

Signe Brekke Harbak

# Habitat use of sea trout (*Salmo trutta*) veterans in two Norwegian estuaries

Master's thesis in Ocean Resources

Supervisor: Jan Grimsrud Davidsen

Co-supervisor: Sindre Håvarstein Eldøy and Eva Bonsak Thorstad

May 2022



Signe Brekke Harbak

# **Habitat use of sea trout (*Salmo trutta*) veterans in two Norwegian estuaries**

Master's thesis in Ocean Resources

Supervisor: Jan Grimsrud Davidsen

Co-supervisor: Sindre Håvarstein Eldøy and Eva Bonsak Thorstad

May 2022

Norwegian University of Science and Technology

Faculty of Natural Sciences

Department of Biology



Kunnskap for en bedre verden





## Acknowledgements

I would like to thank everyone who helped me make this master thesis possible. My project was part of two larger projects at Orkanger and Hellstranda funded by Trondheim Port Authority and Nye Veier via Acciona Construction and Rambøll, respectively. Thanks to all contributors during field work. In Orkanger, Anette, Sindre and Ingvild Grimsrud Davidsen and Aslak and Andreas Løvås Sjørnsen are thanked for great help with catching and tagging of sea trout during a challenging time period with Covid-19 restrictions. Thanks to Geir Mikael Reijners for catching of sea trout in Orkanger and operation manager of Orkanger harbour Bjørn Steinshaug for easy access to the port terminal. Furthermore, I would like to thank Eikem Thamshavn and the boat club Terna for the permission to place receivers at their harbour areas. Thanks to Avinor and Forsvarsbygg for access to their areas during deployment and maintenance of receivers. A special thanks to the members of the Stjørdal hunting and fishing association for assistance during fieldwork and for sharing your coffee on cold days. Thanks to Øystein Nordeide Kielland, Lars Rønning, Anette, Ingvild and Sindre Grimsrud Davidsen for help during catching and tagging of sea trout and Atlantic salmon at Hellstranda and in river Stjørdalselva.

I also want to thank Aslak Darre Sjørnsen for very needed fishing-tips and for teaching me how to read fish-scales. Thank you to Marc André Francis Daverdin for creating maps and to Mohsen Falahati for conducting genetic analysis. I would like to thank fellow master students Mikkel Emil Lange Friis, Enghild Steinkjer, Håvard Vedeler Nilsen, Nanna Norderud, Christianne Dalsbotten Solvåg, Hanne Bjørnås Krogstie and Johan Otto Munkeby for shearing knowledge and nice moments together at the NTNU University Museum during the past two years. A special thanks to Catrine Schulze for support and encouragement through all new experiences and steep learning curves together.

A big thank you to my family and friends for always being supportive.

Finally, I would like to express my gratitude to my supervisors Jan Grimsrud Davidsen and Sindre Håvarstein Eldøy for the opportunity to join a such inclusive and inspiring team at the NTNU University Museum, for all the hours spent together out in the field and for guidance through the thesis. A big thank you also to supervisor Eva Bonsak Thorstad for help during field work, valuable feedback and encouraging words.

*Signe Brekke Harbak*

*Trondheim, May 2022*

## Abstract

Estuaries are important habitats for sea trout (*Salmo trutta*) in all seasons and can be used by individuals also during the winter months as an alternative strategy to the more common freshwater overwintering. In the present study, acoustic telemetry was used to map estuarine habitat use of sea trout veterans from two populations in Orkanger ( $n = 30$ , tracked through April 2020-April 2021) and Stjørdal ( $n = 97$ , tracked through August 2020-September 2021 or May 2021-September 2021), in Trøndelag county in Norway.

In both estuaries, the river channel and sheltered intertidal mudflats were utilized by tagged sea trout in all seasons. There was a clear difference in the proportion of tagged individuals that resided in the estuary during winter between Orkanger (13%) and Stjørdal (62%), suggesting local adaptations or differences in the suitability for overwintering in the estuaries.

For estuarine overwintering individuals in Stjørdal, the sheltered intertidal mudflats were the preferred overwintering habitat with 68% of total time spent in this estuarine habitat type. In Orkanger, 50% of total time spent in the estuary during winter was spent in the sheltered intertidal mudflats. The sea trout in both estuaries, had during the late spring and summer months the highest residence time in the exposed intertidal mudflats and fjord habitat, possibly because the habitats provided good forage availability. In both estuaries, sea trout experiencing higher water temperatures in the estuary than in the fjord, were more likely to reside in the former habitat. In Stjørdal, males had higher probability of presence in the estuary than females, possibly linked to the difference between sexes related to body size and reproductive success. In Stjørdal, the probability of presence in the estuary decreased with date (May-August), possibly due to the upstream migration of sea trout. In Orkanger, no correlation was found between sex and date and the probability of presence in the estuary.

The tagged sea trout present in all estuarine habitats in Orkanger during the time period from April throughout May 2020, resided in water masses with a lower average temperature ( $4.8\text{ }^{\circ}\text{C}$ ,  $\text{SD} = 1.3\text{ }^{\circ}\text{C}$ ) than the average temperature in marine water masses ( $6.5\text{ }^{\circ}\text{C}$ ,  $\text{SD} = 0.4\text{ }^{\circ}\text{C}$ ). This tendency was also observed in Stjørdal during winter and spring, indicating that the sea trout resided in fresh- and brackish water masses and not in seawater. However, during the spring, in Stjørdal the sea trout experienced a temperature shift after decreased influx of melt water in the rivers, where the sea trout resided in water masses with a higher average temperature ( $10.1\text{ }^{\circ}\text{C}$ ,  $\text{SD} = 4.4\text{ }^{\circ}\text{C}$ ) than in the marine environment ( $6.7\text{ }^{\circ}\text{C}$ ,  $\text{SD} = 2.0$ ). In both estuaries, the study showed no correlation between total body length and water temperature experienced by the fish in the time period May-August, indicating that body size did not influence the water temperatures experienced by the species in the two estuaries.

The present study shows that estuaries provide important microhabitats utilized by sea trout during all seasons and for different purposes. Estuaries are under a continuous and increasing pressure from coastal development, where knowledge on habitat use as presented in this study, is essential for management and conservation efforts.

## Samandrag

Elvemunningar er eit viktig habitat for sjøaure (*Salmo trutta*) til alle årstider, og kan brukast gjennom vinterhalvåret som ein alternativ strategi til den meir vanlege overvintringa i ferskvatn. I denne studien blei akustisk telemetri brukt for å kartlegge bruken av elvemunningen hos sjøaureveteranar frå to populasjonar, henholdsvis i Orkanger ( $n = 30$ , følgt frå april 2020-april 2021) og Stjørdal ( $n = 97$ , følgt frå august 2020-september 2021 eller mai 2021-september 2021), i Trøndelag fylke i Midt-Norge.

I begge elvemunningane blei elvekanalen og den beskytta tidevassona brukt av merka sjøaure gjennom alle årstider. Det var ein klar skilnad i andelen av merka sjøaure som oppheldt seg i elvemunningen gjennom vinteren mellom Orkanger (13%) og Stjørdal (62%), noko som kanskje kan forklarast av lokale tilpassingar og variasjon i kor egna elveosane var for overvintring.

I Stjørdal blei den beskytta tidevassona brukt til å overvintre, med 68% av total tid brukt i habitatet. I Orkanger brukte fisken som var til stade gjennom vinteren 50% av total tid i den beskytta tidevassona. I begge elvemunningane hadde den eksponerte tidevassona og fjord habitatet høgast opphaldstid gjennom våren og sommarmånadane, kanskje fordi habitatet gav god tilgang på mat. Sjøaure som opplevde høgare vassstemperaturar hadde større sannsyn for å vere til stade i elvemunningen enn i meir marine områder, noko som indikerte ein temperaturskilnad mellom dei to habitatata. I Stjørdal hadde hannfisk større sannsyn for å vere til stade i elvemunningen enn hofisk, noko som mest truleg er knytt til forskjellen mellom kjønn relatert til kroppsstørrelse og reproduktivsuksess. I Stjørdal sank sannsynet for at fisken var til stade i elvemunningen med dato (mai-august), noko som kan forklarast av migrasjon opp i elva. I Orkanger blei ingen korrelasjon funne mellom kjønn og dato, og sannsyn for opphald i elvemunningen.

Sjøaure som var til stade i elvemunningen frå april og gjennom mai 2020, oppheldt seg i vatn med lågare gjennomsnittstemperatur ( $4.8\text{ °C}$ ,  $SD = 1.3\text{ °C}$ ) enn gjennomsnittstemperaturen i sjøvatn ( $6.5\text{ °C}$ ,  $SD = 0.4\text{ °C}$ ). Denne tendensen blei også observert i Stjørdal gjennom vinteren og våren, noko som indikerte at fisken oppheldt seg i fersk- og brakkvatn og ikkje i marint vatn. På våren opplevde sjøaura i Stjørdal eit temperaturskifte, som følgje av lågare tilkomst av smeltevatn i elvene, og fisken oppheldt seg i vassmassar med høgare gjennomsnittstemperatur ( $10.1\text{ °C}$ ,  $SD = 4.4\text{ °C}$ ) enn i sjøvatn ( $6.7\text{ °C}$ ,  $SD = 2.0$ ). Studien fann ingen korrelasjon mellom total kroppslengde og vassstemperatur som fisken oppheldt seg i for tidsperioda mai-august.

Denne studien viser at elvemunningar består av viktige mikrohabitat, som brukast av sjøaure gjennom alle årstider og til ulike formål. Elvemunningar er under eit kontinuerleg og aukande press frå kystutvikling, og kunnskap om habitatbruk til sjøaure er viktig for kunne utføre godt forvaltnings og bevaringsarbeid.

# TABLE OF CONTENT

1. Introduction .....	1
2. Materials and methods.....	4
2.1 Study sites.....	4
2.1.1 Orkanger.....	4
2.1.2 Stjørdal .....	5
2.1.3 Defining zones and habitats at receiver locations .....	6
2.2 Collection of data .....	7
2.2.1 Fish capture and tagging.....	7
2.2.2 Acoustic transmitters .....	8
2.2.3 Tracking of tagged fish.....	9
2.2.4 Receiver performance.....	10
2.2.5 Environmental parameters.....	10
2.3 Scale analysis and sex determination .....	10
2.4 Data analysis.....	11
2.4.1 Calculation of condition factor.....	11
2.4.2 Filtration of telemetry data .....	11
2.4.3 Statistical analysis .....	12
2.4.4 Calculating residence time .....	13
3. Results .....	14
3.1 Environmental conditions.....	14
3.2 Study groups.....	15
3.3 Number of detected fish .....	16
3.4 Residence time .....	18
3.5 Probability of presence in estuary vs. adjacent fjord.....	20
3.6 Temperature use .....	21
3.7 Modelling temperature use.....	23
4. Discussion .....	25
5. References .....	33
Appendix 1 .....	39
Residence zones through seasons.....	39
Generalized linear models of presence in estuary vs. adjacent fjord.....	41
Generalized linear models of temperature use .....	42

# 1. INTRODUCTION

Estuaries and continental shelf areas comprise 5.2% of the Earth's surface (Wolanski & Elliott, 2016). These areas support many of the world's megacities and their associated demands on the estuarine, adjacent marine and freshwater systems (Jiang *et al.*, 2001; Sekovski *et al.*, 2012). Estuaries are among the most populated areas worldwide, they are used as transport routes, and have high biological productivity, which sustain a high level of food production (Wolanski & Elliott, 2016). Despite their importance, estuaries are unproportionally exploited and regarded among the most ecologically threatened ecosystems worldwide (Froneman, 2018). Growing pressure from increasingly diverse human activities coupled with climate change impacts can have irreversible environmental consequences, degrade habitats and lead to fatal outcomes for ecosystems (Moksness *et al.*, 2013). Human utilization of land, such as forest clearing, wetland draining, and infrastructure development threatens species living in coastal habitats (Sekovski *et al.*, 2012; Wolanski & Elliott, 2016). Habitat destruction has far-reaching ecological consequences, modifying the structure and function of estuarine ecosystems and contributing to the decline of biodiversity (Kennish, 2002). In order to ensure effective management of estuarine habitats and conservation of its species, proper understanding of the function of the habitat for the species of interest is crucial (Kennish, 2002; Moksness *et al.*, 2013).

Estuaries are characterized by highly variable hydrodynamics driven by river inflow and the tidal cycle, mixing freshwater and saltwater resulting in a unique habitat (Wolanski & Elliott, 2016; Zhang *et al.*, 2021). As a result of the shape and size, in addition to variation in river flows, sediment input, tides, wind and evaporation, the physical functioning varies greatly among estuaries (Wolanski & Elliott, 2016). River estuaries are heterogenous regarding temperature and salinity and may present the inhabitants with a range of thermal and saline habitats, where the need to respond to salinity change may be rapid, such as during tidal cycles (McCormick, 2001). Stratification occurs when water masses with different densities form distinct layers, where less dense brackish and often warmer water lies over the denser and usually colder seawater (Jordan, 2012; Wolanski & Elliott, 2016). Such water layers allow mobile organisms to actively seek areas with profitable temperature and salinity, performing behavioural thermoregulation (Moore *et al.*, 2012). The great variation in abiotic conditions creates several microhabitats within the estuaries, which may be utilized for various purposes by the inhabitants. Variation in microhabitats may influence the behavioural patterns and foraging decisions of the inhabitants in the estuary (Kennish, 2002).

Anadromous brown trout (*Salmo trutta L.*, hereafter referred to as sea trout) is a species providing important ecosystem services. Recreational sea trout fisheries contribute to recreational activities for local communities, local cultural heritage and transfer of ecological knowledge (Liu *et al.*, 2019). Sea trout exploit several types of habitats and exhibits complex movement and behavioural patterns driven by factors not yet fully understood (Jonsson, 1985). In recent years, several studies have aimed for quantifying the marine habitat use of sea trout (Eldøy *et al.*, 2015; Kristensen *et al.*, 2019). These efforts have increased the knowledge on marine migration of sea trout, but at the same time highlighted the extensive variation in behaviour and habitat utilization within the species (Strøm *et al.*, 2021). Sea trout have the ability to migrate between freshwater and saltwater (Klemetsen *et al.*, 2003), thus utilize habitats with distinct characteristics. Sea trout veterans (sea trout that have previously performed one or more marine migrations) perform feeding migrations to estuarine and marine

habitats, often annually during their life time (Thorstad *et al.*, 2016). This life-history strategy often implies improved feeding opportunities and growth rate, enhancing the reproductive potential and fitness (Jonsson & Jonsson, 1993). However, migration also includes several risks and stressors. The costs of migrating to marine habitats can be related to the physiological demands needed to adjust to different salinities, energetic investment in locomotion, increased risk of predation and exposure to novel pathogens (Thorstad *et al.*, 2016). Thus, there is a continuous trade-off between survival and growth that determines the life-history decisions and behavioural patterns (Nevoux *et al.*, 2019). Today, many sea trout populations in Norway are under pressure, mainly caused by several human-derived factors (Jonsson & Jonsson, 2011; Thorstad *et al.*, 2016). A rapport from 2022 investigating Norwegian sea trout populations (Anon, 2022), found that less than a quarter of the 1251 investigated watercourses, were classified as in good or in very good state, while almost 40% were regarded as in bad state, very bad state or lost. Thus, knowledge on how and why the sea trout utilize estuaries is essential to conserve populations and maintain their ecosystem service for local communities.

The main determinants of individual's fitness are survival and growth, whereas the relative value of feeding habitats in terms of survival and growth often changes seasonally or in relation to the developmental stage of the sea trout (Nevoux *et al.*, 2019). Thus, sea trout exhibit ontogenetic niche shifts related to size and developmental stage (Klemetsen *et al.*, 2003). There is large variation in timing and duration of marine migrations, with some of the most influential factors being temperature, physiological state, and size of the sea trout (Drenner *et al.*, 2012). A study by Eldøy *et al.* (2021) showed that females were more likely to migrate to the sea than males. As the reproductive success of males and females is unequally dependent on size, where female breeding success is strongly positive to body size (Fleming, 1998; Heinimaa & Heinimaa, 2004), the benefit of marine feeding migrations is potentially larger for females. When at sea, the migrating sea trout often feed close to the surface and near costal areas within 80 km of their river of origin, but large individuals may sometimes undertake even longer migrations at sea (Klemetsen *et al.*, 2003; Thorstad *et al.*, 2016; Kristensen *et al.*, 2019). Several studies show that relatively large proportions of the fish use the estuary areas of their natal rivers. In a study by Middlemas *et al.* (2009), 37% of the fish were detected less than 6 km from their natal river. The results was comparable to findings by Finstad *et al.* (2005) and Thorstad *et al.* (2007), where 53% of the sea trout were detected within 9 km and 25% within 9.5 km, respectively. Many populations have also been found to utilize estuarine areas during the winter months as an alternative to the more common overwintering upstream in freshwater (Knutsen *et al.*, 2004; Rikardsen *et al.*, 2006).

Temperature is a characteristic of the habitat, being one axis of its multidimensional niche, contributing directly and indirectly to the fitness of the individual (Magnuson *et al.*, 1979). Temperature influences many aspects of the life cycle of brown trout, including timing of spawning, egg hatching, timing of smolt migration etc. (Jonsson & Jonsson, 2009b). As an ectothermic organism, water temperature influences the rate of biochemical reactions affecting the performance of the individual (Angilletta Jr *et al.*, 2002). An experimental study testing the temperature preferences of sea trout reported that the sea trout preferred temperatures correlated to the optimal growth temperature of the species (Larsson, 2005). It is suggested that sea trout have a growth optimum at 16-17°C (Forseth & Jonsson, 1994; Elliott & Hurley, 2000; Ojanguren *et al.*, 2001), with diet as an important factor of growth. Kristensen *et al.* (2018) found that sea trout in the marine phase adjusted to temperature with a gradual increase in residence depth as temperatures increased, as well as sudden responses if internally measured

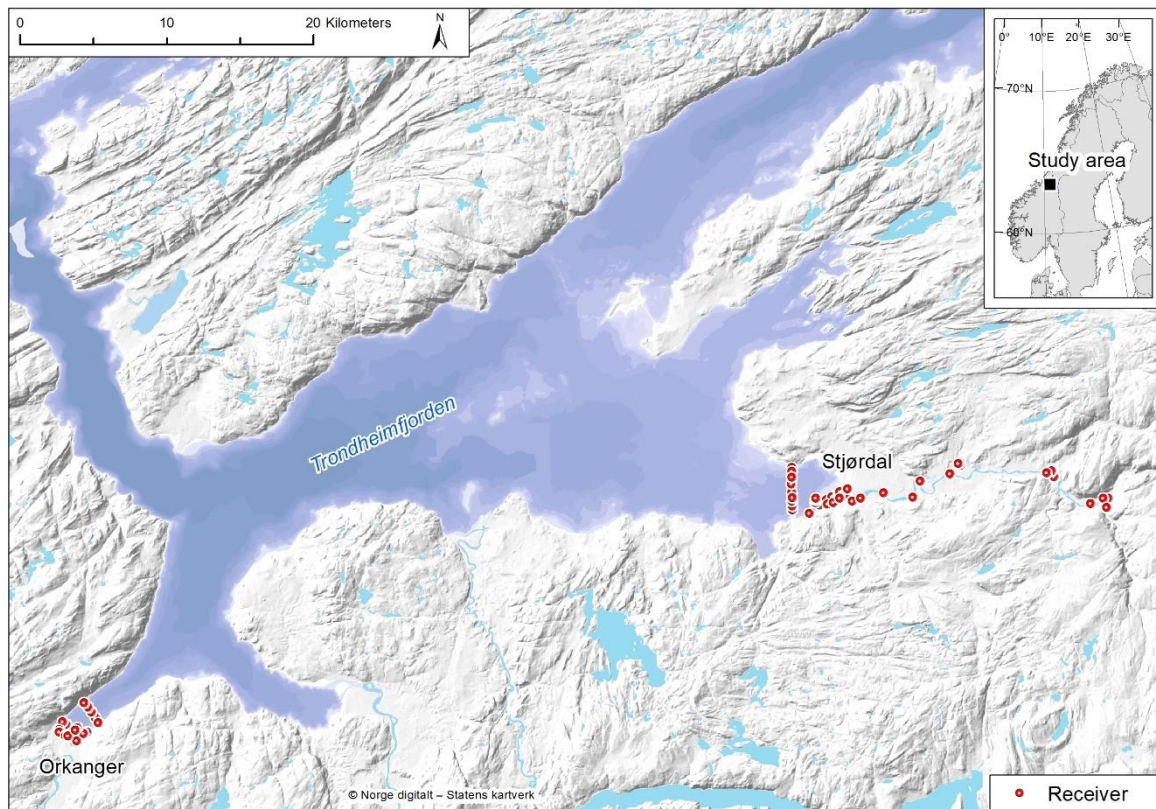
temperatures rose above 17 °C. At low water temperatures, slower biochemical reactions are found to reduce prey capture probability and predator avoidance, due to reduced swimming ability (Watz & Piccolo, 2011). It is shown that smaller fish are more susceptible to fluctuations in water temperature than larger fish, due to the buffer effect a large body mass can give when thermal equilibrium occurs in the fish (Elliott & Elliott, 2010). In addition, low water temperatures compromise the hypo-osmoregulatory ability, meaning that the combination of low temperatures and high salinity may be challenging due to insufficient ion-transport mechanisms (Koed *et al.*, 2007). Similar as for temperature, it is shown that tolerance for salinity is linked to fish size, where larger fish have better osmoregulatory capacity than smaller fish due to the more favourable surface-area-to-volume ratio for larger fish (McCormick & Saunders, 1987; Finstad & Ugedal, 1998; Jonsson & Jonsson, 2011). This size dependent salinity and temperature tolerance may be reflected in the habitat use in the river mouth, where fish of different sizes prefer or avoid microhabitats with distinct abiotic characteristics.

The aim of this study was to examine the habitat use of sea trout, where spatial and temporal distribution of tagged fish were recorded using acoustic telemetry in two estuaries in Trøndelag county, central Norway. The thesis was part of two larger research projects at NTNU University museum (Davidsen *et al.*, 2021a; Davidsen *et al.*, 2021b), and included data used for impact assessments of upcoming infrastructure developments in the two study areas. The aim was to gain a better understanding of how veteran sea trout migrants used the estuaries, and how individual characteristics (total body length and sex) influenced the extent of the estuarine habitat use and temperature use. It was hypothesized that (1) the sea trout in Orkanger and Stjørdal utilize the estuaries through all seasons, (2) the estuarine habitats in Orkanger and Stjørdal are utilized in similar ways, with variation within the estuaries, and (3) temperature use is influenced by body length; shorter fish use warmer water temperatures.

## 2. MATERIALS AND METHODS

### 2.1 Study sites

The study was conducted in two fjords with associating estuaries located in Orkland and Stjørdal municipalities (Figure 1), both in Trøndelag county, central Norway. The study site in Orkanger was divided into four zones, which were (1) exposed intertidal mudflats, (2) river channel, (3) sheltered intertidal mudflats, and (4) other. The study site in Stjørdal was divided into five zones, which were (1) exposed intertidal mudflats, (2) river channel, (3) sheltered intertidal mudflats, (4) fjord, and (5) upstream in river. When investigating the habitat utilization of sea trout, the main focus was on zone 1-3 within the estuaries.



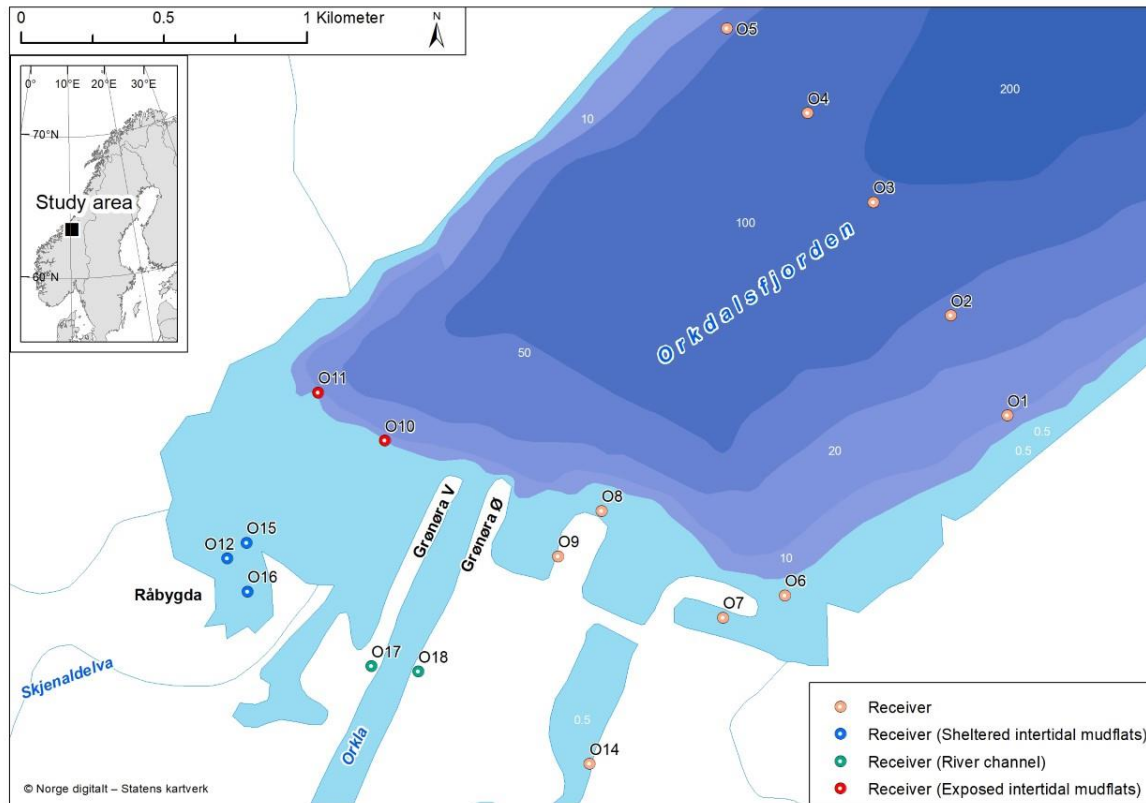
**Figure 1:** Map of the study sites in Orkanger and Stjørdal with all deployed receivers represented by a red dot.

#### 2.1.1 Orkanger

The study area in Orkland municipality was located in Orkanger and included the river outlet of River Orkla and River Skjenaldelva, shallow sandbanks at Råbygda estuary, and port areas of Grønøra west and east (Figure 2). The Orkla watercourse has a drainage basin of 3092 km<sup>2</sup>, a mean annual water discharge of 71 m<sup>3</sup>/s and a distance of 88 km accessible for anadromous fish. The river mouth of River Skjenaldelva is located 400 meters west of the river mouth of River Orkla. River Skjenaldelva has a drainage basin of 132 km<sup>2</sup> and a mean annual water discharge of 5.5 m<sup>3</sup>/s. The river delta of River Orkla was channelized in the 1960s and 70s, building the port area of Grønøra. During the construction, large areas of wetland was lost, with todays remaining wetland areas at the Råbygda estuary. The wetlands at Råbygda are sheltered by sandbanks and little exposed to waves from the Orkdal fjord. However, the estuary area of Råbygda is influenced by tides and freshwater input from River Skjenaldelva. At low tide,



larger areas of sea bottom consisting of mud and sand, as well as areas with coarse sandy bottom and pebbles, are exposed to air. The area outside the sandbanks is exposed to waves, influenced by seawater, and has an increasing depth. River Orkla is channelized through the port area of Grønøra, where the water discharge is strongly affected by a hydropower regulation further upstream in the watercourse.

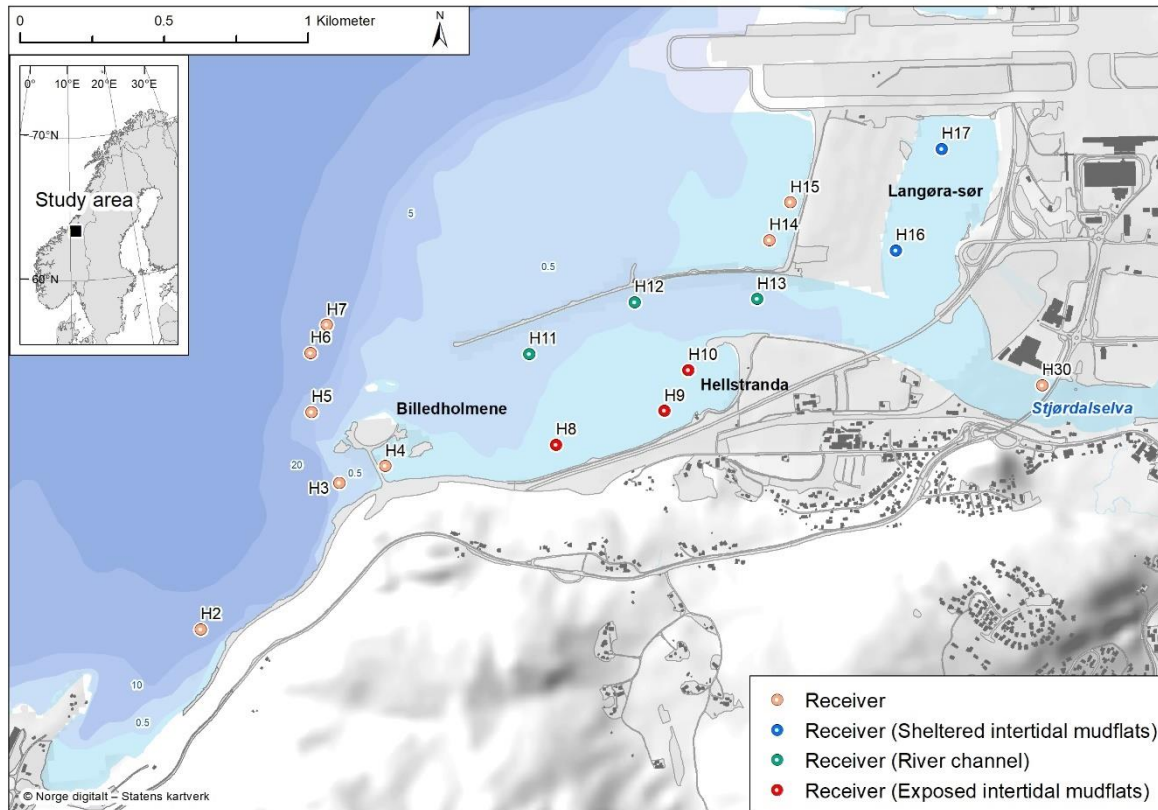


**Figure 2:** Map of the study site in Orkanger with receivers deployed in the exposed intertidal mudflats (red dots), sheltered intertidal mudflats (blue dots), river channel (green dots), and harbour and fjord areas (orange dot).

### 2.1.2 Stjørdal

The study site in Stjørdal municipality included the river outlet of River Stjørdalselva, the former river outlet inside Langøra-south and a shallow water pool between Billedholmene and Hellstranda (Figure 3). River Stjørdalselva has a drainage basin of 2111 km<sup>2</sup>, a mean annual water discharge of 79 m<sup>3</sup>/s and a 55 km long section accessible for anadromous fish. The original river outlet of River Stjørdalselva was moved in 1954 due to the expansion of Værnes airport. A new river outlet was formed through Langøra, resulting in a new straight river channel entering the fjord towards Billedholmene (Davidsen *et al.*, 2017b). A one km long stone pier was built, forming a shallow water pool between Billedholmene and Hellstranda. This area is a transition zone between freshwater from the river and saltwater from the Stjørdal fjord. The former river outlet, Langøra-south, is a shallow area with intertidal mudflats and brackish water, partly encapsulated and sheltered from marine water from the fjord by the Langøra land area and a weir constructed by stones in the river channel. The exposed intertidal mudflats at Hellstranda are highly affected by the tide and large areas are frequently exposed to air. Hellstranda is exposed to waves and marine water coming in from the fjord. The main river channel of River Stjørdalselva goes along the pier, and is influenced

by the tide, with shifting salinities and currents. The waterflow in the river is strongly affected by a hydropower dam further upstream the watercourse.



**Figure 3:** Map of the study site in Stjørdal with receivers deployed in the exposed intertidal mudflats (red dots), sheltered intertidal mudflats (blue dots), river channel (green dots), and fjord and upstream river (orange dot).

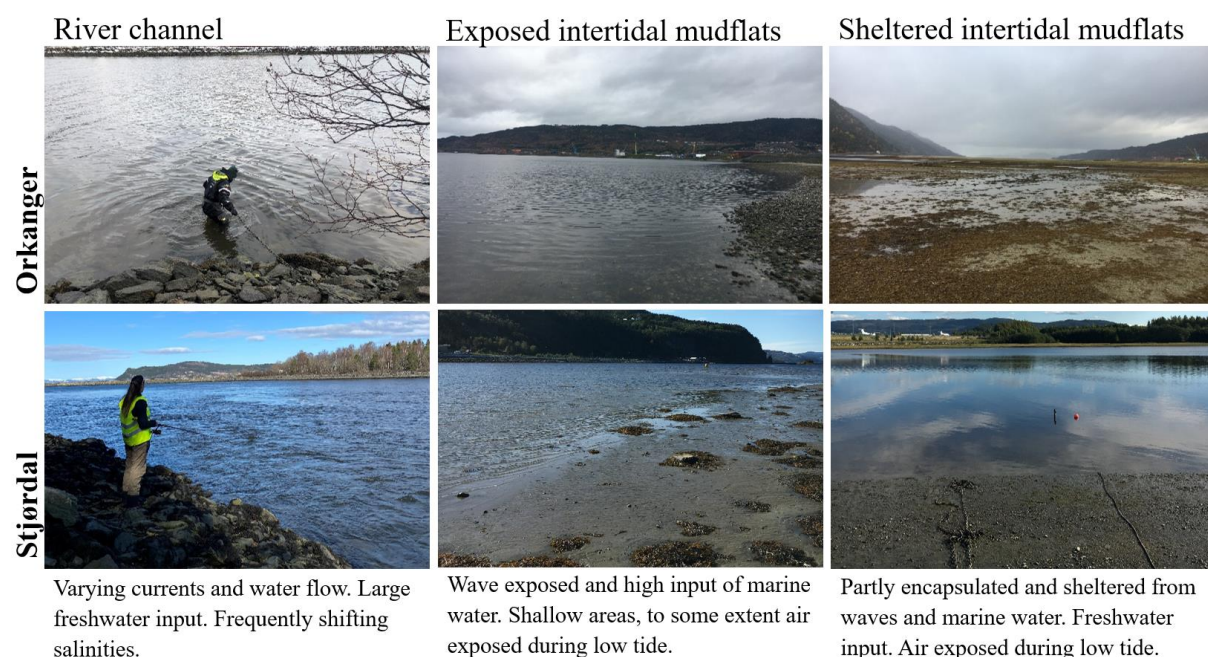
### 2.1.3 Defining zones and habitats at receiver locations

The area within the range of each receiver was categorized into a zone (1-5, Table 1), depending on exposure to seawater, shelter from waves, as well as freshwater input. Measured salinities were either defined as freshwater (<5‰), brackish water (5-30‰) or saltwater (>30‰). Varying degree of marine- and freshwater input and shelter from marine waves created different types of habitats. Orkanger and Stjørdal had corresponding zones with similar bathymetry and salinity levels, providing similar habitats available for the sea trout to explore (Figure 4). However, the two study locations were not identical and comparisons without considering differences and confounding factors were not possible. Langøra-south in Stjørdal had a similar habitat as Råbygda in Orkanger, with shallow and sheltered areas less exposed to waves. However, one main difference was the fresh water source in Orkanger, River Skjenaldelva, running through Råbygda, while no freshwater source drained directly through the sheltered area at Langøra-south. In addition, the exposed intertidal mudflats in Stjørdal were shallower than the exposed intertidal mudflats in Orkanger and more frequently air exposed. The number of receivers placed in the different habitats varied between the study sites (Table 1), covering different ranges of the habitats. In Stjørdal, the sheltered intertidal mudflats and the exposed intertidal mudflats were physically separated by the river channel (Figure 3). In Orkanger, the sheltered intertidal mudflats and the exposed intertidal mudflats were neighbouring areas, separated from the river channel due to the channelization of the river course (Figure 2).

When exploring the habitat use in the estuaries of River Orkla in Orkanger and River Stjørdalselva in Stjørdal, the main focus was on zone 1-3 located in the estuaries. Estuary in its rightful terms consist of the tidal mouth of the rivers, which includes an area influenced of tidewaters further upstream the river outlets. In this study, the term estuary is used about the lower and more marine parts of the estuarine areas.

**Table 1:** Division of zones in Orkanger and Stjørdal, with descriptions of zones/habitats 1-5. Receivers included in each zone are listed.

<b>Zone – Habitat</b>	<b>Receivers in Orkanger</b>	<b>Receivers in Stjørdal</b>
1 – Exposed intertidal mudflats	O10, O11	H8, H9, H10
2 – River channel	O17, O18	H11, H12, H13
3 – Sheltered intertidal mudflats	O12, O15, O16	H16, H17
4 – Fjord	O1-O9, O14	H1-H7, H14, H15, H60-H68
5 – Upstream	NA	H30-H32, H34-H40, H42, H80, H81



**Figure 4:** Estuarine habitats in Orkanger and Stjørdal.

## 2.2 Collection of data

### 2.2.1 Fish capture and tagging

A total of 127 sea trout veterans, divided into three groups based on capture location and year (Table 2), were captured and tagged with individually coded acoustic transmitters implanted into the abdominal cavity. In Orkanger, 30 fish were tagged during 7-13 April 2020, while 97 fish were tagged in Stjørdal during 3 August 2020-19 May 2021. In Orkanger, 25 fish were captured in the estuarine parts of River Orkla and 5 fish at Råbygda. Fish from Stjørdal were captured in the river mouth or lower parts of River Stjørdalselva. All fish were captured by

using fishing rod and line. The fish were held in keep nets placed in low current areas of the river, for up to four hours until tagging.

The fish were anesthetized in a tarpaulin-covered tank containing Benzoac Vet (ACD Pharmaceuticals AS) with a dilution of 15-20 ml per 100 L for 3-4 minutes. The total body length and weight of the fish were measured. The fish were placed in a tube with water continuously administered over the gills during the surgical procedure. A scalpel was used to make a 2-3 cm incision on the side of the *linea alba* anterior to the pelvic gridle (Wagner *et al.*, 2011; Eldøy *et al.*, 2015). A sterilized acoustic transmitter was inserted into the body cavity. The incision was closed with two separate non-biodegradable sutures (Resorba Wundversorgung GmbH & Co; Resolon 3/0). A small piece of the adipose fin was collected using sterile scissors, for later genomic verification of species and sex. In addition, approximately 10 scales were sampled from each fish for age determination. The scales were collected from an area close to the caudal fin, above the lateral line, using a forceps. After sampling, the fish were kept in recovery tanks for 5-10 minutes, until showing normal swimming behaviour and breathing rate and then released in calm water close to capture site. The experimental procedures were approved and done in accordance with the regulations set by the Norwegian National Animal Research Authority (Orkanger: 20/113613 and Stjørdal: 20/60513).

**Table 2:** Tagging date, number of sea trout veterans (*n*), sex distribution, total body length and mass with mean, standard deviation (SD) and range given for each group of tagged fish. Two individuals tagged in Stjørdal during spring 20 had not sex determined.

Tagging group	Date	<i>n</i>	Female:Male ( <i>n</i> )	Total body length (mm)		Body mass (g)	
				Mean ± SD	Range	Mean ± SD	Range
<b>Orkanger spring 2020</b>	07.04.- 13.04.2020	30	16:14	367 ± 85	270- 550	516 ± 449	160- 1760
<b>Stjørdal autumn 2020</b>	03.08.- 20.12.2020	46	23:21 2 NA	388 ± 60	290- 550	600 ± 334	220- 2000
<b>Stjørdal spring 2021</b>	26.03.- 19.05.2021	51	16:35	390 ± 77	272- 615	539 ± 353	155- 2100

### 2.2.2 Acoustic transmitters

In Orkanger, one size of cylindrically shaped transmitters from Thelma Biotel (Trondheim, Norway) were used for all fish (Table 3). In Stjørdal, transmitters of different sizes from Thelma Biotel and Vemco Inc. (Halifax, Canada) were used, depending on the total body length of the fish. The acoustic transmitters emitted a unique sound signal (69 or 71 kHz), which was recorded when the fish were within range of a listening station. The signals were sent with a random time interval, with a minimum of 40 seconds and maximum 80 seconds between each signal.

The acoustic transmitters used at both study sites had temperature sensors. The information was stored each second time the fish ID-number was sent to the receivers, approximately every other



minute. As sea trout are poikilothermic, their core temperature is similar dependent on the temperature of surrounding water masses. Hence, temperature measured by the fish transmitters could be used as a measure for the water temperature were the fish resided, with precaution of a small delay.

**Table 3:** Group of tagged fish, number of tagged fish (*n*), battery lifetime, transmitter size and weight, and signal strength for each transmitter type used.

<b>Transmitter type</b>	<b>Tagging group</b>	<b><i>n</i></b>	<b>Battery lifetime (days)</b>	<b>Transmitter size (mm)</b>	<b>Weight in air (g)</b>	<b>Signal strength (dB re 1uPa @ 1m)</b>
<b>T-MP9</b>	Orkanger spring 20	30	365	9 x 27	4.3	146
<b>ADT-LP9-L</b>	Stjørdal autumn 20	11	380	9 x 28	5.1	142
	Stjørdal spring 21	18				
<b>T-LP9-L</b>	Stjørdal spring 21	29	576	9 x 28	4.3	142
<b>V9T-2L</b>	Stjørdal autumn 20	35	410	9 x 31	4.6	146
<b>ADT-LP6</b>	Stjørdal spring 21	4	70	6 x 18	1.3	137

### 2.2.3 Tracking of tagged fish

The tagged sea trout in Orkanger were tracked using 17 acoustic receivers from Thelma Biotel AS (ThelmaBiotel TBR700), which operated from April 2020 to April 2021. The receivers were located at Råbygda, the harbour area and in an array across the Orkdal fjord (Figure 2). Receivers O2-O5 and O10-O11 were placed 15 m below the water surface and attached to a 14 mm rope, with floating elements at the top. An anchor and acoustic release system (Sub Sea Sonic model ARI-60-E, Sub Sea Sonic inc., San Diego, USA) were attached at the bottom of the rope. Remaining receivers were either attached to a pole that was placed into the sediments or to a rope, which had a floating element at the surface and anchor at the sea floor. Receiver O10 and O11 at Grønøra west were placed at a relatively exposed site and the habitat was categorized as exposed intertidal mudflats. Receiver O17 and O18 were placed in the main river channel of river Orkla, and O12, O15 and O16 at Råbygda were placed at the sheltered intertidal mudflats.

In Stjørdal, 17 receivers were operating from August 2020 to August 2021 in the estuary and adjacent marine areas (Figure 3). In addition, an array of nine receivers were placed further out in the fjord and 11 receivers placed upstream the river mouth (Figure 1). Due to the use of acoustic transmitters from two different companies, with non compatible receivers, both receivers from Vemco (Vemco models: VR2 and VR2-AR) and Thelma Biotel AS (ThelmaBiotel TBR700) were used on each receiver station. Receiver H1, H5-H7 and H11-H13 were attached to a 14 mm rope and placed approximately 15 meters below the water surface with a floating element at the top rope end, in addition to an anchor and an acoustic

release system (VR2-AR) attached at the bottom rope end. Remaining receivers were either attached to a pole placed into the sediments or to a rope, which had a floating element at the surface and anchor at the sea floor. Receiver H8, H9 and H10 at Hellstranda were placed in a habitat categorized as exposed intertidal mudflats. Receiver H11, H12 and H13 were placed in the river channel and receiver H16, and H17 at Langøra-south were categorized as the sheltered intertidal mudflats.

#### 2.2.4 Receiver performance

The receiver performance varied with salinity, ocean currents and wind, which affected the sensitivity to incoming signals from the acoustic transmitters. The estuaries in both Orkanger and Stjørdal were complex, with large variation in salinity, water temperature, and flow patterns, which caused large spatial and temporal differences in the environmental variables. To evaluate the effectiveness of the receiver lines in recording passing fish, three control tags were placed at receiver nr. O4, O9, and O15 (Figure 2) in Orkanger as well as receiver H1, H5-H7, and H11-H13 (Figure 3) in Stjørdal. Evaluation of the recorded signals from neighboring receivers showed that the range (50-400m) was equal to other similar studies (Eldøy *et al.*, 2015; Bordeleau *et al.*, 2018), with shorter range in areas with layers of varying salinity or temperature and in areas with counter currents.

#### 2.2.5 Environmental parameters

Water temperature and salinity were monitored at three different locations in Stjørdal and two different locations in Orkanger by data loggers (DST Milli-CT, Star-Oddi Ltd., Reykjavik, Iceland). In Orkanger, recordings were stored every second hour, while in Stjørdal, recordings were stored every 30 minutes. Data loggers in Orkanger were placed at receiver O9 in the port area of Grønøra east and receiver O15 in Råbygda estuary in the time period between 03.04.20 and 18.03.21. The data logger placed at receiver O15 had no measurements in the time period between 08.10.20-05.04.21 due to technical errors. Temperature and salinity were measured at 3-5 meters depth (depending on the tide) at receiver O9 and from 0-1 meter depth at receiver O15. Data loggers in Stjørdal were placed at receiver H8, H10 and H17 (Figure 3) in the period between 03.08.20 and 16.09.21. The data loggers were attached to receiver H8 close to the Hell-tunnel, H10 at Hellstranda, and H17 at Langøra-south, which were placed on poles 10 cm above the sea floor, thus, depth varied from 0-2 meters dependent on the tide. All data from periods in air exposure were removed.

### 2.3 Scale analysis and sex determination

Fish scales from tagged fish were stored in paper envelopes and analysed using a light microscope at the NTNU University Museum. The most intact and readable scales for age analysis were selected to determine previous sea migrations and age of each individual fish. An imprint of the selected scales was made by pressing the scales onto 1 mm Lexan plates. The imprints were analysed using a computer-controlled stereoscope (Leica M165C with camera Leica MC170 HD, Sankt Gallan, Switzerland) and connecting software, LAS V4.5. Calculation of age and number of previous marine migrations were completed in accordance with the method described by Lea (1910) and Dahl (1910). In the scale samples from Orkanger, 27 of 30 scales had high enough quality to be analysed. In Stjørdal, scale samples from 60 of 97 individuals were analysed.

To genetically verify the species and sex of the tagged sea trout, DNA samples from adipose fin clips were analyzed at the NTNU University Museum DNA lab as described in Eldøy *et al.* (2021).

## 2.4 Data analysis

### 2.4.1 Calculation of condition factor

Individual condition factor (Fulton's Condition factor,  $K$ ) was used to estimate the physical condition of the fish and was calculated using the formula (Ricker, 1975):

$$K = \frac{\text{wet body mass (g)} * 100}{\text{total body length (cm)}^3}$$

Fulton's condition factor made it possible to compare seasonal changes in nutritional condition. The general pattern in adult fishes is a decrease during times of low temperature and/or low food availability, and an increase in marine phase towards the spawning season, followed by a sharp decline after spawning (Froese, 2006).

### 2.4.2 Filtration of telemetry data

False detections is a known challenge in acoustic telemetry studies, and can cause biased or erroneous outcomes in the data analysis (Simpfendorfer *et al.*, 2015). The false registrations occur from acoustic noise in the sea, or when transmissions from two or more transmitters collide, making the receiver detect a different transmitter ID-code that is not present (Pincock, 2012). The colliding signals can be detected as an unknown transmitter ID-code or as a transmitter ID-code identical to another transmitter in the study, which will be more difficult to filter out from the dataset (Simpfendorfer *et al.*, 2015). False registrations are likely when several tagged fish stay in the detection range of the receiver at the same time, thus, receivers in estuaries have an increased chance to detect false detections (Pincock, 2012). Complete elimination of false detections is not possible, but identification and removal of errors give a more realistic dataset. Still, filtering the dataset may contribute to a risk of removing real data.

At the 17 receivers deployed in Orkanger, the initial number of detections was 1 239 459 in the time period April 2020 to April 2021. A visual inspection of the dataset showed few false ID registrations. Non-active ID-codes in the study were removed with no further filtration. A total of 935 970 registrations remained after removal of non active ID-codes and control tags and were considered as valid registrations. This included 38 084 registrations in the exposed intertidal mudflats, 303 831 registrations in the river channel, and 481 038 registrations in the sheltered intertidal mudflats. The remaining 113 017 registrations were at the receivers placed in the harbour and fjord area, categorized as zone 'other'.

The filter used for the study population in Stjørdal, required at least two registrations from a unique ID-code within a time span of 10 minutes to accept the registration as valid. There was a total of 4 317 284 registrations of active ID-codes at the receivers deployed in Stjørdal in the time period between August 2020 to August 2021. After filtering and removal of false registrations, 2 789 745 detections remained of the sea trout tagged in Stjørdal autumn 20, in addition to 830 082 detections of sea trout tagged in Stjørdal spring 21. For both tagging groups in Stjørdal, the exposed intertidal mudflats had 385 224 registrations through the study period,

994 444 registrations in the river channel, in addition to 1 694 800 registrations in the sheltered intertidal mudflats. The receivers categorized as fjord zone had 139 282 registrations and the upstream river zone had 406 077 registrations.

### 2.4.3 Statistical analysis

Statistical analyses were conducted in RStudio version 2021.09.0 (RStudio Team, 2021) by using R version 4.0.2. (R Core Team, 2020). The statistical significance level was determined to  $p < 0.05$ . Normality was tested by performing the Shapiro-Wilk test of normality for one variable by using the R function `shapiro.test`. In addition, a visual inspection was done by making density and Q-Q plots with the `ggpubr` r-package. Kruskal-Wallis test by rank was used to test for differences between groups in total body length, weight, and condition factor, as the data did not meet the assumption of normality. Wilcoxon-tests were used to perform pairwise comparisons of residence time between the study populations.

Mixed effect models were used to examine the influence of individual biological characteristics, date, and zone on the use of water masses with different temperatures. Function ‘`lme`’ in package ‘`nlme`’ (Pinheiro J, 2022) was used to model the water temperature experienced by the fish in response to sex, total body length, date and habitat, using fish ID as random variable. A generalized linear model with binomial error structure (‘`glmer`’ in ‘`lme4`’ R package) was used to investigate the decision to reside in the estuary versus adjacent fjord areas, with sex, date, total body length, and daily water temperature experienced as explanatory variables and fish ID as random factor.

All models were conducted separately for the two study locations and covered the time period May-August 2020 for Orkanger and May-August 2021 for Stjørdal. Daily mean temperature experienced was calculated for individual fish IDs from all registrations. Data with missing information were excluded from the models. Two fish (ID no. 162 and 163) from Stjørdal did not have sex determined and were excluded from models where sex was included as explanatory variable using the function ‘`complete.cases`’ in the ‘`base`’ package in R. In Orkanger, the models consisted of 169 detections in the exposed mudflats, 745 detections in the river channel and 404 detections in the sheltered mudflats ( $n = 24$ ). In Stjørdal, the models consisted of 1804 detections in the exposed mudflats, 2433 detections in the river channel and 1582 detections in the sheltered mudflats ( $n = 73$ ). All numeric variables were standardized using the base R ‘`scale`’ function prior to modelling. Condition-factor was not included as an explanatory variable due to the long time span between tagging date and the time period the models were based on.

Function ‘`check_collinearity`’ in R package ‘`performance`’ was used to check the models for collinearity and showed low collinearity between variables within models ( $VIF \leq 1.63$ ). Automated model selection and model averaging were performed by using function ‘`dredge`’ in package `MuMIn` in R. Second order Akaike’s Information Criteria (AICc) was used to rank and identify the best fitted models for both study groups (Burnham & Anderson, 2003; Burnham *et al.*, 2011). The second order Akaike’s Information Criteria was chosen due to a low sample size relative to number of parameters in some of the models.  $\Delta AICc < 2$  was set as limit when selecting the most parsimonious models (Burnham & Anderson, 2003). When a single model could not be identified, conditional model averaging was used to calculate parameter estimates of the models with  $\Delta AICc < 4$ .



#### 2.4.4 Calculating residence time

Calculating residence time in each zone required a set of assumptions. In cases with no daily registrations, it was assumed that the fish was present in the zone it was last detected in until entering and being detected in another zone. The three zones in Stjørdal were surrounded by receivers included in the fjord and upstream zones, giving few opportunities to leave a zone without being detected in another zone. In Orkanger, there were no receivers placed upstream River Orkla and River Skjenaldelva resulting in uncertainty when calculating residence time in the river channel and the sheltered intertidal mudflats. The fish may have migrated upstream River Orkla, while still being assumed present in the river channel. Likewise, fish may have been assumed present in the sheltered intertidal mudflats, after moving upstream River Skjenaldelva.

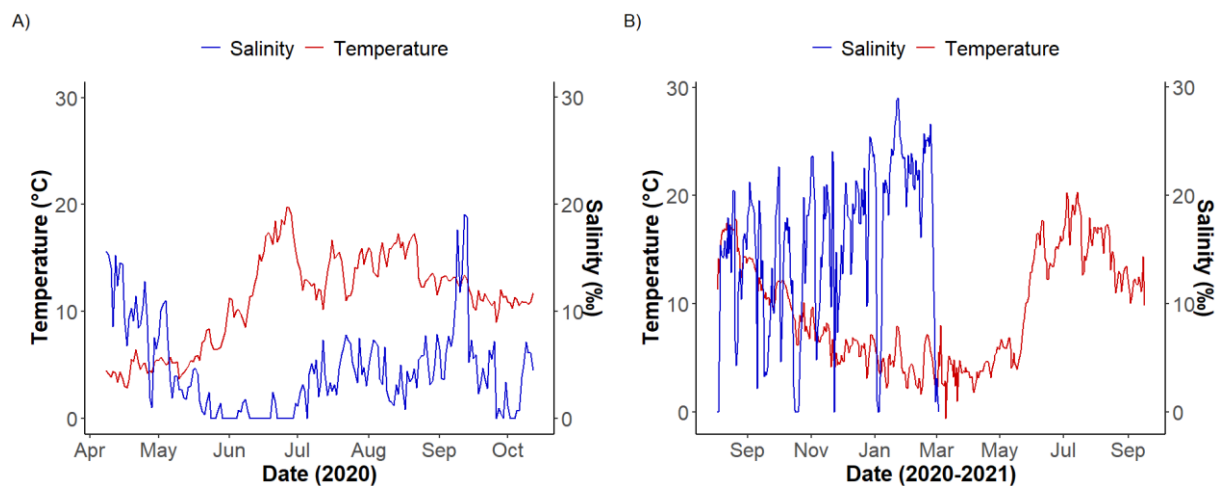
### 3. RESULTS

#### 3.1 Environmental conditions

In Orkanger, mean daily temperature in the sheltered mudflats (receiver O15, Figure 2) ranged from 2.9 °C to 19.8 °C in the time period from April to October 2020, with an overall average of 11.1 °C (SD = 4.3 °C). The water temperature increased from May to the end of June 2020, followed by a decrease in July (Figure 5). Average temperature in the time period May to August 2020 was 12.2 °C (SD = 4.2 °C, range 3.7-19.8 °C).

In Stjørdal, mean daily temperature in the exposed mudflats (receiver H8, Figure 3) ranged from -0.6 °C to 20.3 °C in the time period from August 2020 to September 2021, with an overall average of 9.3 °C (SD = 5.0 °C). Water temperatures increased from May, peaking in mid July 2021. Average water temperature in the time period May to August 2021 was 13.2 °C (SD = 4.1 °C, range 3.9-20.3 °C).

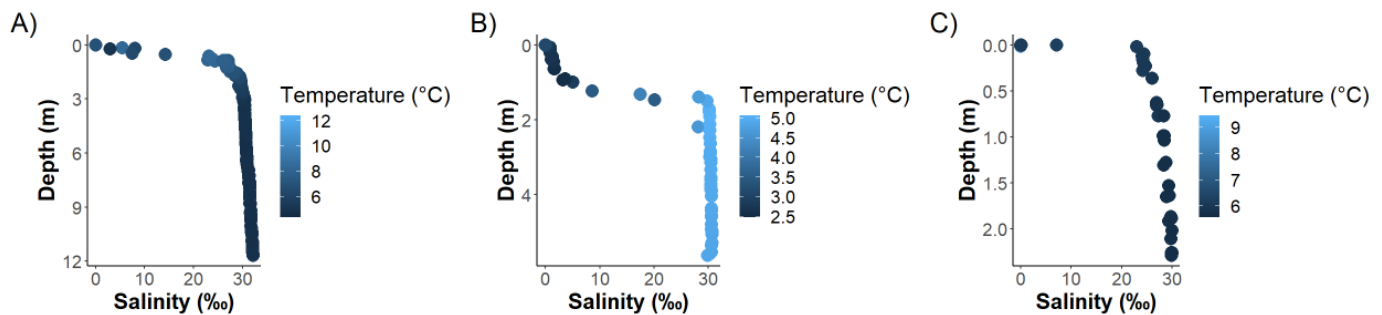
The salinity in both areas was highly influenced by tides, resulting in large daily fluctuations. However, the calculated daily average hides the daily variation (Figure 5). In Orkanger, the mean daily salinity at the sheltered mudflats (receiver O15) ranged from 0.0 to 19.1 ‰ from April to October 2020. In Stjørdal, the mean daily salinity measured at the exposed mudflats (receiver H8) ranged from 0 to 29 ‰ during August 2020 to March 2021.



**Figure 5:** Mean daily water temperature and salinity recorded in Orkanger and Stjørdal. A) Recorded in Orkanger at the sheltered mudflats (receiver O15) from April to October 2020, measured at 0-1 meters depth. Recordings from air exposed periods were removed. There were no recordings from 08.10.2020-05.04.2021 due to technical fails. B) Recorded in Stjørdal at the exposed mudflats (receiver H8) from August 2020 to September 2021, measured at 0-2 meters depth, dependent on tides. There were no salinity recording from 3 March 2021 due to technical fails.

In Stjørdal, the water temperature and salinity measured vertically in the water column, revealed layering of freshwater and saltwater (Figure 6). The marine areas at receiver H6 (Figure 6A) had a relatively homogenous water mass. The river channel had a characteristic thermocline and halocline with distinct layering of the water column. Freshwater with a temperature range between 2.5-3.5 °C created the upper layer, with marine water masses (30 ppt.) at 5 °C from

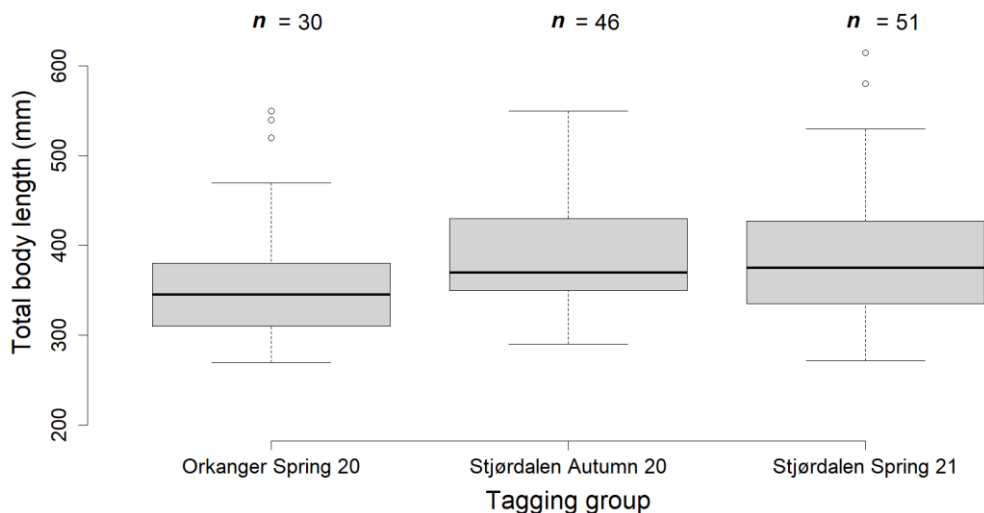
approximately 1.5 meters depth (Figure 6B). The CTD, taken during high tide in the sheltered mudflats, showed large influx of marine water (Figure 6C).



**Figure 6:** Water temperature and salinity in Stjørdal at different depths measured in A) marine habitat (receiver H6) 20 April 2021, B) river channel (receiver H11) 19 April 2021, and C) sheltered intertidal mudflats (receiver H17) 19 April 2021. Temperature given by graded blue colour from light blue (warmer water) to dark blue (colder water). NB the scale of the y-axes differs between panel A, B, and C.

### 3.2 Study groups

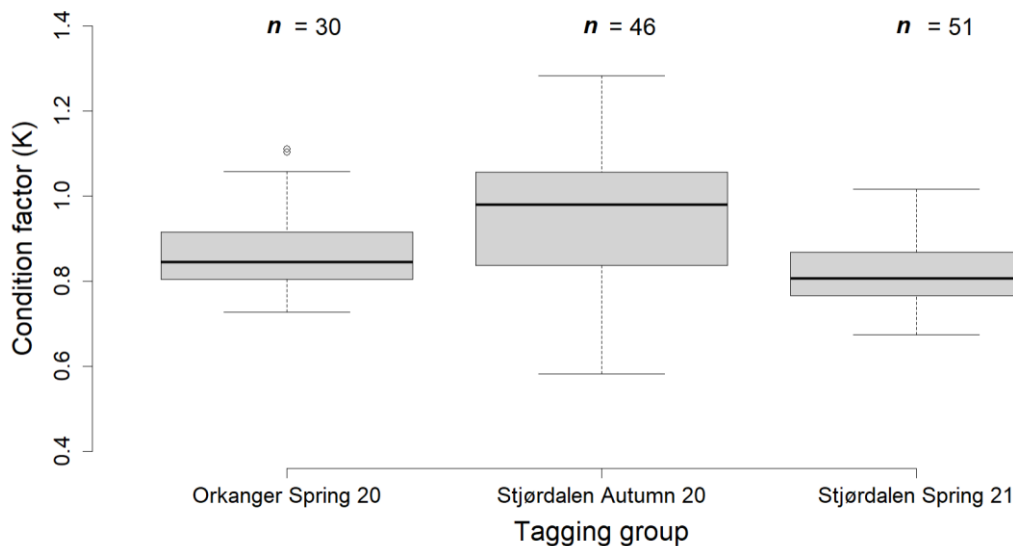
There were no differences in total body length between the three tagging groups (Figure 7, Kruskal-Wallis rank sum test;  $p$ -value = 0.103).



**Figure 7:** Total body length (mm) for three tagging groups of sea trout, named after location, tagging season and year.  $n$  is the number of fish in each tagging group. Each box represents the interquartile range (IQR), and the 5<sup>th</sup> and 95<sup>th</sup> percentiles (whiskers). The dots represent outliers and the bold lines show the median value of each tagging group.

Scale analysis of tagged sea trout in Orkanger, indicated 23 immature individuals, with one ( $n = 15$ ), two ( $n = 7$ ) or three ( $n = 1$ ) marine seasons. The largest individuals ( $n = 4$ ) had spent 3-5 seasons at sea and spawned 2-4 times. In Stjørdal, mean age was 4.7 years (SD = 1.0, range 3-8 years). In both study populations, the sea trout that had spawned had matured after 2-3 seasons at sea.

Mean Fulton's body condition factor fish tagged in Orkanger spring 20 (0.87, Figure 8) was lower than of fish tagged in Stjørdal autumn 2020 (Wilcoxon rank sum test; 0.95,  $p$ -value = 0.008). In addition, the tagged sea trout in Orkanger spring 20 had a higher condition factor than sea trout tagged in Stjørdal spring 20 (0.82,  $p$ -value = 0.03). Sea trout tagged in Stjørdal spring 20 had lower condition factor than sea trout tagged in Stjørdal autumn 20 ( $p$ -value < 0.05).



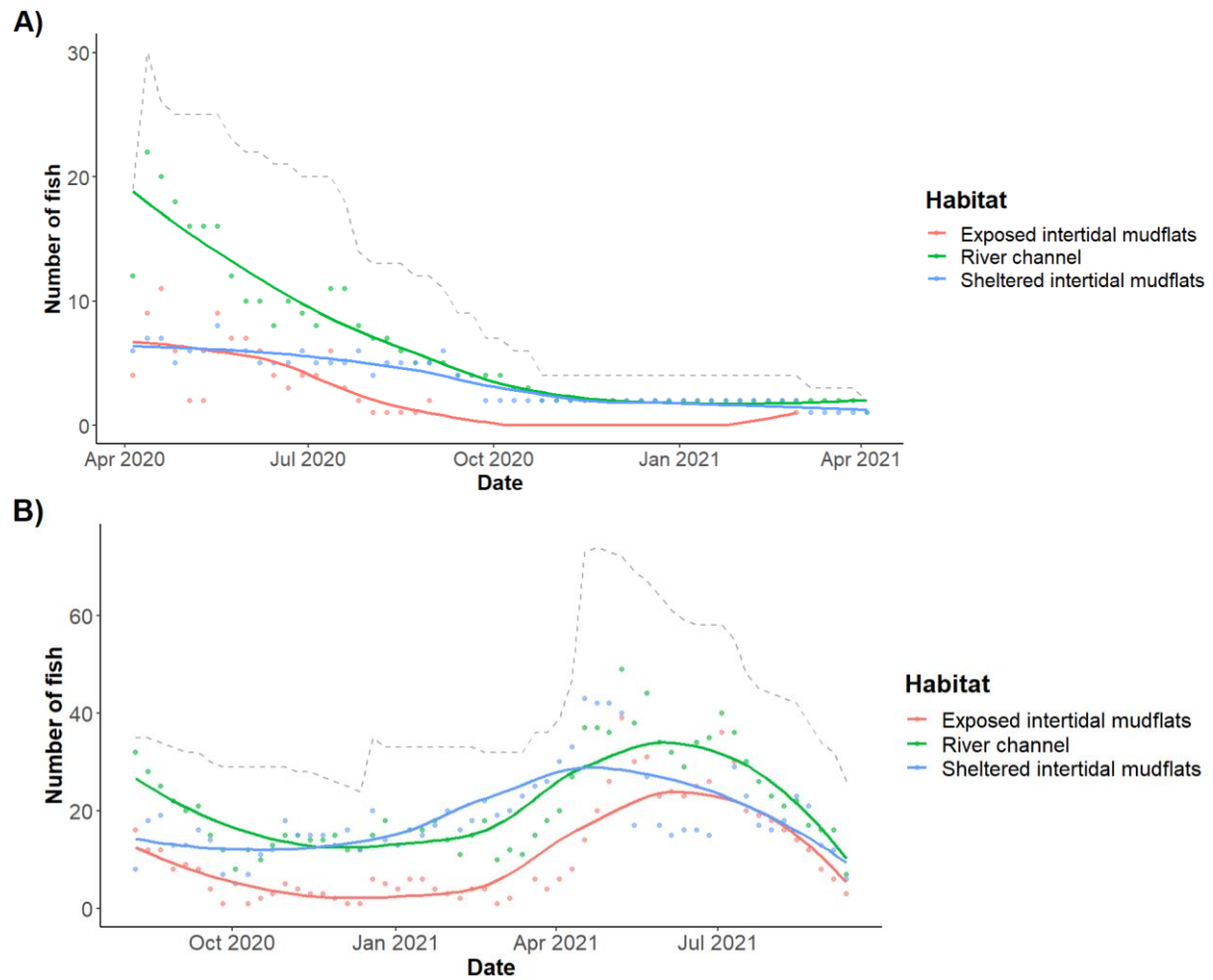
**Figure 8:** Fultons's condition factor (K) for three tagging groups of sea trout, named after location, tagging season and year.  $n$  is the number of fish in each tagging group. Each box represents the interquartile range (IQR), and the 5<sup>th</sup> and 95<sup>th</sup> percentiles (whiskers). The dots represent outliers and the bold lines show the median value of each tagging group.

### 3.3 Number of detected fish

In Orkanger, all of the 30 tagged sea trout were detected in the study area the 12 April 2020, with several fish entering more than one zone the following week, where the highest number of fish was detected in the river channel ( $n = 22$ , 74% of detected fish in any habitat). The weekly number of fish detected in the three estuarine habitats in Orkanger decreased from the time of tagging and throughout the study period. Four individuals were detected during the winter months (13% of tagged fish, Figure 9A), where two fish were detected in the river channel and two fish were detected in the sheltered intertidal mudflats.

In Stjørdal, a total of 35 tagged sea trout were detected the first weeks after tagging in August 2020 (Figure 9B), with the highest number of fish detected in the river channel ( $n = 32$ , 92% of fish detected in any habitat). In the first week of January 2021, 13 individuals (39% of fish detected in any habitat) were detected in the river channel, 13 individuals in the sheltered mudflats and 4 individuals (12%) in the exposed mudflats. Tagging of additional sea trout in April 2021 resulted in an increase in detected individuals, with the highest number of fish detected through the study period in April ( $n = 74$ ), corresponding with 56% detected in the sheltered mudflats, 50% detected in the river channel and 27% detected in the exposed mudflats. Individuals moved between zones during spring and summer, utilizing different types of

habitats. The number of detected fish decreased throughout the summer months, with 26 individuals detected at the end of the study period.



**Figure 9:** Weekly number of fish detected in A) Orkanger (April 2020-April 2021), and B) Stjørødal (August 2020-August 2021). Exposed intertidal mudflats, river channel and sheltered intertidal mudflats are represented by different colours. Fish can be registered in several habitats during one week. Grey dotted line represents total registered fish IDs each week on all receivers (including habitat upstream and fjord). NB the scale of the x-axes differs between panel A and B.

### 3.4 Residence time

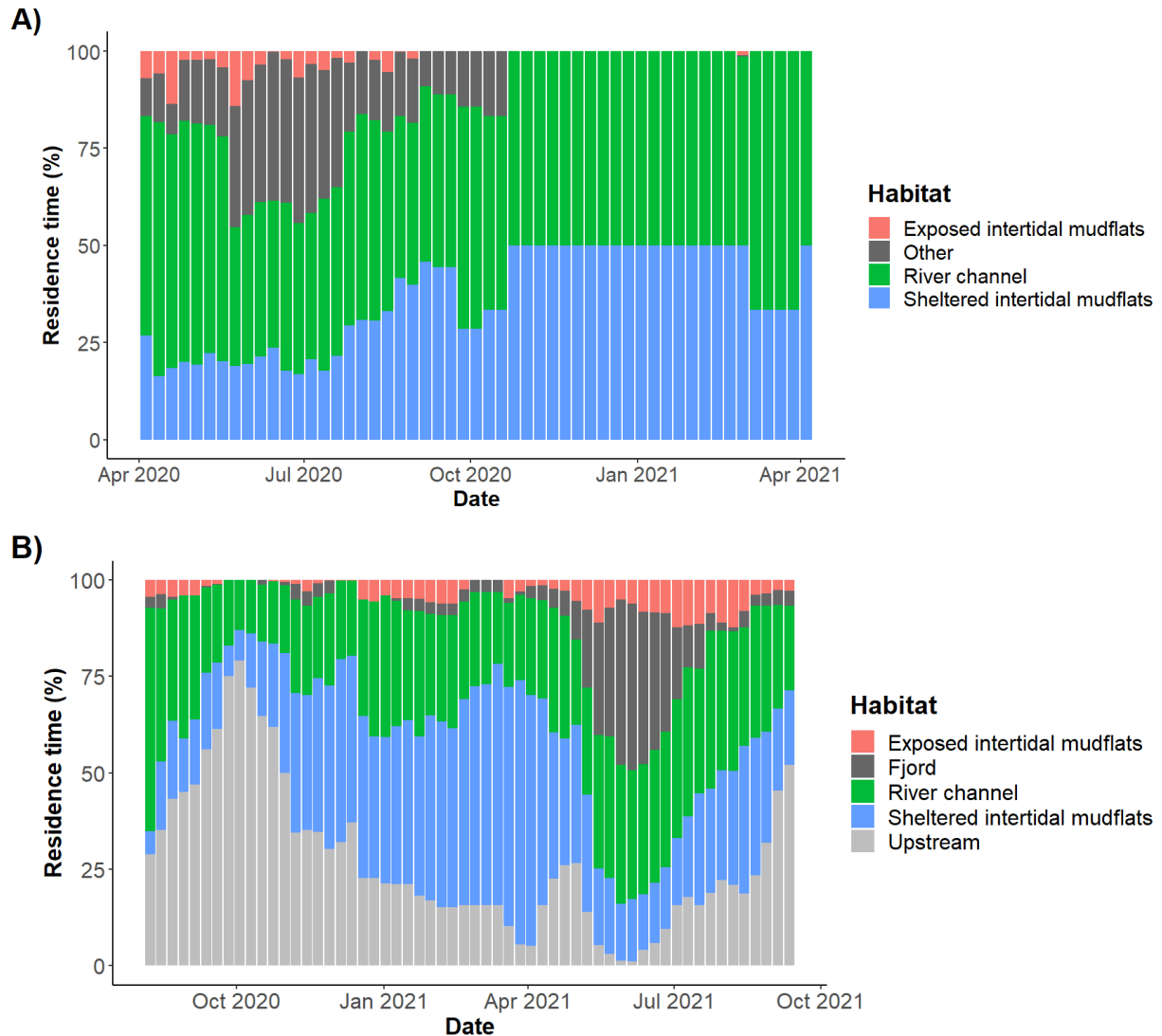
In Orkanger, the exposed mudflats (Figure 10A) had the highest percentage residence time with 14% of total time spent in the exposed mudflats in late April (19-25 April) and late May (24-30 May). There were no registrations in the exposed mudflats during the winter, except one individual detected in the week starting with the 28 February 2021, with a residence time of 1% of total time. In Stjørdal, the tagged sea trout spent more time in the exposed mudflats during the summer period (May-September) than in the winter period (November-April, Wilcoxon Rank Sum Test;  $p < 0.001$ ), with the highest weekly residence time of 63% of total time (Figure 10B) in the week starting with the 3 July ( $n = 35$  of in total 57 detected fish).

In both estuaries, the sheltered mudflats were used by tagged sea trout during all seasons. In Orkanger, 50% of total time was spent in the sheltered mudflats from 25 October 2020 to 21 February 2021 (Figure 10A). During winter, two of four detected fish in Orkanger were resident in the sheltered mudflats. From 7-28 March, 34% of total time was spent in the sheltered mudflats ( $n = 1$  of in total 3 detected individuals). In Orkanger, the lowest residence time in the sheltered mudflats was recorded in the spring and summer. In Stjørdal, the tagged sea trout had a higher average weekly time spent in the sheltered mudflats during the winter (November-April) than in the summer (May-September, Wilcoxon Rank Sum Test;  $p < 0.001$ ), with the highest weekly residence time in the sheltered mudflats at 68% of total in late March 2021 time ( $n = 26$  of in total 36 individuals detected). The lowest residence time was recorded in August 2020, with 6% of total time spent in the habitat ( $n = 8$  of in total 35 detected individuals).

In both estuaries, the river channel was used throughout the study period. In Orkanger, 22 of 30 individuals detected in mid May, spent time in the river channel, corresponding to 65% of total time (Figure 10A). From 11 November 2020 to 21 February 2021, 50% of total time was spent in the river channel. The highest percentage time was recorded in March 2021, with 67% of total time spent in the river channel ( $n = 2$  of in total 3 individuals detected). In Stjørdal, there was no difference between average weekly time spent in the river channel during the summer (May-September) and during the winter (November-April, Wilcoxon Rank Sum Test;  $p = 0.17$ ). The highest percentage residence time spent in the river channel (Figure 10B) was recorded in the week starting with the 8 August 2020, with 58% of total time spent in the river channel ( $n = 32$  of in total 35 individuals detected). The lowest residence time spent in the river channel (13%) was recorded in the first week of November 2020 ( $n = 8$  of in total 29 individuals detected). From 19 December 2020 to 13 February 2021 the residence time varied from 26-37% of total time, and about half of all detected fish were spending time in the river channel. In the summer months of 2021, 30-40% of total time was spent in the river channel.

In Orkanger, the highest residence time in the habitat characterized as other (including receivers in the fjord habitat) was recorded in the summer, with 38% of total time spent in the fjord during the second week of July (Figure 10A). In Orkanger, tagged sea trout were only detected in this habitat from April to mid October. In Stjørdal, tagged sea trout were detected in the fjord through all seasons, nevertheless, with a lower average weekly time spent during the winter (November-April) than in the summer (May-September, Wilcoxon Rank Sum Test;  $p = 0.02$ ). The highest residence time in the fjord, was recorded in June 2021 (Figure 10B), with 43% of total time spent in the fjord ( $n = 36$  of 61 detected individuals). Residence time in the fjord decreased into the autumn with only 1% residence time recorded the first week of August, and only two of 42 detected fish, spending time in the habitat.

In Stjørdal, 79% of total time was spent upstream the river first week of October, with corresponding 25 of 29 individuals detected (Figure 10B). Time spent upstream the river decreased through the winter period and reached a minimum level at 1% in the last week of May and first week of June 2021. In River Orkla in Orkanger, no receivers were placed upstream the river, and similar calculations could not be done.



**Figure 10:** Weekly residence time in different habitats for study population A) Orkanger (April 2020-April 2021) and B) Stjørdal (2020-August 2021), given in percent of total time. Habitats are presented by different colours. NB the scale of the x-axes differs between panel A and B.

### 3.5 Probability of presence in estuary vs. adjacent fjord

Generalized linear models were made to explore the effect of sex, total body length, date, and mean daily water temperature experienced by the fish on the probability of presence in the estuary versus adjacent fjord areas. In Orkanger, the model selection resulted in four equally well fitted models ( $\Delta\text{AICc} < 2$ ) exploring the probability of presence in estuary versus adjacent fjord areas (Table 4). All of the best models included date and mean daily water temperature experienced by the fish as explanatory variables. In addition, sex and total body length were included in some of the best models. In Stjørdal, two binomial regression models were equally well fitted, exploring the presence in estuarine versus adjacent fjord areas (Table 5). The models indicated that mean daily water temperature experienced by the fish, date, sex, and total body length influenced whether the sea trout were present in the estuary or in the nearby fjord ( $\Delta\text{AICc} < 2$ , Table 5). The explanatory variables date, experienced water temperature, and sex were included in both of the two best models.

In Orkanger, the estimates from the model averaging (Figure 11A) indicated a temperature difference between the estuary and adjacent fjord areas, where recorded water temperature experienced by the fish in the estuary were higher than in adjacent fjord areas. The probability of presence in the estuary increased with increasing date during the period May-August. Further, the probability of residence of males in the estuary was lower than the probability of residence of females, and smaller fish were more likely to reside in the estuary than larger individuals. However, the standard errors of the estimates of sex and body length were relatively large (Table A1, Appendix). For the study population in Stjørdal, the model conditional averaging showed that fish with a higher mean daily water temperature experienced by the fish were more likely to stay in the river estuary than in the nearby fjord areas in the time period May-August 2021 (Figure 11B). The probability of staying in the estuary decreased with increasing date from May throughout August. The probability of presence of males in the estuary was higher than the probability of females. In addition, the conditional model averaging indicated that total body length had limited effect as the standard error was close to the estimate value (Table A2, Appendix).

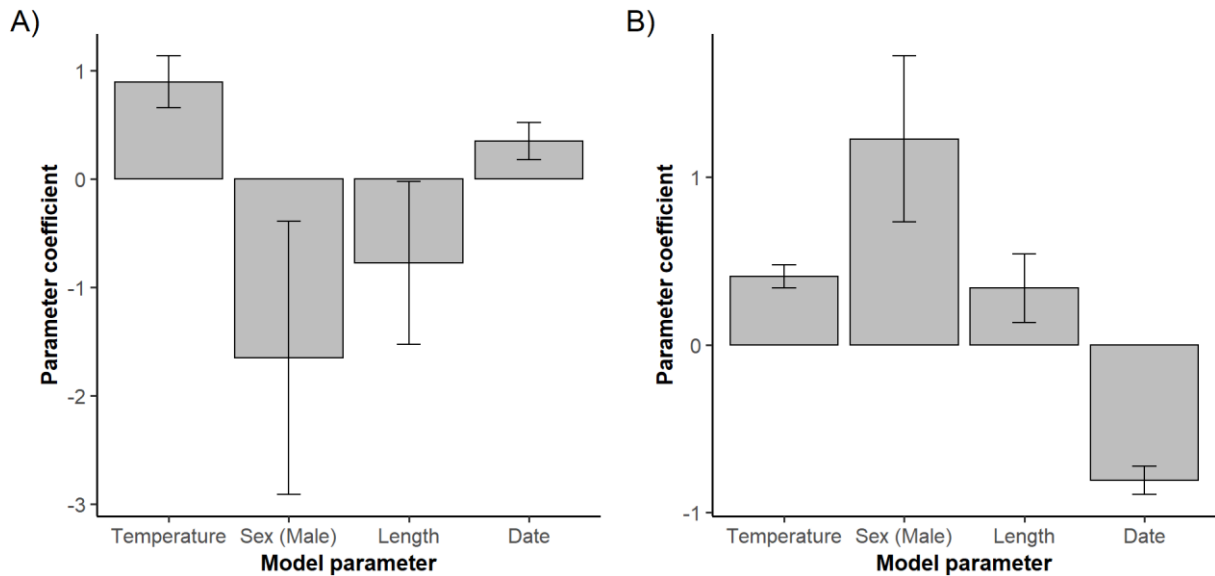
**Table 4:** Models estimating the determinants for presence in estuarine areas in Orkanger versus nearby fjord areas, from May throughout August 2020. Based on the explanatory variables mean daily water temperature experienced by the fish (T), date (D), sex (S), and total body length (L). The models are ranked by decreasing  $\Delta\text{AICc}$  value, with supported models on grey background ( $\Delta\text{AICc} < 2$ ). df is the number of parameters.

Model	AICc	$\Delta$ AICc	AICc Weights	df
[T, D]	609.6	0.00	0.234	4
[T, D, S]	609.7	0.13	0.220	5
[T, D, L]	610.4	0.81	0.157	5
[T, D, S, L]	610.8	1.24	0.126	6
[T]	611.7	2.09	0.082	3
[T, S]	611.8	2.24	0.077	4
[T, L]	612.4	2.84	0.057	4
[T, S, L]	612.9	3.29	0.045	5
[D]	621.9	12.30	0.001	3



**Table 5:** Models estimating the determinants for presence in the estuary in Stjørðdal versus nearby fjord areas, from May throughout August 2021. Based on the explanatory variables mean daily water temperature experienced by the fish (T), date (D), sex (S), and total body length (L). The models are ranked by decreasing  $\Delta AICc$  value, with supported models on grey background ( $\Delta AICc < 2$ ). df is the number of parameters.

Model	AICc	$\Delta AICc$	AICc Weights	df
[T, D, S, L]	3202.5	0.00	0.507	6
[T, D, S]	3203.1	0.63	0.370	5
[T, D]	3206.5	4.05	0.067	4
[T, D, L]	3206.9	4.39	0.056	5



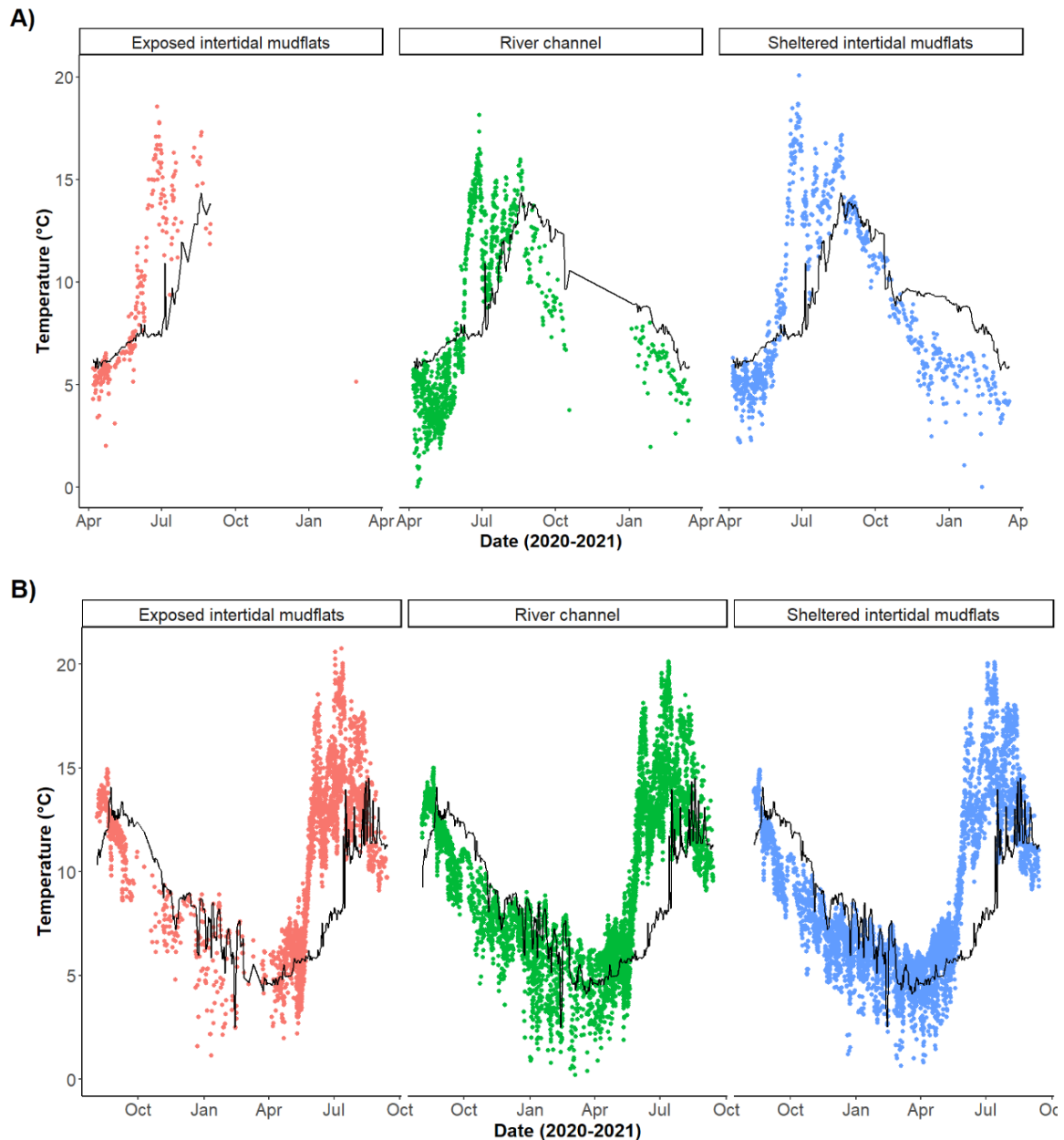
**Figure 11:** Estimated effects of mean daily water temperature experienced by the fish, sex (male), total body length, and date on probability of presence in estuaries A) Orkanger, and B) Stjørðdal, based on conditional model averaging ( $\Delta AICc < 4$ ). A positive parameter coefficient indicates a positive relationship between the parameter and the probability of presence in estuarine areas. Error bars show standard error of each parameter coefficient.

### 3.6 Temperature use

In Orkanger from April throughout May, the mean daily water temperature experienced by the fish in the exposed mudflats, river channel and sheltered mudflats were 6.0 °C (SD = 1.0 °C), 4.3 °C (SD = 1.3 °C), and 5.2 °C (SD = 1.0 °C), respectively. The mean daily temperature of marine water at approximately 10 meters depth in the exposed mudflats (receiver O10) was 6.5 °C (SD = 0.4 °C) in the same time period. From June throughout August 2020, the mean daily water temperature experienced by the fish in the exposed mudflats, river channel and sheltered mudflats were 13.2 °C (SD = 2.8 °C), 11.0 °C (SD = 3.2), and 10.7 °C (SD = 4.1 °C), respectively. The mean daily temperature of marine water was 9.5 °C (SD = 2.3 °C) in the same time period. The tagged sea trout in Orkanger experienced through the study period a mean daily temperature range in the exposed mudflats, river channel and sheltered mudflats from 2.0 °C-18.6 °C, 0.0 °C-18.1 °C, and 0.0 °C-20.1 °C, respectively (Figure 12A).

In Stjørðdal from September 2020 to May 2021, the mean daily water temperature experienced by the fish in the exposed mudflats, river channel and sheltered mudflats were 7.9 °C (SD = 2.7 °C), 7.2 °C (SD = 2.5 °C) and 6.5 °C (SD = 1.9 °C), respectively. The mean daily temperature of marine water at 16 meters depth at receiver H7 was 7.9 °C (SD = 2.6 °C) in the same time

period. From May to August 2021, the mean daily water temperature experienced by the fish in the exposed mudflats, river channel and sheltered mudflats were 11.1 °C (SD = 4.2 °C), 10.3 °C (SD = 4.3 °C) and 9.0 °C (SD = 4.5 °C), respectively. The mean daily temperature of marine water was 6.7 °C (SD = 2.0 °C) in the same time period. The tagged sea trout in Stjørðal experienced through the study period a mean daily temperature range in the exposed mudflats, river channel and sheltered mudflats from 1.1 °C-20.8 °C, 0.2 °C-20.1 °C, and 0.6 °C-20.1 °C, respectively (Figure 12B).



**Figure 12:** Experienced water temperature by the tagged sea trout in A) Orkanger (April 2020-April 2021), and B) Stjørðal (August 2020-August 2021), registered by internal transmitters. Habitats are represented by different colours and panels. Each dot represents mean daily water temperature experienced by a fish. Black line gives mean daily temperature in marine water registered at receiver A) O10 at approximately 10 meters depth, and B) H7 at approximately 16 meters depth. NB the scale of the x-axes differs between panel A and B.

### 3.7 Modelling temperature use

Influence of sex, total body length, season, and zone on the water temperature experienced by the fish was tested for the study populations in Orkanger ( $n = 24$ , 1 May-31 August 2020) and Stjørdal ( $n = 73$ , 1 May-31 August 2021). Total body length was initially hypothesized to have an impact on the use of water temperatures in both estuaries and was included in the models together with sex, season and zone as explanatory variables.

In Orkanger, there were four equally well fitted models ( $\Delta\text{AICc} < 2$ , Table 6) exploring the water temperature experienced in the time period from May through out August 2020. The models indicated that experienced water temperature was influenced by a combination of date, zone, sex, and total body length. Date and zone were included as explanatory variables in all of the best models. For the study population in Stjørdal, three models were equally well fitted ( $\Delta\text{AICc} < 2$ , Table 7) exploring the temperature use. The models indicated that experienced water temperature was influenced by a combination of date, zone, sex, and total body length. Date and zone were included as explanatory variables in all of the best models.

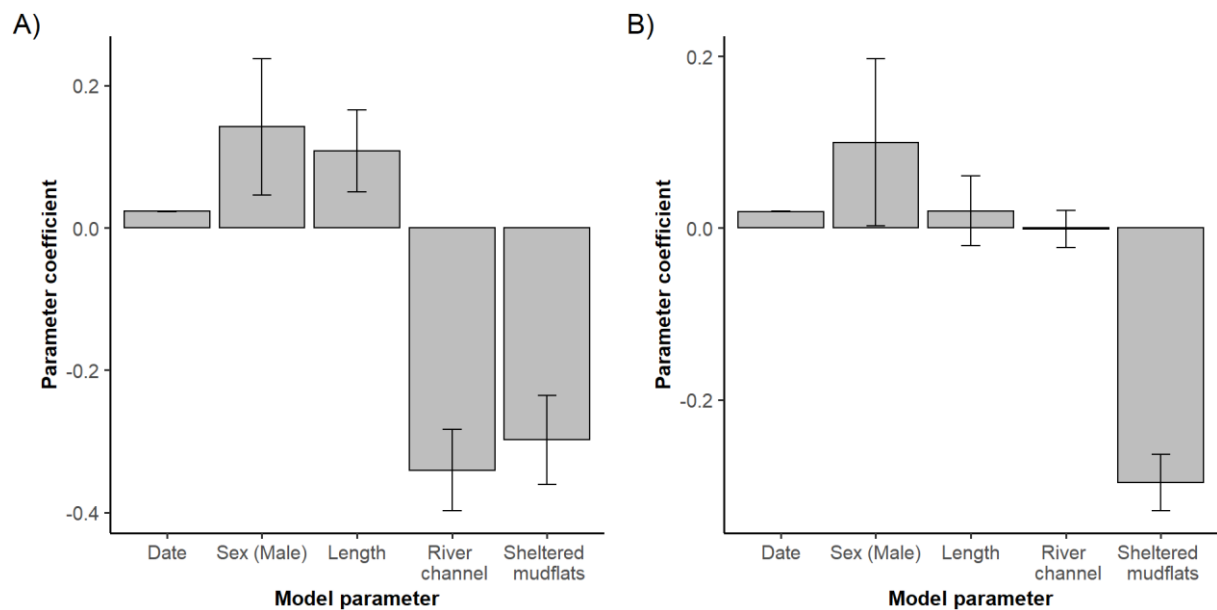
For both study populations, the conditional model averaging showed relatively large variation in intercept values compared to parameter estimates of the explanatory variables (date, zone, sex, and total body length), suggesting that these variables only explained a small part of the observed variation in experienced water temperature (Table A3 and A4, Appendix). However, for both study populations, the estimates from the conditional model averaging indicated a positive correlation between date and temperature use between May-August, with an increase in experienced temperatures from May to August (Figure 13A and B). In Orkanger, the estimated parameters indicated a difference in experienced water temperatures between habitats, where individuals in the exposed mudflats experienced higher mean daily water temperatures than individuals in the river channel and the sheltered mudflats during the time period May to August. In both estuaries, the estimated effects of sex and total body length showed that males and larger individuals utilized higher water temperatures. However, for the study population in Stjørdal the standard errors of the estimates of sex and total body length were relatively large. In Stjørdal, the model averaging showed that the estimated effect of the river channel had standard errors exceeding the parameters. However, estimated parameters indicated a difference in temperature use between the exposed- and sheltered mudflats, where individuals in the sheltered mudflats utilized lower water temperatures than individuals in the exposed mudflats (Figure 13B).

**Table 6:** Models for estimating water temperature experienced by the fish in Orkanger from May to August 2020, based on the explanatory variables date (D), zone (Z), sex (S), and total body length (L). The models are ranked by decreasing  $\Delta\text{AICc}$  value, with supported models on grey background ( $\Delta\text{AICc} < 2$ ). df is the number of parameters.

Model	AICc	$\Delta$ AICc	AICc Weights	df
[D, Z, L]	2231.0	0.00	0.341	7
[D, Z, S, L]	2231.0	0.04	0.335	8
[D, Z, S]	2232.2	1.19	0.188	7
[D, Z]	2232.8	1.83	0.136	6
[D, L]	2268.8	37.83	0.000	5
[D, S, L]	2269.3	38.35	0.000	6

**Table 7:** Models for estimating the water temperature experienced by the fish in Stjørdal from May to August 2021, based on the explanatory variables date (D), zone (Z), sex (S), and total body length (L). The models are ranked by decreasing  $\Delta\text{AICc}$  value, with supported models on grey background ( $\Delta\text{AICc} < 2$ ). df is the number of parameters.

Model	AICc	$\Delta\text{AICc}$	AICc Weights	df
[D, Z]	12207.7	0.00	0.440	6
[D, Z, S]	12208.7	1.00	0.267	7
[D, Z, L]	12209.5	1.82	0.177	7
[D, Z, S, L]	12210.4	2.67	0.116	8
[D]	12300.5	92.83	0.000	4
[D, S]	12301.2	93.51	0.000	5



**Figure 13:** Estimated effects of date, sex, total body length, and zone on water temperature experienced by the fish in A) Orkanger and B) Stjørdal, based on conditional model averaging ( $\Delta\text{AICc} < 4$ ). A positive parameter coefficient indicates a positive relationship with the daily temperature use in the two estuarine areas. Error bars show standard error of each parameter coefficient.

## 4. DISCUSSION

Estuarine areas are important habitats for anadromous brown trout and are in many areas used during all seasons (Jonsson & Jonsson, 2002; Jensen & Rikardsen, 2012; Lacroix, 2013). With increasing human activity, climate change impacts and pressure on estuarine ecosystems, knowledge on how sea trout utilize these habitats is important for well funded management and conservation efforts. The present study investigated the habitat use in two estuaries in Trøndelag county, by tracking tagged fish for a period of one year.

Sea trout were present in the estuary throughout the study period in both Orkanger and Stjørdal. The number of present individuals varied over the study period, but the estuary appeared to be a highly important habitat for the sea trout during all seasons. The defined estuary areas were rather small, and a long section upstream of the river mouths, influenced by the tides, were excluded from the term estuary for both study locations. Residence upstream the river mouths was not investigated, as river Orkla not had receivers placed upstream. Skjenaldelva is known for inhabiting a sea trout population (Foldvik *et al.*, 2017), thus, the tagged sea trout in Orkanger may have migrated upstream river Skjenaldelva to overwinter.

In Orkanger, 13% of the tagged individuals were detected in the estuary during the winter period, with estuarine overwintering individuals detected in the river channel and in the sheltered intertidal mudflats. In River Stjørdalselva, 61% of the tagged sea trout veterans was detected in the estuary during the winter months. These results indicated a difference in the proportion of estuarine overwintering individuals between the sea trout populations in Orkanger and Stjørdal. River Orkla and River Stjørdalselva are both relatively large rivers with good overwintering conditions and in such rivers, sea trout are known for returning to the river for spawning and overwintering (Jonsson, 1985). In rivers with poor overwintering conditions, often smaller rivers, many individuals may choose to stay in the estuary during the autumn and winter to utilize the sea for feeding (Jonsson & Jonsson, 2002; Knutsen *et al.*, 2004; Olsen *et al.*, 2006; Jensen & Rikardsen, 2008). Rikardsen *et al.* (2006) hypothesized that the harsh overwintering conditions upstream, made it more beneficial for sea trout to migrate to sea despite the risk of predation. The sea trout populations in Orkanger and Stjørdal were purely riverine where the stable overwintering lake environments was missing, and the advantages of residing in freshwater in relation to migrating to the estuaries might have been reduced (Jensen & Rikardsen, 2008). In addition, previous studies have suggested that in general, north Norwegian sea trout populations overwinter in freshwater (Berg & Berg, 1989), whereas southern populations are more frequently observed in marine habitats (Knutsen *et al.*, 2004; Olsen *et al.*, 2006). This tendency is assumed caused by the low marine water temperatures at higher latitudes, resulting in higher stress related to osmoregulation. However, several recent studies have showed that also northern populations utilize marine habitats during winter (Rikardsen *et al.*, 2006; Jensen & Rikardsen, 2008; 2012).

The sheltered intertidal mudflats were important areas for estuarine overwintering sea trout in both estuaries. The available overwintering habitats in each estuary may have been of different suitability, influenced by the hydrological conditions and the shape of the estuary. In Stjørdal, the sheltered intertidal mudflats were directly connected to the river channel, making it possible for the sea trout to move between the sheltered intertidal mudflats and the river channel without transferring through marine water masses with higher salinities. In Orkanger, the sheltered intertidal mudflats were physically separated from the river channel by the Grønøra-west

harbour area, requiring the fish to transfer in marine water masses between the two habitats. In both estuaries, overwintering individuals were likely exposed to stress in form of shifting salinities several times a day due to the tide, indicating that the sea trout at least were partly adapted to cold temperatures in brackish, and possibly also saltwater (Jensen & Rikardsen, 2008). However, the short distance between the sheltered mudflats and the river channel in Stjørdal, gave the sea trout the advantage of easily moving upstream during high tides when water masses reached unfavorable high salinities. Consequently, the sheltered mudflats in Langøra-south in Stjørdal, were suggested as a more suitable overwintering area for the sea trout than the sheltered mudflats in Orkanger. In addition, observations suggested that the sheltered mudflats in Orkanger and Stjørdal were in varying degree influenced by the tide, resulting in larger air exposed areas and lower water levels in the sheltered mudflats in Orkanger than in Stjørdal. Unpublished studies from Gaute Kjærstad showed that the sheltered mudflats in Stjørdal, had the highest number of benthic organisms compared to all estuary habitats in Stjørdal in the months March-November 2021, in addition to a different composition of benthic organisms than the exposed intertidal mudflat and the habitat upstream of the river mouth. Previous studies have shown that benthic feeding (crustacea and annelids) was more important for sea trout during the winter, while midwater and surface organisms (young fish and insects) were preferred in the summer (Pemberton, 1976). Hence, the sheltered mudflats may have provided more desirable feeding grounds during the winter months, compared to the upstream habitat and more marine areas.

One individual sea trout in Stjørdal was detected in the more marine fjord areas during the winter months, possibly seeking to optimize forage possibilities, in accordance with earlier studies (Knutsen *et al.*, 2004; Olsen *et al.*, 2006; Rikardsen *et al.*, 2006; Spares *et al.*, 2014). The tendency of overwintering in freshwater during the winter period, is thought to be driven by low salinity tolerance at low seawater temperatures (Koed *et al.*, 2007). However, sea trout have been shown to tolerate full-salinity at water temperatures as low as 1-2 °C (Rikardsen, 2004; Jensen & Rikardsen, 2012). It is suggested that the choice of overwintering habitat is regulated by the trade-off between risks and benefits (Jensen & Rikardsen, 2008; Halttunen *et al.*, 2013). In the estuarine habitat, sea trout can benefit from characteristics similar to those found in both marine and freshwater systems. As only one individual stayed in the fully marine environment during the winter, it was suggested that a higher proportion of individuals resided in the estuary, benefiting of both low-risk and increased feeding. A study by Spares *et al.* (2014) showed that the marine overwintering life-strategy appeared to be a feeding migration in which the sea trout continuously increased their body condition, representing an alternative to the more common overwintering strategy of starvation in freshwater. Marine feeding from autumn to spring has been shown as a valuable energy source, especially for sea trout whose condition factor has decreased after freshwater fasting and spawning (Rikardsen *et al.*, 2006). The present study included several individuals likely to have spawned the previous season, thus possibly willing to migrate to marine habitats in the winter period to increase their food availability and following condition factor. It is suggested that individual salmonids that can energetically afford to do so, overwinter in the river, whereas individuals with low energy reserves in harsh overwintering conditions immediately return to marine habitats after spawning (Rikardsen *et al.*, 2006; Halttunen *et al.*, 2013). Despite lower marine production during winter, there are prey (fish, amphipods, euphausiids) available in the marine habitat through all seasons (Halttunen *et al.*, 2013). Davidsen *et al.* (2014) found that sea trout, captured in the spring after overwintering and feeding in the estuary of River Snilldalselva, had a higher condition factor than sea trout captured in the same river the previous autumn. It was suggested that the findings indicated that

estuary overwintering sea trout experienced growth during the winter period. However, feeding in marine habitats at low temperatures during the winter months does not necessarily result in somatic growth. Stomach fullness of marine overwintering sea trout has been found to be at the highest during the winter period, indicating that the individuals fed, although the digestion virtually ceased at low temperatures (Spares *et al.*, 2014). A study on seasonal variation in marine growth by Olsen *et al.* (2006), showed no evidence of growth during winter, and suggested that the extended marine stay during winter may have trade-off benefits other than growth. Still, overwintering in marine habitats with no growth, may be of higher benefit than experiencing reduced condition in freshwater.

At both Orkanger and Stjørdal, the river channel was heavily used in the spring period from April 2020 in Orkanger and April 2021 in Stjørdal. In the first week of April, 63% of all detected fish in Orkanger and 51% of all detected fish in Stjørdal spent time in the river channel. The river channel was a natural transport route for marine migrating sea trout, after upstream overwintering during the winter months. The river channel was an important transition zone between the two habitats, with brackish water creating an intermediate environment with stepwise demands to full salinity tolerance (Wolanski & Elliott, 2016). Previous studies have suggested that sea trout typically stay close to the river mouth during the first weeks after entering the estuary (Jonsson & Jonsson, 2011), where the fish may actively seek preferred water layers separated by the halocline (Wang *et al.*, 2015; Thorstad *et al.*, 2016). With increasing water temperatures during the spring and summer period, an increasing number of sea trout was detected in more marine habitats, possibly due to more favorable water temperatures for the required osmoregulation in seawater and initiation of the main feeding and growth season of the sea trout.

From the spring towards summer, many sea trout utilized fjord areas outside the estuary, although there were fish utilizing the estuary also throughout the summer. During summer months the exposed intertidal mudflats were more frequently used than during the other seasons. About half of all detected individuals in both estuaries, visited the exposed intertidal mudflats during the summer, although with relatively short residence times. It is possible that the fish used the exposed intertidal mudflats to feed but resided in other habitats to digest and rest. In addition, the exposed mudflats in both estuaries, had large areas frequently exposed to air, making the area occasionally inaccessible for the sea trout and consequently limiting the possible time spent in the habitat. Exposed intertidal mudflats likely represent a valuable feeding area for species living in the estuaries and are regarded as vulnerable and decreasing habitats (Husa & Kutti, 2022). Unpublished data from Gaute Kjærstad showed a rich and diverse fauna of benthic organisms in the estuary of Stjørdalselva, where the exposed intertidal mudflats were dominated by Gammaridae, Nematoda and Oligochaeta. Knutsen *et al.* (2001) found that sea trout feeding in estuarine habitats, hunted smaller fish and invertebrates such as polychaetes, crustaceans and surface living arthropods. Several studies have showed that sea trout are opportunistic feeders that may take a wide variety of prey species and have large seasonal variation in diet and within habitats (Grønvik & Klemetsen, 1987; Knutsen *et al.*, 2001; Knutsen *et al.*, 2004). As a relatively large proportion of the marine prey typically are caught in shallow and brackish water and the sea trout prefer to use inner and warmer parts of the fjord to feed (Knutsen *et al.*, 2001; Rikardsen *et al.*, 2007b), it is plausible to suggest that the exposed intertidal mudflats were quite suitable feeding grounds in the summer period with high foraging opportunities as well as low predation risk. However, it is found an ontogenetic shift in feeding niche when the sea trout are about 25 cm long, where the fish becomes largely

piscivorous, hunting littoral and small pelagic fish (Knutsen *et al.*, 2001; Morinville & Rasmussen, 2006; Rikardsen *et al.*, 2007a). Thus, it is suggested that the sea trout veterans sought to the more marine areas during the summer months to feed on pelagic prey.

The sea trout in both study populations, spent relatively short time in the sheltered intertidal mudflats during the summer months. In Stjørdal, 6% of total time was spent in the sheltered intertidal mudflats in the start of August. As larger sea trout becomes more piscivorous (Jonsson & Jonsson, 2011; Davidsen *et al.*, 2017a), it is suggested that the sheltered intertidal mudflats in Stjørdal were of less interest during the summer months due to poorer forage opportunities than in more marine habitats. In addition, the shallow mudflats were quickly heated by sun radiation possibly causing unfavorable water temperatures. The study population in Orkanger, showed the same tendencies of habitat use during the summer months as the study population in Stjørdal. However, the sheltered intertidal mudflats at Råbygda may have provided a more diverse feeding habitat than the sheltered mudflats in Stjørdal due to the freshwater influx of River Skjenaldelva. A study by Strøm *et al.* (2021) found that variation in migratory behaviour were likely influenced by spatiotemporal differences in habitat quality between sites, indicating that local habitat variation may promote populations-specific responses.

In present study, residence time in the estuary versus adjacent fjord areas in the summer months was influenced by date and mean daily water temperature experienced by the fish, for both study populations. The estuary may have offered a habitat minimizing stress related to osmoregulation, lower predation risk and temperatures closer to the optimal growth temperature (Jonsson & Jonsson, 2011). Still, temperatures in the shallow areas of the estuaries, occasionally exceeded the optimal growth temperature during the summer months, causing unfavorable environmental conditions. The adjacent fjord areas had higher salinities, demanding higher efforts in osmoregulation, as well as a possibly higher experienced predation pressure and exposure to diseases (Bordeleau *et al.*, 2018). Nevertheless, the marine habitat may have offered better foraging conditions and less competition for space and food. Pemberton (1976) found that the availability of food was the main factor influencing the presence or absence of trout. The models conducted in present study, indicated a higher experienced temperature for sea trout resident in the estuary than in the fjord areas. The estuarine water masses had a temperature shift in May-June where temperatures experienced by the fish exceeded marine water temperatures and remained higher throughout the summer. These results may indicate that the sea trout resided in water layers consisting of brackish water, holding a different temperature than the marine water masses, possibly to limit the energy use on osmoregulation, which is higher in the salinities experienced in marine water masses (McCormick & Saunders, 1987).

The effect of date on the probability of presence in the estuary was inconsistent between the two study populations, indicating that the likelihood for presence in the estuary increased from May to August in Orkanger, whereas the opposite effect was observed in Stjørdal. However, the standard error of the estimate in Orkanger was relatively large, indicating a limited effect on the probability of presence in the estuary. In Stjørdal, date was found negative correlated to the probability of presence in the estuary, indicating that the probability of presence decreased with date, from May to August. This tendency was consistent with the number of fish detected in the estuary from May with a decrease towards September. A large number of individuals was detected in the river channel during spring, possibly explained by migration towards marine habitats after spawning and overwintering in the river (Thorstad *et al.*, 2016). Through the summer and autumn, the number of detected individuals decreased, possibly explained by the



upstream river migration. The timing of the upstream migration shows good conformity with earlier literature (Jonsson & Jonsson, 2002; Sjørnsen *et al.*, 2020; Norderud *et al.*, 2021; Sjørnsen *et al.*, 2021), with a relatively wide range of starting date for the upstream migration, from April to December. The model also indicated higher likelihood for presence in adjacent fjord areas as date increased, which may be a consequence of individuals leaving the estuary for upstream migration, and remaining individuals seeking an alternative overwintering strategy in the fjord system (Knutzen *et al.*, 2004; Jensen & Rikardsen, 2008).

The models in the present study provided some but limited support to the influence of total body length and sex on habitat use in terms of staying in the estuary versus fjord. Sex and total body length had limited effect on use of the two habitats in Orkanger. In Stjørdal, the probability of presence of males in the estuary were higher than the probability of females. Several studies have showed that females were more likely to migrate to the sea than males, instead of remaining in the estuarine areas of the rivers (Bordeleau *et al.*, 2018; Eldøy *et al.*, 2021). The increased feeding opportunities in marine areas are possibly of greater benefit to females than males due to the strong correlation between female body size and the number of eggs produced (Elliott, 1995). Thus, to optimize the reproductive success, females actively sought the more productive foraging areas in the fjord to enhance growth. The reproductive success of males are shown not as size dependent as for females, although a larger body size may be a competitive advantage during mating (Fleming & Reynolds, 2004). When choosing marine habitat, the balance between feeding opportunity and survival in the estuary may be favorable for males, while females may have stronger benefits of longer and more risky migrations to maximize growth.

Total body length was not identified as an important factor for the probability of presence in the estuary versus adjacent fjord areas in the time period from May to August. However, it is possible that body length had a larger effect on habitat use during the first period at sea after marine migration in the time period from April to May, not revealed by the models. The predation pressure in the different habitats were suggested as part of the trade-off between optimizing fitness and reduce risks (Thorstad *et al.*, 2016). Several studies show that experienced predation pressure is correlated to body size (Dieperink *et al.*, 2001; Dieperink *et al.*, 2002; Flaten *et al.*, 2016). Smaller individuals would be more vulnerable than larger individuals to the increased predation pressure caused by gulls *Larus* spp., cormorants *Phalacrocorax carbo* (L.), harbour seals *Phoca vitulina* L. and gadids present outside the river outlet (Koed *et al.*, 2006; Jonsson & Jonsson, 2009a; Suuronen & Lehtonen, 2012). As smaller individuals have a lower probability of survival due to poorer swimming performance, osmoregulatory ability and sensor perception (Fuiman & Magurran, 1994; Finstad & Ugedal, 1998), it is suggested that smaller individuals would benefit of being resident closer to the estuary with lower salinities and shelter providing protection from predators (Werner & Hall, 1988; Petersson & Järvi, 2006). However, the present study found no correlation between total body length and choice of habitat (estuary versus fjord). Both study sites included a relatively short marine distance, with receivers placed a few kilometers out from the river mouth. Correlations between individual biological characteristics, as sex and total body length, could be clearer if receivers placed further out in the fjord were included. This would have required a longer and tougher migration distance for the sea trout, possibly revealing more distinct characteristics of fish physically able and favoured to conduct this migration (Flaten *et al.*, 2016).

The water temperatures experienced by the fish in both study populations, were only to a small degree explained by the explanatory variables (date, zone, sex, and total body length), suggesting that other variables not included in the models were of higher importance. The experienced temperatures in the estuarine habitats ranged from 2 °C-21 °C for both study populations in the time period May to August. Temperature is known to be an important abiotic factor influencing the metabolic process and growth in fish (Jonsson & Jonsson, 2011), and sea trout have been found to prefer water temperatures closely related to their optimal temperature for growth at approximately 16 °C (Forseth & Jonsson, 1994; Larsson, 2005; Elliott & Elliott, 2010). Sea trout were detected in all estuarine habitats during summer, despite water temperatures occasionally exceeding favorable temperatures. Therefore, it was assumed that the habitat choice was influenced by a trade-off including several external factors, such as salinity, temperature, food availability and predation pressure. For migrating sea trout, estuarine habitats are generally regarded as having three primary advantages, which are productive foraging, relative refuge from predators, and an intermediate environment with stepwise change in demands of osmoregulation (Thorpe, 1994; Jensen & Rikardsen, 2012; Thorstad *et al.*, 2016). Thus, the sea trout may have chosen to reside in the estuarine habitats despite relatively high water temperatures. Jensen *et al.* (2014) found that the likelihood for finding sea trout in the outer areas of the fjord started to increase when water temperatures in the inner parts of the fjord was measured to around 14 °C. In addition, several studies have showed that sea trout tended to reside in deeper water layers as the surface water increased in temperature (Eldøy *et al.*, 2017; Kristensen *et al.*, 2018), and performing deeper dives when water temperature exceed 17 °C (Kristensen *et al.*, 2018). However, present study did not investigate depth use.

For both study populations, zone had the strongest effect on mean daily water temperature experienced by the fish, in the time period from May to August. For the study population in Orkanger, the conditional model average indicated a difference in the experienced water temperatures between individuals in the exposed intertidal mudflats and the two other estuarine habitats, the river channel and sheltered mudflat, where individuals experienced higher water temperatures in the exposed mudflats. A similar tendency was shown by the model averaging for the study population in Stjørdal, where individuals present in the exposed mudflats and the river channel experienced higher water temperatures than individuals present in the sheltered mudflats. These differences in experienced temperatures between habitats may be explained by other factors or benefits supplied by the habitat. It is suggested that the sea trout in Orkanger transferred from the river channel and the sheltered mudflats when temperatures exceeded preferred temperatures, because the habitats not provided other benefits more important than the temperature. Contrary, the sheltered mudflats may have provided better forage availability, resulting in a prolonged residency despite unfavorable temperatures. Hence, experienced water temperatures may have depended on the preferred temperatures of prey and not the preferred temperature of the sea trout. A previous study has shown that the relationship between temperature and habitat use not corresponded to the species optimal growth temperatures, but to their previously documented temperature preferences (Jensen *et al.*, 2014). These results suggest a possible adaptation to local environments, where the optimal and preferred temperatures may vary among populations and within fish size (Elliott & Elliott, 2010).

For the study population in Stjørdal, total body length and sex were not identified as important factors explaining the water temperature experienced by the fish in the time period May to August. It was initially hypothesized that shorter fish used water with higher temperatures than larger fish, thus actively seeking habitats with higher temperatures, compared to larger

individuals. This behaviour would have been explained by a difference in optimal growth temperatures between smaller and larger individuals (Jonsson & Jonsson, 2009b), in addition to the fact that ionic regulation at low temperature in sea water is easier for large than small fish (Tanguy *et al.*, 1994; Ugedal *et al.*, 1998). However, modeling the water temperatures experienced by the fish in Stjørdal, based on measurements from internal transmitters, showed no correlation between experienced water temperature and total body length. Contrary, for the study population in Orkanger, sex and total body length were identified as factors influencing the experienced water temperature by the sea trout. The estimates of sex and total body length were positive correlated to temperature, indicating that males and larger individuals experienced higher temperatures than females and smaller individuals. As earlier mentioned, females have been found to have a higher tendency to migrate to the sea than males, due to the female fecundity increasing with size (Jonsson & Jonsson, 1993; Elliott, 1995; Eldøy *et al.*, 2021). Thus, males remaining in the estuary would experience water masses with higher temperatures than females migrating to more marine areas during the summer. Although several studies have suggested an optimal growth temperature at 16 °C (Larsson, 2005; Elliott & Elliott, 2010), a higher optimum growth temperature has been suggested for individuals with increased energy intake (Elliott & Hurley, 2000). The studies by Elliott and Hurley (2000) and Forseth and Jonsson (1994) showed that the optimum temperature for growth are strongly linked to energy intake. As larger sea trout are found to have a more energy rich piscivorous diet in the marine habitat, the optimal temperature for growth may also increase for larger individuals.

From April throughout May 2020, the tagged sea trout present in all estuarine habitats in Orkanger resided in water masses with an average temperature lower than the average temperature in marine water masses. Melt water influx in River Orkla and River Skjenaldelva may have created a colder fresh- and brackish water layer over the warmer, more marine, and denser water masses in the estuary. This tendency was also observed in Stjørdal, where the sea trout resided in water masses with an average temperature lower than marine water, during the winter and spring. The CTD-measurement from the river channel in River Stjørdalselva in late April 2021, showed a clear distinction between the two water layers. After decreased melt water influx in the spring, a shift in temperature was observed and the sea trout resided in water masses with a higher average temperature than in marine water. The temperature use demonstrated their preference for water masses with lower salinities, possibly to minimize stress related to osmoregulation.

In conclusion, the present study shows that estuarine habitats are important areas for sea trout during all seasons. Findings indicated that the study population in Stjørdal had a higher proportion of estuarine overwintering individuals than the study population in Orkanger. Local adaptations and distinct overwintering strategies were plausible explanations to the observed difference between the study populations. The estuaries were shaped and influenced by abiotic factors in different ways and in varying degrees, providing habitats of varying suitability for overwintering. Even though the numbers of estuarine overwintering sea trout in present study must be regarded as minimum numbers, the study shows that estuarine areas can be important for sea trout populations during the winter, in accordance with several studies (Knutsen *et al.*, 2004; Jensen & Rikardsen, 2012). It is therefore likely to assume that the sea trout can be negatively affected by anthropogenic pressure in coastal areas during the winter. During the summer, the sea trout had a relatively high residence time in the estuarine habitats. Individuals residing in brackish water in the estuary may have benefited of reduced stress related to osmoregulation and possibly avoided exposure to pathogens and lice from aquaculture sites

further out in the fjord. In a management perspective, the knowledge provided by this study highlights the importance of investigating the habitat use in estuaries on a spatial and temporal scale. It is shown that the estuaries provided several microhabitats that were utilized in different seasons and consequently to different purposes. As estuarine habitats are under a continuous and increasing pressure from coastal development, knowledge on sea trout habitat use is essential for management and conservation efforts.

## 5. REFERENCES

- Angilletta Jr, M. J., Niewiarowski, P. H. & Navas, C. A. (2002). The evolution of thermal physiology in ectotherms. *Journal of thermal Biology* **27**, 249-268.
- Anon (2022). Klassifisering av tilstanden til sjøørret i 1279 vassdrag. In *Temarapport fra Vitenskapelig råd for lakseforvaltning*, 170 p. Trondheim.
- Berg, O. K. & Berg, M. (1989). The duration of sea and freshwater residence of the sea trout, *Salmo trutta*, from the Vardnes River in northern Norway. *Environmental biology of fishes* **24**, 23-32.
- 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.
- Burnham, K. P. & Anderson, D. R. (2003). *Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach*. 488 p. New York, NY: Springer New York, New York.
- Burnham, K. P., Anderson, D. R. & Huyvaert, K. P. (2011). AIC model selection and multimodel inference in behavioral ecology: some background, observations, and comparisons. *Behavioral ecology and sociobiology* **65**, 23-35.
- Dahl, K. (1910). *Alder og vekst hos laks og ørret belyst ved studiet av deres skjæl*. 16-25 p. Kristiania.
- Davidsen, J. G., Eldøy, S. H., Sjørnsen, A. D., Rønning, L., Thorstad, E. B., Næsje, T. F., Uglem, I., Aarestrup, K., Whoriskey, F. & Rikardsen, A. (2014). Habitatbruk og vandringer til sjøørret i Hemnfjorden og Snillfjorden. *NTNU Vitenskapsmuseet naturhistorisk rapport* **6**, 1-55.
- Davidsen, J. G., Knudsen, R., Power, M., Sjørnsen, A. D., Rønning, L., Hårsaker, K., Næsje, T. F. & Arnekleiv, J. V. (2017a). 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., Sjørnsen, A. D., Rønning, L., Davidsen, A. S. G. & Daverdin, M. (2017b). Kartlegging av sjøørret i habitatområde ved utløpet av Stjørdalselva, Nord-Trøndelag og konsekvensanalyse av tre utfyllingsalternativer. *NTNU Vitenskapsmuseet naturhistorisk rapport* **4**, 32.
- Davidsen, J. G., Sjørnsen, A. D. & Davidsen, A. S. G. (2021a). Utbygging av Orkanger havn - kartlegging av områdebruk til sjøørret og forslag til kompenserende tiltak. *NTNU Vitenskapsmuseet naturhistorisk rapport* **6**, 29.
- Davidsen, J. G., Sjørnsen, A. D., Rønning, L., Davidsen, A. S. G., Eldøy, S. H., Daverdin, M. & Kjærstad, G. (2021b). Utbygging av ny E6 ved Hellstranda – kartlegging av områdebruk til sjøørret og laks, samt forslag til kompenserende tiltak. *NTNU Vitenskapsmuseet naturhistorisk rapport* **10**, 63.
- Dieperink, C., Pedersen, S. & Pedersen, M. I. (2001). Estuarine predation on radiotagged wild and domesticated sea trout (*Salmo trutta* L.) smolts: Estuarine predation on smolts. *Ecology of freshwater fish* **10**, 177-183.
- 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**.
- Eldøy, S. H., Davidsen, J. G., Thorstad, E. B., Whoriskey, F., Aarestrup, K., Næsje, T. F., Rønning, L., Sjørnsen, A. D., Rikardsen, A. H. & Arnekleiv, J. V. (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., Naesje, 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: marine depth use of *salmo trutta*. *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.
- Elliott, J. M. (1995). Fecundity and egg density in the redd for sea trout. *Journal of Fish Biology* **47**, 893-901.
- 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. *J Fish Biol* **77**, 1793-1817.
- Finstad, B. & Ugedal, O. (1998). Smolting of sea trout (*Salmo trutta* L.) in northern Norway. *Aquaculture* **168**, 341-349.
- Finstad, B., Økland, F., Thorstad, E. B., Bjørn, P. A. & McKinley, R. S. (2005). Migration of hatchery-reared Atlantic salmon and wild anadromous brown trout post-smolts in a Norwegian fjord system. *Journal of Fish Biology* **66**, 86-96.
- Flaten, A. C., Davidsen, J. G., Thorstad, E. B., Whoriskey, F., Rønning, L., Sjørnsen, A. D., Rikardsen, A. H. & Arnekleiv, J. V. (2016). The first months at sea: marine migration and habitat use of sea trout *Salmo trutta* post-smolts. *J Fish Biol* **89**, 1624-1640.
- Fleming, I. A. (1998). Pattern and variability in the breeding system of Atlantic salmon (*Salmo salar*), with comparisons to other salmonids. *Canadian journal of fisheries and aquatic sciences* **55**, 59-76.
- Fleming, I. A. & Reynolds, J. D. (2004). *Salmonid breeding systems*. 264-294 p. New York.
- Foldvik, A., Einum, S., Finstad, A. G. & Ugedal, O. (2017). Linking watershed and microhabitat characteristics: effects on production of Atlantic salmonids (*Salmo salar* and *Salmo trutta*). *Ecology of freshwater fish* **26**, 260-270.
- Forseth, T. & Jonsson, B. (1994). The Growth and Food Ration of Piscivorous Brown Trout (*Salmo trutta*). *Functional ecology* **8**, 171-177.
- Froese, R. (2006). Cube law, condition factor and weight-length relationships: history, meta-analysis and recommendations. *Journal of applied ichthyology* **22**, 241-253.
- Froneman, W. (2018). *Estuary*. 126 p. London.
- Fuiman, L. A. & Magurran, A. E. (1994). Development of predator defences in fishes. *Reviews in fish biology and fisheries* **4**, 145-183.
- Grønvik, S. & Klemetsen, A. (1987). Marine food and diet overlap of co-occurring Arctic charr *Salvelinus alpinus* (L.), brown trout *Salmo trutta* L. and Atlantic salmon *S. salar* L. off Senja, N. Norway. *Polar biology* **7**, 173-177.
- Halttunen, E., Jensen, J. L. A., Næsje, T. F., Davidsen, J. G., Thorstad, E. B., Chittenden, C. M., Hamel, S., Primicerio, R. & Rikardsen, A. H. (2013). State-dependent migratory timing of postspawned Atlantic salmon (*Salmo salar*). *Canadian journal of fisheries and aquatic sciences* **70**, 1063-1071.
- Heinimaa, S. & Heinimaa, P. (2004). Effect of the female size on egg quality and fecundity of the wild Atlantic salmon in the sub-arctic River Teno. *Boreal environment research* **9**, 55-62.

- Husa, V. & Kutti, T. (2022). Forslag til metode for kartlegging av sårbare arter og naturtyper på grunt vann (0-50 meters dyp) til søknader om akvakultur i sjø-Kunnskapsleveranse til Fiskeridirektoratet. *Rapport fra havforskningen* **9**, 34.
- 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. (2012). Archival tags reveal that Arctic charr *Salvelinus alpinus* and brown trout *Salmo trutta* can use estuarine and marine waters during winter. *J Fish Biol* **81**, 735-749.
- 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*. *J Fish Biol* **84**, 1640-1653.
- Jiang, Y., Kirkman, H. & Hua, A. (2001). Megacity development: managing impacts on marine environments. *Ocean & coastal management* **44**, 293-318.
- 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. (2009a). Migratory timing, marine survival and growth of anadromous brown trout *Salmo trutta* in the River Imsa, Norway. *J Fish Biol* **74**, 621-638.
- Jonsson, B. & Jonsson, N. (2009b). 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. *J Fish Biol* **75**, 2381-2447.
- Jonsson, B. & Jonsson, N. (2011). *Ecology of Atlantic Salmon and Brown Trout : Habitat as a template for life histories*. 708 p. Netherlands.
- Jonsson, N. & Jonsson, B. (2002). Migration of anadromous brown trout *Salmo trutta* in a Norwegian river. *Freshwater biology* **47**, 1391-1401.
- Jordan, S. J. (2012). *Estuaries : classification, ecology, and human impacts*. p. Hauppauge, NY: Nova Science Publishers.
- Kennish, M. J. (2002). Environmental threats and environmental future of estuaries. *Envir. Conserv* **29**, 78-107.
- 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. A., Knutsen, H., Gjørseter, J. & Jonsson, B. (2001). Food of anadromous brown trout at sea. *Journal of Fish Biology* **59**, 533-543.
- Knutsen, J. A., Knutsen, H., Olsen, E. M. & Jonsson, B. (2004). Marine feeding of anadromous *Salmo trutta* during winter. *Journal of Fish Biology* **64**, 89-99.
- Koed, A., Baktoft, H. & Bak, B. D. (2006). Causes of mortality of Atlantic salmon (*Salmo salar*) and brown trout (*Salmo trutta*) smolts in a restored river and its estuary. *River Res. Applic* **22,17**, 69-78.
- Koed, A., Nielsen, C., Madsen, S. S. & Thomsen, D. 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.
- Kristensen, M. L., 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**, 209-224.

- Kristensen, M. L., Pedersen, M. W., Thygesen, U. H., Del Villar-Guerra, D., Baktoft, H. & Aarestrup, K. (2019). Migration routes and habitat use of a highly adaptable salmonid (sea trout, *Salmo trutta*) in a complex marine area. *Animal biotelemetry* **7**, 1-13.
- Lacroix, G. L. (2013). Population-specific ranges of oceanic migration for adult Atlantic salmon (*Salmo salar*) documented using pop-up satellite archival tags. *Canadian journal of fisheries and aquatic sciences* **70**, 1011-1030.
- 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.
- Lea, E. (1910). Contributions to the methodics in herring-investigation. *ICES Journal of Marine Science* **1**, 7-33.
- Liu, Y., Bailey, J. L. & Davidsen, J. G. (2019). Social-cultural ecosystem services of sea trout recreational fishing in Norway. *Frontiers in Marine Science* **6**.
- Magnuson, J. J., Crowder, L. B. & Medvick, P. A. (1979). Temperature as an ecological resource. *American zoologist* **19**, 331-343.
- McCormick, S. D. & Saunders, R. L. (1987). Preparatory physiological adaptations for marine life of salmonids: osmoregulation, growth, and metabolism. *American Fisheries Society Symposium* **1**, 211-229.
- McCormick, S. D. (2001). Endocrine control of osmoregulation in teleost fish. *American zoologist* **41**, 781-794.
- Middlemas, S. J., Stewart, D. C., Mackay, S. & Armstrong, J. D. (2009). Habitat use and dispersal of post-smolt sea trout *Salmo trutta* in a Scottish sea loch system. *J Fish Biol* **74**, 639-651.
- Moksness, E., Dahl, E. & Støttrup, J. G. (2013). *Global challenges in integrated coastal zone management*. 260 p. Ames, Iowa: Wiley-Blackwell.
- Moore, A., Bendall, B., Barry, J., Waring, C., Crooks, N. & Crooks, L. (2012). River temperature and adult anadromous Atlantic salmon, *Salmo salar*, and brown trout, *Salmo trutta*: Temperature and salmonids. *Fisheries management and ecology* **19**, 518-526.
- Morinville, G. R. & Rasmussen, J. B. (2006). Marine feeding patterns of anadromous brook trout (*Salvelinus fontinalis*) inhabiting an estuarine river fjord. *Canadian journal of fisheries and aquatic sciences* **63**, 2011-2027.
- Nevoux, M., Finstad, B., Davidsen, J. G., Finlay, R., Josset, Q., Poole, R., Höjesjö, J., Aarestrup, K., Persson, L., Tolvanen, O. & Jonsson, B. (2019). Environmental influences on life history strategies in partially anadromous brown trout (*Salmo trutta*, Salmonidae). *Fish and fisheries* **20**, 1051-1082.
- Norderud, N., Davidsen, J. G. & Eldøy, S. H. (2021). River migration of sea trout *Salmo trutta* in River Beiarelva, Northern Norway. 37 p.: NTNU.
- Ojanguren, A. F., Reyes-Gavilán, F. G. & Braña, F. (2001). Thermal sensitivity of growth, food intake and activity of juvenile brown trout. *J Therm Biol* **26**, 165-170.
- Olsen, E. M., Knutsen, H., Simonsen, J. H., Jonsson, B. & Knutsen, J. A. (2006). Seasonal variation in marine growth of sea trout, *Salmo trutta*, in coastal Skagerrak. *Ecology of freshwater fish* **15**, 446-452.
- Pemberton, R. (1976). Sea trout in North Argyll sea lochs: II. diet. *Journal of Fish Biology* **9**, 195-208.
- Petersson, E. & Järvi, T. (2006). Anti-predator response in wild and sea-ranched brown trout and their crosses. *Aquaculture* **253**, 218-228.
- Pincock, D. G. (2012). False detections: what they are and how to remove them from detection data. *Vemco Application Note* **902**, 1-11.



- Pinheiro J, B. D., R Core Team (2022). nlme: Linear and Nonlinear Mixed Effects Models. R package version 3.1-157, 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/>.
- Ricker, W. E. (1975). Computation and interpretation of biological statistics of fish populations. *Journal of the Fisheries Research Board of Canada* **191**, 1-382.
- Rikardsen, A. H. (2004). Seasonal occurrence of sea lice *Lepeophtheirus salmonis* on sea trout in two north Norwegian fjords. *Journal of Fish Biology* **65**, 711-722.
- 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 (2021). RStudio: Integrated Development Environment for R. Boston, MA: RStudio, PBC. URL: <http://www.rstudio.com/>.
- Sekovski, I., Newton, A. & Dennison, W. C. (2012). Megacities in the coastal zone: Using a driver-pressure-state-impact-response framework to address complex environmental problems. *Estuarine, coastal and shelf science* **96**, 48-59.
- 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.
- Sjursen, A. D., Rønning, L. & Davidsen, J. G. (2020). Overvåkning av anadrome laksefisk i Fjærevassdraget, Nordland. Resultater fra videoovervåkning 2019. *NTNU Vitenskapsmuseet naturhistorisk rapport* **3**, 1-18.
- Sjursen, A. D., Rønning, L. & Davidsen, J. G. (2021). Overvåkning av anadrome laksefisk i Botnvassdraget i Nordland 2018-2020. *NTNU Vitenskapsmuseet naturhistorisk rapport* **2**, 1-29.
- Spares, A. D., Dadswell, M. J., MacMillan, J., Madden, R., O'Dor, R. K. & Stokesbury, M. J. W. (2014). To fast or feed: an alternative life history for anadromous brook trout *Salvelinus fontinalis* overwintering within a harbour. *J Fish Biol* **85**, 621-644.
- Strøm, J. F., Jensen, J. L. A., Nikolopoulos, A., Nordli, E., Bjørn, P. A. & Bøhn, T. (2021). Sea trout *Salmo trutta* in the subarctic: home-bound but large variation in migratory behaviour between and within populations. *Journal of Fish Biology* **99**, 1280-1291.
- Suuronen, P. & Lehtonen, E. (2012). The role of salmonids in the diet of grey and ringed seals in the Bothnian Bay, northern Baltic Sea. *Fisheries research* **125-126**, 283-288.
- Tanguy, J. M., Ombredane, D., Baglinière, J. L. & Prunet, P. (1994). Aspects of parr-smolt transformation in anadromous and resident forms of brown trout (*Salmo trutta*) in comparison with Atlantic salmon (*Salmo salar*). *Aquaculture* **121**, 51-63.
- Thorpe, J. (1994). Salmonid fishes and the estuarine environment. *Estuaries* **17**, 76-93.
- Thorstad, E. B., Økland, F., Finstad, B., Sivertsgård, R., Plantalech, N., Bjørn, P. A. & McKinley, R. S. (2007). Fjord migration and survival of wild and hatchery-reared Atlantic salmon and wild brown trout post-smolts. *Hydrobiologia* **582**, 99-107.

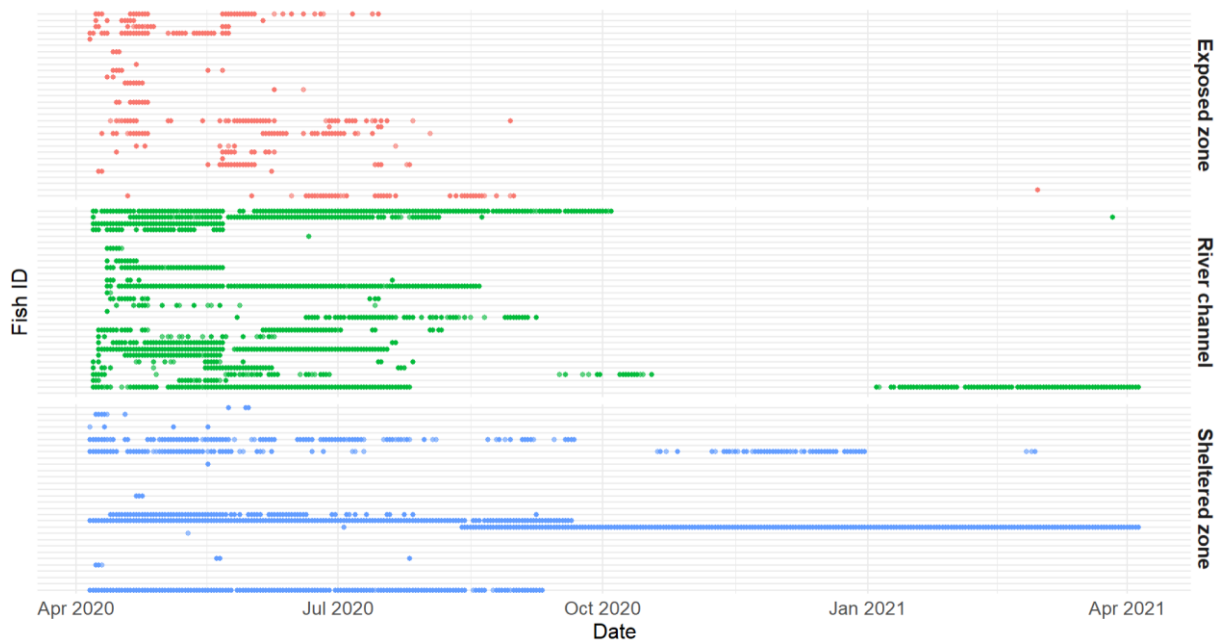
- Thorstad, E. B., Todd, C. D., Uglem, I., Bjørn, P. A., Gargan, P. G., Vollset, K. W., Halttunen, E., Kålås, S., Berg, M. & Finstad, B. (2016). Marine life of the sea trout. *Marine biology* **163**, 1-19.
- Ugedal, O., Finstad, B., Damsgård, B. & Mortensen, A. (1998). Seawater tolerance and downstream migration in hatchery-reared and wild brown trout. *Aquaculture* **168**, 395-405.
- Wagner, G. N., Cooke, S. J., Brown, R. S. & Deters, K. A. (2011). Surgical implantation techniques for electronic tags in fish. *Reviews in fish biology and fisheries* **21**, 71-81.
- Wang, T., Geyer, W. R., Engel, P., Jiang, W. & Feng, S. (2015). Mechanisms of tidal oscillatory salt transport in a partially stratified estuary. *Journal of physical oceanography* **45**, 2773-2789.
- Watz, J. & Piccolo, J. J. (2011). The role of temperature in the prey capture probability of drift-feeding juvenile brown trout (*Salmo trutta*). *Ecology of freshwater fish* **20**, 393-399.
- Werner, E. E. & Hall, D. J. (1988). Ontogenetic Habitat Shifts in Bluegill: The Foraging Rate-Predation Risk Trade-off. *Ecology (Durham)* **69**, 1352-1366.
- Wolanski, E. & Elliott, M. (2016). *Estuarine ecohydrology : an introduction*. 321 p. Amsterdam: Elsevier Science.
- Zhang, Y., Ren, J., Zhang, W. & Wu, J. (2021). Importance of salinity-induced stratification on flocculation in tidal estuaries. *Journal of hydrology (Amsterdam)* **596**, 126063.

# APPENDIX 1

## Residence zones through seasons

Daily residence zones for each unique fish ID were investigated, giving an overview of the habitat use for each fish throughout the study period. All registrations were included, indicating presence in the zone, not considering residence time in each zone.

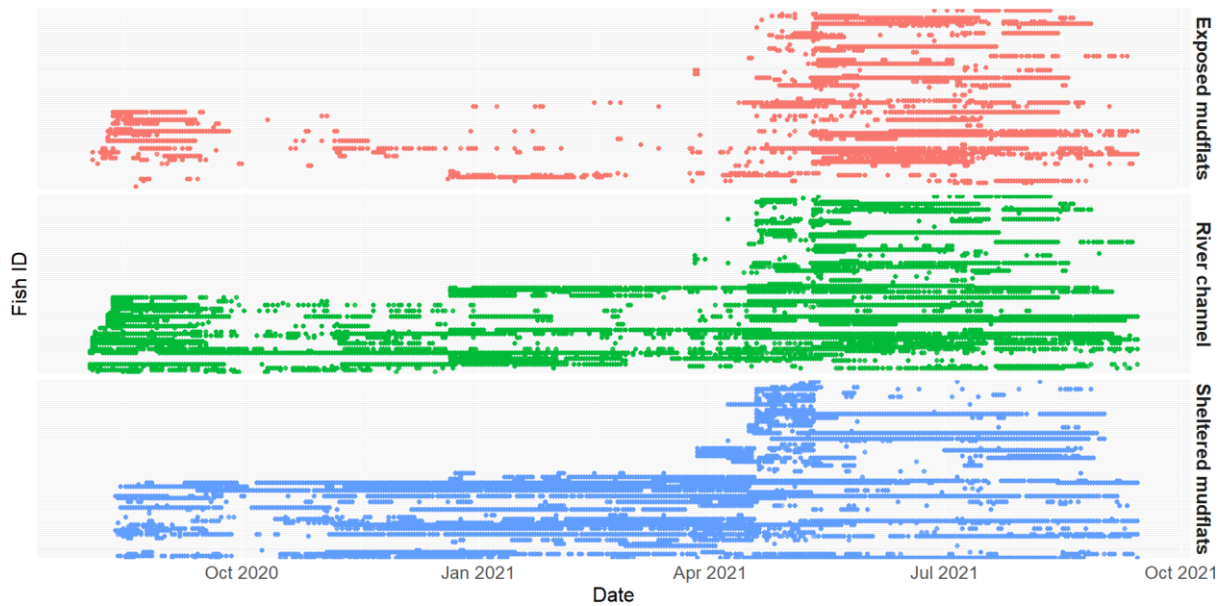
Most of the tagged sea trout in Orkanger ( $n = 30$ ) were registered in the river channel from April to September 2020, with a decreasing use of this habitat towards late autumn and winter season (Figure A1). Several individuals were also in the timespan April-August 2020 registered in the exposed mudflats. From November and through the winter months, two individuals were registered in the sheltered mudflats (Råbygd fjæra) and seemed to be resident in the habitat throughout the winter period. Two individuals were detected in the river channel of River Orkla during the winter. One of the individuals overwintered in the habitat.



**Figure A1:** Daily residence zone for each unique fish ID in tagging group Orkanger represented on individual lines. Exposed intertidal mudflats (red dots), river channel (green dots), and sheltered intertidal mudflats (blue dots) are represented in different colours and panels.

In Stjørdal, a higher proportion of tagged sea trout was detected in the exposed mudflats during the summer months June and July than in the winter (Figure A2). The river channel was frequently used by the sea trout throughout the study period, with a high number of fish present in September-October 2020. The tagged sea trout used the sheltered mudflats throughout the study period (Figure A2). A large proportion of the tagged sea trout in the autumn 2020 were resident in the sheltered mudflats during the winter months. Several of the individuals tagged in spring 2021 were present in the sheltered mudflats during April, followed by less detections in June and July. The sheltered intertidal mudflats were more frequently used during the winter

than during the summer. Five individuals tagged in the spring 2021 were resident in the sheltered mudflats during the summer months.



**Figure A2:** Daily residence zone for each unique fish ID in Stjørðal represented on individual lines, in time period August 2020–October 2021. Fish IDs from tagging group Stjørðal autumn 20 and Stjørðal Spring 21 included. Exposed intertidal mudflats (red dots), river channel (green dots), and sheltered intertidal mudflats (blue dots).

## Generalized linear models of presence in estuary vs. adjacent fjord

**Table A1:** Parameter estimates and estimated standard errors of the effect date (D), mean daily body temperature (T), sex (S), and total body length (L) on residency in the estuary versus nearby fjord areas for tagging group Orkanger in the time period from May through out August 2020. The estimated are based on conditional model averaging ( $\Delta AICc < 4$ ) of generalized linear models. The parameter estimates are scaled and indicate the magnitude of each effect relative to the other effects.

	<b>Estimate</b>	<b>Std. Error</b>
<b>(Intercept)</b>	-3.2304	0.8926
<b>Mean daily temperature</b>	0.9752	0.2640
<b>Date</b>	0.3462	0.1713
<b>Sex (Male)</b>	-1.6616	1.2693
<b>Total body length</b>	-0.7866	0.7553

**Table A2:** Parameter estimates and estimated standard errors of the effect of date, mean daily body temperature, sex, and total body length on the probability of presence in estuary versus adjacent fjord areas for tagging group Stjørødal from May throughout August 2021. The estimated are based on conditional model averaging ( $\Delta AICc < 4$ ) of generalized linear models. The parameter estimates are scaled and indicate the magnitude of each effect relative to the other effects.

	<b>Estimate</b>	<b>Std. Error</b>
<b>(Intercept)</b>	-3.12329	0.40016
<b>Mean daily temperature</b>	0.40633	0.06940
<b>Date</b>	-0.80882	0.08357
<b>Sex (Male)</b>	1.22627	0.49529
<b>Total body length (L)</b>	0.33652	0.20472

## Generalized linear models of temperature use

**Table A3:** Parameter estimates and estimated standard errors of the effect of date, zone, sex, and total body length on body temperature in tagging group Orkanger from May to August 2020. The estimates are based on conditional model averaging ( $\Delta AIC_c < 4$ ) of generalized linear models. The parameter estimates are scaled and indicate the magnitude of each effect relative to the other effects.

	<b>Estimate</b>	<b>Std. Error</b>
<b>(Intercept)</b>	-430.76641	9.8283112
<b>Date</b>	0.0233826	0.0005336
<b>River channel</b>	-0.3406936	0.0570598
<b>Sheltered mudflats</b>	-0.2978498	0.0625472
<b>Sex (Male)</b>	0.1419234	0.0954518
<b>Total body length</b>	0.1082915	0.0574350

**Table A4:** Parameter estimates and estimated standard errors of the effect of date, zone, sex, and total body length on temperature use in tagging group Stjørdal from May to August 2021. The estimates are based on conditional model averaging ( $\Delta AIC_c < 4$ ) of generalized linear models. The parameter estimates are scaled and indicate the magnitude of each effect relative to the other effects.

	<b>Estimate</b>	<b>Std. Error</b>
<b>(Intercept)</b>	-360.75857	5.52009
<b>Date</b>	0.0191879	0.0002937
<b>River channel</b>	-0.0011385	0.0215483
<b>Sheltered mudflats</b>	-0.2967060	0.0328092
<b>Sex (Male)</b>	0.0997811	0.0972253
<b>Total body length</b>	0.0198904	0.0407694

