smaller than the fish in this study (400-3000 g). Salinity tolerance is known to increase with fish size in salmonids (Parry, 1960), and thus the fish in the present study probably had a higher salinity tolerance compared to the fish studied by McKay and Gjerde. Nevertheless, staying in less saline waters may decrease energy expenditure related to osmoregulation and therefore increase the potential for growth.

The fjord migrating fish in 2017 was shown to experience salinities up to 34 ‰ almost immediately after marine entry in April, followed by a decrease in salinities in June and July. No acclimatization period in the fjord was observed by these fish, which contrasts another study by Kristensen *et al.* (2019). They tracked eight post-spawned anadromous brown trout for their marine migrations and found that after migrating to sea, the fish spent the first fifteen days in brackish waters. This indicates some form of acclimatization period to the higher salinities in the marine environment. One possible explanation for the seemingly lacking acclimatization period in Tosenfjorden in 2017 may be that the fjord migrating trout already had acclimatized to higher salinities during their stay in the stratified waters of Flostrømmen estuary. Another explanation may be that veteran trout have a high salinity tolerance due to size (Aarestrup *et al.*, 2015). As previously mentioned, larger fish size have been found to affect salinity tolerance positively (e.g. Parry, 1960). Ugedal *et al.* (1998) found size to explain approximately half of the individual variance in salinity tolerance in hatchery-reared migrating brown trout. As the fish in the present study were veteran fish, they might have had a sufficient salinity tolerance for exposure to full strength seawater at first sea entry. The timing of marine entry in 2017 coincided with low temperatures (~ 4 °C) in the fjord, indicating a good tolerance to the

combination of high salinities and low temperatures. Studies have suggested that this combination may be challenging for salmonids due to poor ion regulation in cold water (Finstad *et al.*, 1988; Larsen *et al.*, 2008). However, Larsen *et al.* (2008) found differences in gene expression related to osmoregulatory capacity between two Danish populations of fjord migrating brown trout, which they viewed as strong evidence of adaptation to the local marine environment. It is possible that the fish in the current study also were locally adapted to high salinities in combination with low water temperatures. Considering the differences observed between the estuarine residents and fjord migrating fish under their concurrent stay in Flostrømmen 2017, it might be suggested that differences in salinity tolerance may also exist within populations. This should, however, be studied further.

Studies have indicated that optimal temperature for growth decrease with increasing body size (reviewed in Jonsson & Jonsson, 2009). An effect of total length on experienced temperatures of the fjord migrators and estuarine residents in 2017 was therefore expected, but as this variable did not get included in any of the predictive models no such effect was observed. This was also the case for registered salinities for the two groups. Although previous studies have found a higher salinity tolerance in larger fish (Parry, 1960; Ugedal *et al.*, 1998), no significant relationships were found between total length and salinity use for neither fjord migrating fish nor estuarine residents. Previous studies have correlated size to migration strategy in salmonids, with larger fish shifting their diet to consist of more pelagic fish of increasing prey size (e.g. Garman & Nielsen, 1982; Knutsen *et al.*, 2001; Davidsen *et al.*, 2017). Swimming is also more energetically efficient for larger fish (Nøttestad *et al.*, 1999). Thus, it would be expected that larger fish would experience higher salinities and a corresponding change in temperatures due to them migrating into more pelagic areas. The conditional model averaging for the fjord migrants in 2017 indicated a negative relationship between previous seaward migrations and experienced temperatures. Number of previous seaward migrations are likely to have a positive effect on body size, and therefore size may indirectly be important for the choice of habitat. Thus, a higher number of previous seaward migrations correspond to a larger size and therefore may also a lower optimal temperature for growth. This relationship was, however, not significant. The model averaging for estuarine resident fish in 2017 indicated that fish with a higher number of previous seaward migrations utilized water masses with lower temperatures and lower salinities. However, as a higher number of previous seaward migrations would be expected to impact size positively, these results indicate that larger fish reside in lower salinities

which contradicts the assumptions made above. Number of previous seaward migrations for fjord migrating fish was positively correlated to salinities, but these results were not significant.

The model selection for the fjord migrating fish in 2017 indicated that fish with higher condition factor resided in colder waters. Condition factor had an opposite effect on temperature use for the estuarine residents in 2017, indicating that fish with higher condition factor utilized warmer waters of the estuary. However, as the standard error for the both estimates were relatively high (and  $p$ -value  $> 0.05$ ) these results are likely not representative for the population. Additionally, condition factor had a positive (though non-significant) effect on experienced salinities for the fjord migrants in 2017. These results are contradicting to the predicted impacts on temperature for fjord migrants because for this particular study area, the more saline marine waters were shown to be warmer than the less saline waters. Conditional model averaging indicated that fish with higher condition factor in Flostrømmen estuary resided in saltier waters, but the standard error was high which indicate low accuracy of this estimate. Sex was not an important explanatory variable for experienced temperatures or salinities in any of the models for the estuarine resident fish. One possible explanation to why the models generally had few significant estimates and high standard errors may be the relatively low sample size. Doing a similar study with larger sample size may give a more accurate description of potential effects of biological parameters on temperature and salinity use.

## 5 Conclusion

Large differences in registered temperatures and salinities were found between the fjord habitat and the estuarine habitat, implying significantly different conditions for growth between the groups under their feeding migrations. Higher salinities in the fjord may have been more energy demanding due to osmoregulation, but this was probably compensated for by higher fjord temperatures compared to the estuary and a probability of greater abundance of energy rich prey compared to the estuarine habitat. Additionally, large parts of the fjord residency were spent in brackish waters, which are likely to be more energy efficient to dwell in compared to full-strength sea water. Of especial interest is the possibly higher seawater tolerance or preference observed in fjord migrating fish compared to the estuarine residents, which may partially explain why some fish migrated to the fjord and others remained resident in Flostrømmen. Alternatively, this may be explained by a lower condition factor for the fjord fish and therefore a higher motivation to migrate into the fjord to feed. Total body length, condition factor, sex and number of previous seaward migrations did not seem to be important predictors for the temperature and salinity use of the fish; however, more studies should be conducted on the matter as the sample size in this study might not have been sufficient. With potential increasing water temperatures and higher precipitation rates in the future as predicted by IPCC, the habitats in Tosenfjorden may be altered which may affect the anadromous brown trout in this area. It is possible that increasing surface temperatures will make the growth conditions in the fjord and estuarine area more favorable as the current temperatures are well below the optimal temperature for growth. However, as optimal temperature for growth in marine habitats may be lower than the reported growth optimum for the species in freshwater, the effects of increased fjord temperatures are hard to predict. Optimal conditions for growth are likely affected by the combinations of temperature and salinity, prey composition and size of the fish, indicating complex interactions between a range of factors that should be considered when addressing this issue. Based on the implications that the estuarine residents moved to deeper and saltier water layers when temperatures approached 15 °C, it is possible that increasing temperatures in this habitat may ultimately lead to a higher number of estuarine fish migrating using the fjord as a thermal refuge.

## Literature

- Anderson, D. R., Link, W. A., Johnson, D. H. & Burnham, K. P. (2001). Suggestions for presenting the results of data analyses. *The Journal of Wildlife Management* **65**, 373-378.
- Anon. 2019. Klassifisering av tilstanden til 430 norske sjøørretbestander. Temarapport fra Vitenskapelig råd for lakseforvaltning nr 7. 150 p.
- Bartoń, K. (2020). MuMIn: Multi-Model Inference. R package version 1.43.17. <https://CRAN.R-project.org/package=MuMIn>.
- Berg, O. K. & Berg, M. (1987). Migrations of sea trout, *Salmo trutta* L., from the Vardnes river in northern Norway. *Journal of Fish Biology* **31**, 113-121.
- Bordeleau, X., Davidsen, J. G., Eldøy, S. H., Sjørnsen, A. D., Whoriskey, F. G. & Crossin, G. T. (2018). Nutritional correlates of spatiotemporal variations in the marine habitat use of brown trout (*Salmo trutta*) veteran migrants. *Canadian Journal of Fisheries and Aquatic Sciences* **75**, 1744-1754.
- Bœuf, G. & Payan, P. (2001). How should salinity influence fish growth? *Comparative Biochemistry and Physiology Part C: Toxicology & Pharmacology* **130**, 411-423.
- Chapman, B. B., Skov, C., Hulthén, K., Brodersen, J., Nilsson, P. A., Hansson, L. A. & Brönmark, C. (2012). Partial migration in fishes: definitions, methodologies and taxonomic distribution. *Journal of Fish Biology* **81**, 479-499.
- Cucherousset, J., Ombredane, D., Charles, K., Marchand, F. & Baglinière, J.-L. (2005). A continuum of life history tactics in a brown trout (*Salmo trutta*) population. *Canadian Journal of Fisheries and Aquatic Sciences* **62**, 1600-1610.
- Davidsen, J., Knudsen, R., Power, M., Sjørnsen, A., Rønning, L., Hårsaker, K., Næsje, T. & Arnekleiv, J. (2017). Trophic niche similarity among sea trout *Salmo trutta* in Central Norway investigated using different time-integrated trophic tracers. *Aquatic Biology* **26**, 217-227.
- Davidsen, J. G., Thorstad, E. B., Baktoft, H., Aune, S., Økland, F. & Rikardsen, A. H. (2013). Can sea trout *Salmo trutta* compromise successful eradication of *Gyrodactylus salaris* by hiding from CFT Legumin (rotenone) treatments? *Journal of Fish Biology* **82**, 1411-1418.
- Davidsen, J. G., Daverdin, M., Arnekleiv, J. V., Rønning, L., Sjørnsen, A. D. & Koksvik, J. I. (2014a). Riverine and near coastal migration performance of hatchery brown trout *Salmo trutta*. *Journal of Fish Biology* **85**, 586-596.
- Davidsen, J. G., Daverdin, M., Sjørnsen, A. D., Rønning, L., Arnekleiv, J. V. & Koksvik, J. I. (2014b). Does reduced feeding prior to release improve the marine migration of hatchery brown trout *Salmo trutta* smolts? *Journal of Fish Biology* **85**, 1992-2002.
- Davidsen, J. G., Eldøy, S. H., Sjørnsen, A. D., Rønning, L., Bordeleau, X., Daverdin, M., Bårdsen, M. T., Whoriskey, F. & Koksvik, J. I. 2018. Marine vandringer og områdebruk hos sjøørret og sjørøye i Tosenfjorden. NTNU Vitenskapsmuseet naturhistorisk rapport (ISSN 1894-0056). 84 s.
- del Villar-Guerra, D., Aarestrup, K., Skov, C. & Koed, A. (2014). Marine migrations in anadromous brown trout (*Salmo trutta*). Fjord residency as a possible alternative in the continuum of migration to the open sea. *Ecology of Freshwater Fish* **23**, 594-603.
- Dieperink, C., Bak, B. D., Pedersen, L. F., Pedersen, M. I. & Pedersen, S. (2002). Predation on Atlantic salmon and sea trout during their first days as postsmolts. *Journal of Fish Biology* **61**, 848-852.



- Drenner, S. M., Clark, T. D., Whitney, C. K., Martins, E. G., Cooke, S. J. & Hinch, S. G. (2012). A synthesis of tagging studies examining the behaviour and survival of anadromous salmonids in marine environments. *PLoS one* **7**, e31311-e31311.
- Eldøy, S., Davidsen, J., Thorstad, E., Whoriskey, F., Aarestrup, K., Næsje, T., Rønning, L., Sjørnsen, A., Rikardsen, A. & Arnekleiv, J. (2015). Marine migration and habitat use of anadromous brown trout *Salmo trutta*. *Canadian Journal of Fisheries and Aquatic Sciences* **72**, 1366-1378.
- Eldøy, S. H., Davidsen, J. G., Thorstad, E. B., Whoriskey, F. G., Aarestrup, K., Næsje, T. F., Rønning, L., Sjørnsen, A. D., Rikardsen, A. H. & Arnekleiv, J. V. (2017). Marine depth use of sea trout *Salmo trutta* in fjord areas of central Norway. *Journal of Fish Biology* **91**, 1268-1283.
- Eldøy, S. H., Bordeleau, X., Lawrence, M. J., Thorstad, E. B., Finstad, A. G., Whoriskey, F. G., Crossin, G. T., Cooke, S. J., Aarestrup, K., Rønning, L., Sjørnsen, A. D. & Davidsen, J. G. (2021). The effects of nutritional state, sex and body size on the marine migration behaviour of sea trout. *Marine Ecology Progress Series* **665**, 185-200.
- Elliott, J. M. (1975a). The growth rate of brown trout (*Salmo trutta* L.) fed on reduced rations. *Journal of Animal Ecology* **44**, 823-842.
- Elliott, J. M. (1975b). The growth rate of brown trout (*Salmo trutta*) fed on maximum rations. *Journal of Animal Ecology* **44**, 805-821.
- Elliott, J. M. (1994). *Quantitative ecology and the brown trout*. 286 p. Oxford: Oxford University Press.
- Elliott, J. M. & Hurley, M. A. (2000). Daily energy intake and growth of piscivorous brown trout, *Salmo trutta*. *Freshwater Biology* **44**, 237-245.
- Elliott, J. M. & Elliott, J. A. (2010). Temperature requirements of Atlantic salmon *Salmo salar*, brown trout *Salmo trutta* and Arctic charr *Salvelinus alpinus*: predicting the effects of climate change. *Journal of Fish Biology* **77**, 1793-1817.
- Finstad, B., Staurnes, M. & Reite, O. B. (1988). Effect of low temperature on sea-water tolerance in rainbow trout, *Salmo gairdneri*. *Aquaculture* **72**, 319-328.
- Finstad, B. & Ugedal, O. (1998). Smolting of sea trout (*Salmo trutta* L.) in northern Norway. *Aquaculture* **168**, 341-349.
- Forseth, T. & Jonsson, B. (1994). The growth and food ration of piscivorous brown trout (*Salmo trutta*). *Functional Ecology* **8**, 171-177.
- Fraser, N. H. C. & Metcalfe, N. B. (1997). The costs of becoming nocturnal: feeding efficiency in relation to light intensity in juvenile Atlantic Salmon. *Functional Ecology* **11**, 385-391.
- Fulton, T. W. (1904). The rate of growth in fishes. *Fisheries Board of Scotland Annual Report* **22**, 141-241.
- Garman, G. C. & Nielsen, L. A. (1982). Piscivory by stocked brown trout (*Salmo trutta*) and its impact on the nongame fish community of Bottom Creek, Virginia. *Canadian Journal of Fisheries and Aquatic Sciences* **39**, 862-869.
- Gross, M., Coleman, R. & McDowall, R. (1988). Aquatic productivity and the evolution of diadromous fish migration. *Science (New York, N.Y.)* **239**, 1291-1293.
- Handeland, S. O., Björnsson, Arnesen, A. M. & Stefansson, S. O. (2003). Seawater adaptation and growth of post-smolt Atlantic salmon (*Salmo salar*) of wild and farmed strains. *Aquaculture* **220**, 367-384.
- Henderson, M. A. & Northcote, T. G. (1985). Visual prey detection and foraging in sympatric cutthroat trout (*Salmo clarki clarki*) and Dolly Varden (*Salvelinus malma*). *Canadian Journal of Fisheries and Aquatic Sciences* **42**, 785-790.

- IPCC. 2013. *Climate change 2013: The physical science basis. Contribution of working group I to the fifth assessment report of the Intergovernmental Panel on Climate Change*. [Stocker, T.F., D. Qin, G.-K. Plattner, M. Tignor, S.K. Allen, J. Boschung, A. Nauels, Y. Xia, V. Bex and P.M. Midgley (eds.)]. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA. 1535 p.
- Jensen, A. J., Finstad, B., Fiske, P., Forseth, T., Rikardsen, A. H. & Ugedal, O. (2018). Relationship between marine growth and sea survival of two anadromous salmonid fish species. *Canadian Journal of Fisheries and Aquatic Sciences* **75**, 621-628.
- Jensen, J. L. A. & Rikardsen, A. H. (2008). Do northern riverine anadromous Arctic charr *Salvelinus alpinus* and sea trout *Salmo trutta* overwinter in estuarine and marine waters? *Journal of Fish Biology* **73**, 1810-1818.
- Jensen, J. L. A., Rikardsen, A. H., Thorstad, E. B., Suhr, A. H., Davidsen, J. G. & Primicerio, R. (2014). Water temperatures influence the marine area use of *Salvelinus alpinus* and *Salmo trutta*. *Journal of Fish Biology* **84**, 1640-1653.
- Jonsson, B. (1985). Life history patterns of freshwater resident and sea-run migrant brown trout in Norway. *Transactions of the American Fisheries Society* **114**, 182-194.
- Jonsson, B. & Jonsson, N. (1993). Partial migration: niche shift versus sexual maturation in fishes. *Reviews in Fish Biology and Fisheries* **3**, 348-365.
- Jonsson, B. & Jonsson, N. (2009). A review of the likely effects of climate change on anadromous Atlantic salmon *Salmo salar* and brown trout *Salmo trutta*, with particular reference to water temperature and flow. *Journal of Fish Biology* **75**, 2381-2447.
- Jonsson, N. (1991). Influence of water flow, water temperature and light on fish migrations in rivers. *Nord J Freshw Res* **66**, 20-35.
- Jonsson, N. & Jonsson, B. (2002). Migration of anadromous brown trout *Salmo trutta* in a Norwegian river. *Freshwater Biology* **47**, 1391-1401.
- Klemetsen, A., Amundsen, P. A., Dempson, J. B., Jonsson, B., Jonsson, N., O'Connell, M. F. & Mortensen, E. (2003). Atlantic salmon *Salmo salar* L., brown trout *Salmo trutta* L. and Arctic charr *Salvelinus alpinus* (L.): a review of aspects of their life histories. *Ecology of Freshwater Fish* **12**, 1-59.
- Knutsen, J., Knutsen, H., Gjørseter, J. & Jonsson, B. (2001). Food of anadromous brown trout at sea. *Journal of Fish Biology* **59**, 533-543.
- Knutsen, J., Knutsen, H., Olsen, E. & Jonsson, B. (2004). Marine feeding of anadromous *Salmo trutta* during winter. *Journal of Fish Biology* **64**, 89-99.
- Kristensen, M., Righton, D., Del Villar-Guerra, D., Baktoft, H. & Aarestrup, K. (2018). Temperature and depth preferences of adult sea trout *Salmo trutta* during the marine migration phase. *Marine Ecology Progress Series* **599**.
- Langeland, A. L., L'Abée-Lund, J., Jonsson, B. & Jonsson, N. (1991). Resource partitioning and niche shift in Arctic charr *Salvelinus alpinus* and brown trout *Salmo trutta*. *Journal of Animal Ecology* **60**, 895-912.
- Larsen, P. F., Nielsen, E. E., Koed, A., Thomsen, D. S., Olsvik, P. A. & Loeschcke, V. (2008). Interpopulation differences in expression of candidate genes for salinity tolerance in winter migrating anadromous brown trout (*Salmo trutta* L.). *BMC Genetics* **9**, 12.
- Larsson, S. (2005). Thermal preference of Arctic charr, *Salvelinus alpinus*, and brown trout, *Salmo trutta* – implications for their niche segregation. *Environmental Biology of Fishes* **73**, 89-96.
- MacCrimmon, H. R., Marshall, T. L. & Gots, B. L. (1970). World distribution of brown trout, *Salmo trutta*: further observations. *Journal of the Fisheries Research Board of Canada* **27**, 811-818.

- McKay, L. R. & Gjerde, B. (1985). The effect of salinity on growth of rainbow trout. *Aquaculture* **49**, 325-331.
- NVE (2021). [www.sildre.nve.no](http://www.sildre.nve.no). 05.05.2021.
- Nøttestad, L., Giske, J., Holst, J. & Huse, G. (1999). Length based hypothesis for feeding migrations in pelagic fish. *Canadian Journal of Fisheries and Aquatic Sciences* **56**, 26-34.
- Parry, G. (1960). The development of salinity tolerance in the salmon, *Salmo salar* (L.) and some related species. *Journal of Experimental Biology* **37**, 425-434.
- Pemberton, R. (1976). Sea trout in North Argyll sea lochs: II. diet. *Journal of Fish Biology* **9**, 195-208.
- Pincock, D. G. (2011). False detections: what they are and how to remove them from detection data. *Vemco Application Note*, 1-14.
- Pinheiro, J., Bates, D., DebRoy, S. & Sarkar, D. (2020). nlme: Linear and nonlinear mixed effects models. R package version 3.1-149, URL: <https://CRAN.R-project.org/package=nlme>.
- R Core Team (2020). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL: <https://www.R-project.org/>.
- Rikardsen, A. H., Amundsen, P.-A., Knudsen, R. & Sandring, S. (2006). Seasonal marine feeding and body condition of sea trout (*Salmo trutta*) at its northern distribution. *Ices Journal of Marine Science* **63**, 466-475.
- Rikardsen, A. H., Dempson, J. B., Amundsen, P.-A., Bjørn, P. A., Finstad, B. & Jensen, A. J. (2007a). Temporal variability in marine feeding of sympatric Arctic charr and sea trout. *Journal of Fish Biology* **70**, 837-852.
- Rikardsen, A. H., Diserud, O. H., Elliott, J. M., Dempson, J. B., Sturlaugsson, J. & Jensen, A. J. (2007b). The marine temperature and depth preferences of Arctic charr (*Salvelinus alpinus*) and sea trout (*Salmo trutta*), as recorded by data storage tags. *Fisheries Oceanography* **16**, 436-447.
- RStudio Team (2020). RStudio: Integrated Development for R. RStudio, PBC, Boston, MA URL: <http://www.rstudio.com/>.
- Simpfendorfer, C. A., Huveneers, C., Steckenreuter, A., Tattersall, K., Hoenner, X., Harcourt, R. & Heupel, M. R. (2015). Ghosts in the data: false detections in VEMCO pulse position modulation acoustic telemetry monitoring equipment. *Animal Biotelemetry* **3**, 55.
- Thomsen, D. S., Koed, A., Nielsen, C. & Madsen, S. S. (2007). Overwintering of sea trout (*Salmo trutta*) in freshwater: escaping salt and low temperature or an alternate life strategy? *Canadian Journal of Fisheries and Aquatic Sciences* **64**, 793-802.
- Thorpe, J. E. (1994). Salmonid fishes and the estuarine environment. *Estuaries* **17**, 76-93.
- Thorstad, E. B., Todd, C. D., Uglem, I., Bjørn, P. A., Gargan, P. G., Vollset, K. W., Halttunen, E., Kålås, S., Berg, M. & Finstad, B. (2016). Marine life of the sea trout. *Marine Biology* **163**, 47.
- Ugedal, O., Finstad, B., Damsgård, B. & Mortensen, A. (1998). Seawater tolerance and downstream migration in hatchery-reared and wild brown trout. *Aquaculture* **168**, 395-405.
- Ytrestøyl, T., Takle, H., Kolarevic, J., Calabrese, S., Timmerhaus, G., Rosseland, B. O., Teien, H. C., Nilsen, T. O., Handeland, S. O., Stefansson, S. O., Ebbesson, L. O. E. & Terjesen, B. F. (2020). Performance and welfare of Atlantic salmon, *Salmo salar* L. post-smolts in recirculating aquaculture systems: Importance of salinity and water velocity. *Journal of the World Aquaculture Society* **51**, 373-392.

Aarestrup, K., Baktoft, H., Thorstad, E., Höjesjö, J. & Koed, A. (2015). Survival and progression rates of anadromous brown trout kelts *Salmo trutta* during downstream migration in freshwater and at sea. *Marine Ecology Progress Series* **535**, 185–195.