Catrine Schulze

Habitat use in an estuary - a comparative study of Atlantic salmon (*Salmo salar*) and sea trout (*Salmo trutta*) of two life stages

A study conducted in the Stjørdal river estuary

Hovedoppgave i Msc
Veileder: Jan Grimsrud Davidsen
Medveileder: Sindre Håvarstein Eldøy
Mai 2022

Hovedoppgave

NTNU
Norges teknisk-naturvitenskapelige universitet
Vitenskapsmuseet (VM)
Institutt for naturhistorie

NTNU
Kunnskap for en bedre verden

Catrine Schulze

Habitat use in an estuary - a comparative study of Atlantic salmon (*Salmo salar*) and sea trout (*Salmo trutta*) of two life stages

A study conducted in the Stjørdal river estuary

Hovedoppgave i Msc
Veileder: Jan Grimsrud Davidsen
Medveileder: Sindre Håvarstein Eldøy
Mai 2022

Norges teknisk-naturvitenskapelige universitet
Vitenskapsmuseet (VM)
Institutt for naturhistorie

NTNU
Kunnskap for en bedre verden

NTNU
Norwegian University of
Science and Technology

Habitat use in an estuary - a comparative study of Atlantic salmon *(Salmo salar)* and sea trout *(Salmo trutta)* of two life stages

Catrine Schulze

Master's thesis in MSc Ocean Resources, Ecosystems

Supervisor: Jan Grimsrud Davidsen,

Co-supervisor: Sindre Håvarstein Eldøy and Eva Bonsak Thorstad

Submission date: 16.05.2022

Norwegian University of Science and Technology

Department of Biology

ACKNOWLEDGEMENTS

I would like to express my very great appreciation to Jan Grimsrud Davidsen, for trusting me with this opportunity, and for sharing long-earned knowledge and humor along the way. The genuine effort to push me and my fellow students up and forward in this world has been invaluable, and I believe we are better people and more confident for having been a part of this inspiring environment. I am also forever grateful to my co-supervisor Sindre Håvarstein Eldøy for always taking the time to share constructive feedback, motivation and guidance through a steep learning curve, and co-supervisor Eva Bonsak Thorstad for sharing valuable perspectives and contagious interest of the field.

My special thanks are extended to the staff at NTNU University museum, for opening your doors and including master students in your highly knowledgeable and positive work environment; Lars Rønning for sharing field knowledge and experience in frog picking from smolt traps, Aslak Darre Sjursen for great training in the analysis of fish scales and help catching my first Atlantic salmon, Gaute Kjærstad for sharing valuable data and knowledge on benthic communities from the study area, Mohsen Falahati for conducting genetic analysis. Marc Daverdin for all produced maps of the study area, as well as Anette, Ingvild and Sindre Grimsrud Davidsen for all practical work related to fishing and fish tagging. I would also like to thank Stjørdal hunting and fishing association for great help and experienced fishing efforts. My project was a part of a larger project at Hellstranda funded by Nye Veier, via Acciona Construction and Rambøll. Some additional tags for smolts and the line of receivers at Agdenes were funded by Sjømat Norge via an agreement with Tor Næsje at NINA. Thanks to Avinor and Forsvarsbygg for access to their areas during deployment and
maintenance of receivers.

Lastly, I wish to extend my great thanks to my ever-supportive family making it possible for me to study all these years, and to Signe Brekke Harbak for the close cooperation during this project, Hanne Bjørnås Krogstie, Johan Munkeby, Sigve Arntzen, Aksel-Johan, Christianne and Nanna Orderud, for the much-needed conversation and discussions at NTNU University museum, Sealab and in the field.

Catrine Schulze
Trondheim, May 2022

ABSTRACT

Details on how Atlantic salmon (*Salmo salar*) and sea trout (*Salmo trutta*) utilize estuarine areas are increasingly relevant in coastal management, as they are often subjected to the same conservation strategies, despite their differences in habitat use and migration behavior. To manage them through species-specific strategies, extensive knowledge is required on their use of estuaries and coastal areas and how their requirements ultimately differ. The present thesis investigated the estuarine habitat use of Atlantic salmon and sea trout adults and smolts, from 10 April to 15 September 2021. In total, 450 Atlantic salmon and sea trout adults and smolt were captured and tagged with acoustic tags prior to the spring migration in 2021, in the lower parts of the Stjørdal river. The fish were detected by acoustic receivers placed strategically within the study area.

Exposed intertidal mudflats, sheltered intertidal mudflats and river channel were defined as the three habitats within the Stjørdal river estuary, and all were ultimately used by both species. While Atlantic salmon continued the migration towards marine habitats shortly after they arrived the brackish estuarine areas, sea trout in general stayed here for a much longer period. In total, 56% of sea trout smolt and 54% of sea trout adults were detected in the sheltered intertidal mudflats between 1 May and 30 June. In the same period, 78% Atlantic salmon smolts were observed in the exposed intertidal mudflats, next to 92% of sea trout smolts. During the week of peak migration in May when both species were present in the estuary, Atlantic salmon smolt and adults spent only 31% and 3% of their time, respectively, in the estuarine habitats. In contrast, sea trout spent much more time here, with 36% for smolt and 73% for adults. Sea trout smolts had a longer residency in the nearby marine areas, compared to sea trout adults. The sheltered intertidal mudflats were shown more important for adult sea trout than any other group of tagged fish. During the week of peak migration, they spent 34% of their time here, while adult Atlantic salmon only spent 1%. During the same week, sea trout experienced higher daily averaged water temperatures than Atlantic salmon with 9-10°C for adult sea trout in all estuarine habitats, with sea trout smolts experiencing the highest average of 11°C, in the sheltered intertidal mudflats. Atlantic salmon experienced daily averaged water temperatures around 5-6°C, with smolts experiencing the highest average 7.5°C, in the sheltered intertidal mudflats.

Through these findings, the present study emphasized the importance of gaining species-specific knowledge regarding coastal habitat use and variation within a population, as behavior and needs are shown to differ with both species and life stage. In conclusion, the Stjørdal river estuary had a variety of functions, as a simple migration corridor, microclimate refuge, temporary holding or foraging grounds. The knowledge provided by this study is of value in a coastal management perspective, as there is a continuous pressure on coastal habitats and their inhabitants. In order to mitigate the negative ecological effects of urban activities in estuaries, it is crucial to have more knowledge about the function of estuarine habitats for the species and life stages of concern.

SAMMENDRAG

Detaljer om hvordan atlantisk laks (Salmo salar) og sjøørret (Salmo trutta) utnytter elvemunningsområder blir stadig mer relevante i tråd med økosystembasert forvaltning. Til tross for åpenbare forskjeller i habitatbruk og migrasjonsatferd, er atlantisk laks og sjøørret ofte underlagt de samme forvaltningsstrategiene. For å håndtere dem gjennom artsspesifikke strategier, kreves det omfattende kunnskap om detaljene rundt deres bruk av elvemunninger og kystområder, samtidig hvordan kravene deres som helhet er forskjellige. Fisken ble merket og oppdaget av akustiske mottakere plassert strategisk rundt studieområdet.

Tre brakkvannshabitater ble definert innenfor elveosen tilhørende Stjørdalselva, hvor alle på et tidspunkt ble brukt av begge arter. Laks fortsatte vandringen mot marine habitater kort tid etter at de ankom de brakkvannshabitatene, mens sjøørreten holdt seg generelt her i en mye lengre periode. Laksesmolt og voksen laks tilbrakte henholdsvis 31 % og 3 % av sin tid i elvemunningen i løpet av uken utvandringen var høyest. I motsetning til laks, tilbrakte sjøørreten tid i elvemunningen gjennom hele studieperioden, med 36 % for smolt og 73 % for voksne, i løpet av uken med høyest utvandring. Sjøørretsmolt hadde opphold seg i lengre tid i nærliggende marine områder, enn voksen sjøørret. De skjermede tidevannshabitatene ble vist viktigere for voksen sjøørret enn noen annen gruppe merket fisk gjennom hele studieperioden, hvor de tilbrakte 34 % av sin tid i uken med høyest utvandring. Imidlertid ble 56 % av sjøørretsmolten og 54 % av voksne sjøørreter registrert i de skjermede tidevannshabitatene mellom 1. mai og 30. juni. I samme periode ble det observert 78 % laksesmolt i de eksponerte tidevannshabitatene, ved siden av 92 % av sjøørretsmolten. I løpet av uken med toppvandring opplevde sjøørreten gjennomsnittlige daglige vanntemperaturer rundt 9-10°C i alle brakkvannshabitater, der sjøørretsmolt opplevde det høyeste gjennomsnittet på 11°C, i de skjermede tidevannshabitatene. Laks opplevde daglige gjennomsnittlige vanntemperaturer rundt 5-6°C, hvor smolt opplevde de høyeste gjennomsnittlige 7,5°C, i det skjermede tidevannshabitatet.

Kunnskapen denne studien gir er verdifull i et kystforvaltningsperspektiv, da det er et kontinuerlig press på kysthabitater og arter innenfor tilhørende økosystemer. Å fullstendig beskytte de verdifulle elvemunningshabitatene fra menneskeskapte stressfaktorer kan være utfordrende når myndighetene må balansere mellom byutvikling og naturvern, ettersom mange elvemunninger ligger i områder som allerede er sterkt urbanisert. For å dempe de negative økologiske effektene av urbane aktiviteter i elvemunninger, er det avgjørende å ha mer kunnskap om funksjonen til elvemunningshabitater for artene og livsstadiene som er bekymret.

1. INTRODUCTION

Estuaries are highly productive ecosystems that are culturally, commercially, and recreationally important (Elliott & Whitfield, 2011). They support diverse and abundant ecological communities of plants and animals and provide important habitats for many species, thus being among the most biologically productive environments on earth (Kennish, 2002). Due to the dynamic influence of tides and river flow, estuarine ecosystems are complex habitats. Estuaries contain a gradient of microhabitats with varying levels of salinity and temperature, as well as a variety of vegetation patches and sedimentary bottoms. Uncontrolled development and overpopulated coastal areas have affected nearly all estuaries in the world (Kennish, 2002). As one of the most sensitive coastal areas, estuaries are at an ever-increasing risk from human activity, and deltas categorized as "vulnerable" by the Norwegian Red List for ecosystems and habitats (Erikstad, 2018). Understanding the different values of these ecosystems is therefore important if we are to successfully develop effective management strategies concerning activity and associated impacts on the coastal marine area (Kennish, 2002; Elliott & Whitfield, 2011).

Details on how Atlantic salmon (*Salmo salar*) and sea trout (*Salmo trutta*) utilize estuarine areas are increasingly relevant in line with ecosystem based management (O'Higgins *et al.*, 2020). The variation in the two species migration patterns and life history strategies are still not well understood and needs to be further studied (Birnie-Gauvin *et al.*, 2019). The sea trout and the Atlantic salmon are two central species in many river and estuary ecosystems, as well as being culturally and economically important species of salmonids native to Europe (Forseth *et al.*, 2017; Liu *et al.*, 2019). There has been a sharp decline in Norwegian populations of both sea trout and Atlantic salmon (Anon, 2021), mainly due to multiple stressors related to anthropogenic activities, with the impact of salmon lice (*Lepeophtheirus salmonis*) having the largest negative effect (Anon, 2021). Coastal development and other anthropogenic pressure have conjointly led to lower reproduction capacity in streams as well as loss/degradation of habitat (Anon, 2021). Atlantic Salmon was categorized as «near threatened» in 2021 (Erikstad, 2018) and is therefore in need of careful consideration regarding management of angler activity and coastal development. Temperature, salinity, oxygen content, spawning conditions and productivity in the water course are some of the important environmental factors that affect the distribution and the population abundance of the species (Jonsson & Finstad, 1995). Many ectotherm species will adjust their behavior to keep their body temperature within a species-specific range, as temperature will largely affect their fitness (Martin & Huey, 2008). With estuaries including gradients of different microhabitats including a variation in water temperatures, and the optimal temperature for sea trout reported with a range of 12-17°C, while it spans from 7-20°C for salmon (Elliott & Elliott, 2010), it is likely some estuarine habitats would be more preferable than others depending on the overall environmental conditions.

Atlantic salmon and sea trout migrate through estuaries on their way between breeding and nursery grounds in freshwater and feeding grounds in marine areas, thus enabling them to exploit different habitats and potentially maximize their individual fitness (Harvey *et al.*, 2020). This life history strategy makes sea trout and Atlantic salmon especially vulnerable to anthropogenic stressors, as they may be exposed in both their freshwater habitats and the sea, as well as the migration routes between these habitats. Atlantic salmon migrate to the open ocean for feeding over one to several years before returning to their natal river (Harvey *et al.*, 2020). On the contrary, sea trout often use coastal and nearshore habitats for feeding and often return to the freshwater habitat every fall for spawning and/or overwintering (Lyse *et al.*, 1998; Jensen *et al.*, 2014; Eldøy *et al.*, 2015). Sea trout show large variations in migration behavior, both within and between populations (Strøm *et al.*, 2021), and may switch between different habitats more frequently (Klemetsen *et al.*, 2003; Jonsson & Jonsson, 2011). Some sea trout are known to migrate even shorter distances to their natal river estuary (Bordeleau *et al.*, 2018; Eldøy *et al.*, 2021), indicating better refuge from predation, less intense salinity levels or better conditions for growth (Thorpe, 1994). Several studies have argued that the migratory behavior of sea trout populations should be considered as a continuum rather than fixed choice between becoming a migrant or a freshwater resident (Cucherousset *et al.*, 2005; del Villar-Guerra *et al.*, 2014), while populations of Atlantic salmon in general are known to migrate over great distances in the Atlantic ocean (Thorstad *et al.*, 2012). Because of these inherent differences in life history between Atlantic salmon and sea trout, it is reasonable to expect that these two species utilize the estuarine habitat differently.

The migration from freshwater to marine areas is a vulnerable phase in the life of anadromous salmonid smolts, as they for their first time undergo energy demanding physiological changes in preparation for a life in more saline environments (Thorstad *et al.*, 2012; Harvey *et al.*, 2020). Salmonid marine migrations are influenced by the individual physiological condition, as well as a number of environmental factors (Olsson *et al.*, 2006; Wysujack *et al.*, 2009; Vainikka *et al.*, 2012). The metabolic and/or growth rate may be related to when or if an individual chooses migration (Wysujack *et al.*, 2009; Bordeleau *et al.*, 2018). As the availability for food is higher in marine environments compared to freshwater systems, migrating to sea could sustain the demands for food and energy in individuals with high growth and metabolic rate (Thorpe *et al.*, 1998). A study on migrating salmonid smolt have shown early migrating salmon smolt may not have fully completed the necessary physiological adaptations, thereby delaying sea entry by residing in the lower parts of the river (Strand *et al.*, 2010). Estuarine feeding was suggested as an intermediary strategy for sea trout smolt spending more time in the estuarine rather than marine areas (Davidsen *et al.*, 2014a). According to a study on seawater tolerance of the two species, differences in seawater tolerance, as well as in the development of smoltification, are evident between sea trout and salmon (Quigley *et al.*, 2006; Nemova *et al.*, 2020). Smoltification for sea trout is more flexible than the same process for the Atlantic salmon (Quigley *et al.*, 2006; Nefedova *et al.*, 2018). The salmon decides whether to smoltify based on its reached size the previous year (Stefansson 2008), while the brown trout decides in the spring of smoltification (Nefedova *et al.*, 2018; Nemova *et al.*, 2020). Compared to Atlantic salmon, the osmoregulation for sea trout is therefore often immature until migration for the sea trout, meaning the smoltification is not quite as complete for the sea trout as for the Atlantic salmon (Quigley *et al.*, 2006; Nemova *et al.*, 2020). As adult sea trout, post-smolts have been studied using habitats close to the coast (Lyse *et al.*, 1998; Jensen *et al.*, 2014; Eldøy *et al.*, 2015). Differences in biologic characteristics and life history strategies between life stages, species, and sex equals different needs for shelter from predation, access to prey, water masses with preferred or tolerated salinity levels, as well as different resilience to pathogens (Thorpe, 1994; Thorpe *et al.*, 1998; Strand *et al.*, 2010). The function of estuaries may therefore vary from serving as a simple migration corridor to microclimate refuge, temporary holding or feeding grounds.

Based on the inherent ecological differences among Atlantic salmon and sea trout, and between smolt and adult life stages, it was hypothesized that 1) 1) adult Atlantic salmon have a short residency in the estuary during the marine migration, while adult sea trout will reside there much longer, 2) Smolts of both Atlantic salmon and sea trout have a longer residency in the estuary than adult individuals. Additionally, the use of different areas of the estuary as well as the water temperature experienced by the two species and life stages was explored to gain more knowledge about the function of the estuarine habitat for these two species of conservation concern.

2. MATERIALS AND METHODS

2.1 STUDY AREA

The study was conducted in the Stjørdal river estuary (63.44899 °N, 10.88527°E) located in Stjørdal municipality, Trøndelag. The study area includes the river outlet of the Stjørdal river, as well as the nearby marine areas and parts of the main river (Figure 1), which is subject to the protection regime of national salmon watercourses and empties into the Trondheim fjord, which has been given the status of a national salmon fjord (Anon, 2007). The anadromous stretch in the main river is 55 km long from the river outlet. The river has several tributaries, where Forra and Sona, are both salmon and sea trout carrying watercourses. The present shape of the river outlet is a result of remodeling related to the development of the Trondheim Airport. The original river channel was cut off where the airport runway is now located, and a stone pier of approximately one km was built to channel the Stjørdal river away from the developed airport area. The stone pier reaches from the shallow part of the river outlet (Langøra-sør) and into the Stjørdal fjord, which is an arm of the Trondheim fjord (figure 1).

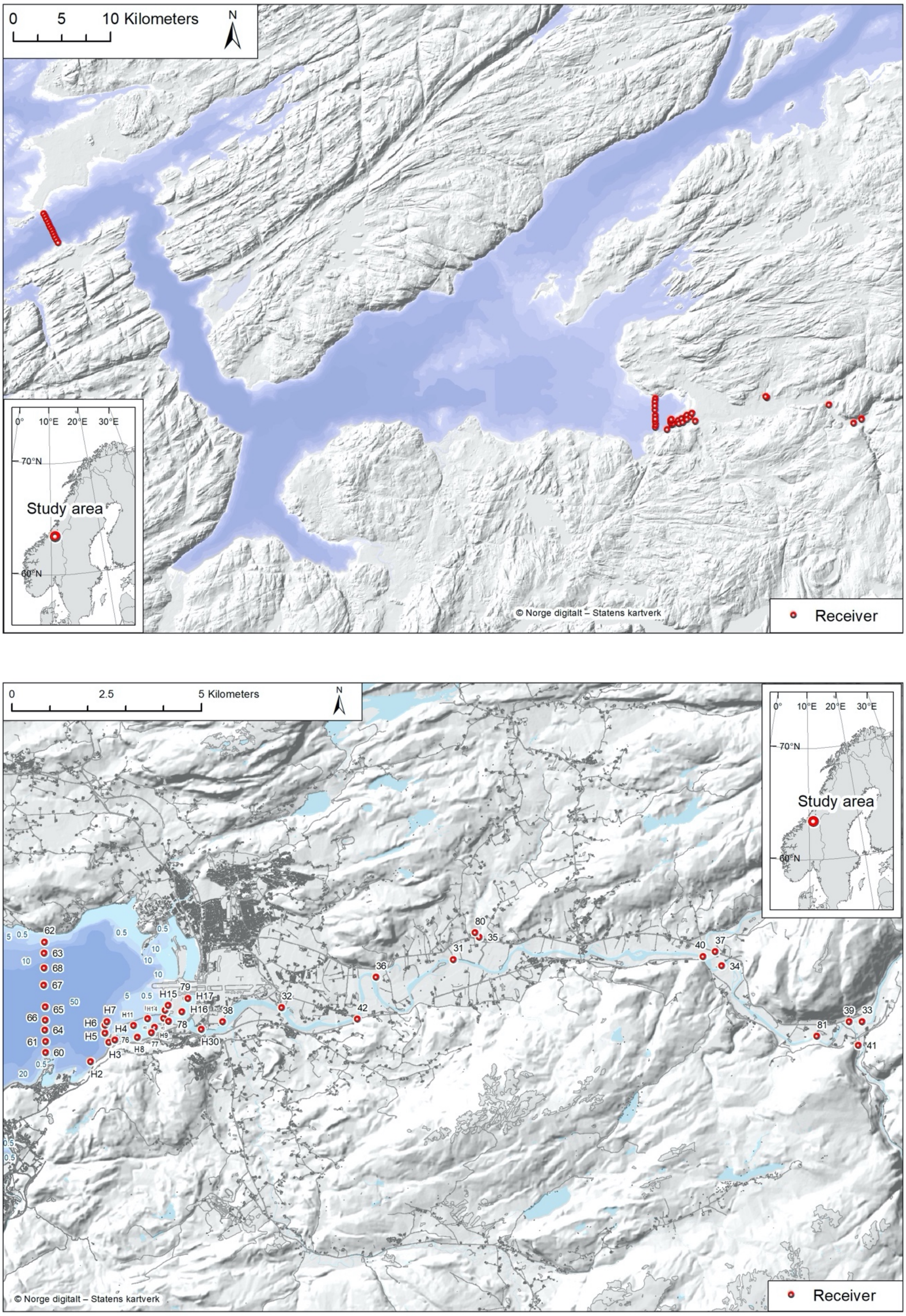


Figure 1: Map of the Stjørdal river study area, where acoustic receivers are marked as red dots. **a)** The full study area, with all included acoustic receivers, from the Stjørdal river to the outer Trondheim fjord. **b)** Acoustic receivers deployed in the Stjørdal river, the Stjørdal river estuary and nearby marine areas.

2.1.1 Description of estuarine habitats

Within the estuary, three defined zones were characterized by differences in hydrological qualities and overall environmental conditions (Table 1). The pier has created a pool with shallow water between Billedholmene and Hellstranda, being strongly impacted by waves from the fjord at high tides. The former river course forms a shallow area inside Langøra with brackish water that is impacted by tides but sheltered from waves from the fjord. The main river channel runs alongside the stone pier, and is an area always submerged by water with strong currents. The variety of potential prey for salmonids between the estuarine areas reflects the differences in substrate, salinity, temperature, and exposure to waves. Salmonid diet was not directly investigated in this project, however based on earlier studies it is assumed that the two species mainly feed on different benthic animals such as crustaceans and worms, and small fish (Grønvik & Klemetsen, 1987). Unpublished studies of benthic animals in the sheltered and exposed intertidal mudflats suggest differences in the composition of benthic species in three areas of the estuary (Kjærstad, 2022).

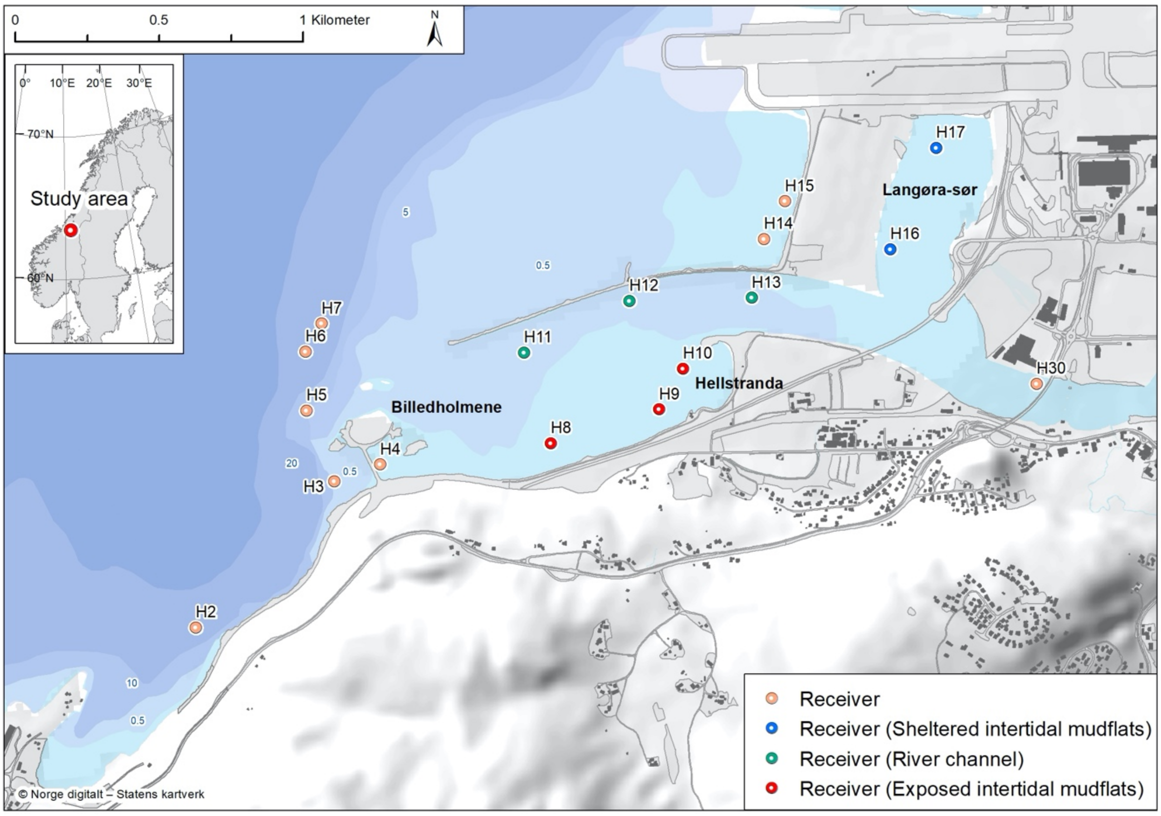


Figure 2: Map of the study area, with focus on the Stjørdal river estuary. Acoustic receivers deployed in the Stjørdal river estuary and nearby marine areas, are marked as dots of different colors representing their respective habitat (red = exposed intertidal mudflats, green = the river channel, blue = sheltered intertidal mudflats, and orange = fjord/upstream).

Table 1: Areas within the study area divided into different zones (habitats) by their overall environmental conditions, with acoustic receivers included in the different habitats. “Zones” are referred to as “habitat” by their respective habitat descriptive title, throughout the present paper.

Zone	Habitat	Acoustic receivers	Environmental conditions
Zone 1	**Exposed intertidal mudflats**	H8, H9 and H10	Highly impacted by waves and change in tidal levels. Shallow area, drained at low tide.
Zone 2	**River channel**	H11, H12 and H13	Main river channel along stone pier. Strong marine, brackish and freshwater currents. Depth of 4-5 m at high tide.
Zone 3	**Sheltered intertidal mudflats**	H16 and H17	Partly enclosed area, impacted by tides. Relatively shallow, with water masses of brackish, marine, and freshwater characteristics.
Zone 4	**Upstream**	H30-32, H34-40, H42, H80 and H81	The Stjørdal main river, with brackish and freshwater.
Zone 5	**Fjord**	H1-7, H14-15, H60-68 H101-103 and H105-112	Marine zone in the inner fjord, including near-coastal and pelagic habitats/open water masses.

Exposed intertidal mudflats (Zone 1)

The exposed intertidal zone is highly influenced by the change in tidal levels, waves and water flow, resulting in drastic variations in temperature and salinity levels during each day and during the season. This shallow pool has its floor alternately submerged and exposed to air twice a day due to the changes in tidal levels, whereas the size of the area exposed to air changes with the phase of the moon. The area seems to be generally characterized by a gradient in salinity levels, with a more marine environment closer to Billedholmene, and a higher degree of brackish water closer to beach Hellstranda. The input of freshwater likely comes in at the tip of Hellstranda, where a backwater is created, bringing the fresh river water into the area. Patches of seaweed occur throughout the zone, although the biomass of seaweed is higher in the more marine areas of this zone. Large parts of the area freeze over in winter, with regular breaks in the large flakes of ice. The samples of benthic species from the exposed intertidal mudflats mainly included Gammarus (amphipod), Nematodes (roundworms) and earthworms in the area close to the beach, and Gammarus, Janiridae (isopod) and eartworms in the area close to Billedholmene. The habitat floor consists mainly of sand and small rocks.

Figur 3. The exposed intertidal mudflats at low tide. Photo, top: Catrine Schulze, photo, left: Jan Grimsrud Davidsen.

River channel (Zone 2)

The river channel has a maximum depth of 4-5 m at high tide. The lower layers of the water column in the channel consists of dense marine water masses coming in from the fjord, while the top layers vary between less dense fresh and brackish water. Variations in temperature and salinity levels are influenced by season, tidal phase and river flow. With strong currents and water masses in constant motion, the area does not freeze in winter. The overall flow pattern in the area is dependent on the tidal influenced incoming and outgoing currents, as well as the outgoing current created by the flow of the river. The river channel floor includes river gravel and rocks.

Figur 4. The river channel, February 2021 (left), and April 2021 (right), photo: Catrine Schulze.

Sheltered intertidal mudflats (Zone 3)

The sheltered intertidal mudflats zone is a relatively shallow area located upstream of the stone pier, in the old river channel. Due to the development of the airport runway, the area is now a partly enclosed part of the old river channel. The area is sheltered from waves from the fjord and has no flow or strong current of water. The amount of marine water coming into the area is controlled by the lunar phase and tidal levels, while the inflow of freshwater depends on the river flow. The lower layers of the area consists of settled marine water, while the top layers vary between fresh and brackish water. Variations in temperature and salinity levels are influenced by season, lunar phase, and time of day. During winter, the area is covered by a relatively solid layer of ice. The marine water layers are warmer in the winter than the freshwater layers. After the spring flow has occurred the relationships is reversed, as the layers of brackish and freshwater become warmer than the marine water. Benthic species samples from the sheltered intertidal mudflats had the highest number of benthic animals, including Mysida (crustacean), Gammarus and Corophiidae (amphipods) and earthworms (Kjærstad, 2022). The sediment in this habitat is mainly characterized by sand and fine particles.

Figure 5. The sheltered intertidal mudflats, photo: Signe Brekke Harbak.

2.2 COLLECTION OF DATA BY ACOUSTIC TELEMETRY

2.2.1 Fish capture and tagging

Fish for the study were caught and tagged in the fall of 2020 and the spring of 2021 (Table X). The adult Atlantic salmon (*n* = 54) and the adult sea trout (*n* = 97) were caught with rod and line in the lower parts of the Stjørdal river and the estuary. Sea trout smolts (*n* = 154) and Atlantic salmon smolt (*n* = 142) were caught with a smolt trap 13 km upstream from Hellstranda in the side river Gråelva, or 24 km upstream from Hellstranda by Sona bridge in the Stjørdal river. Here, 15 of the sea trout smolt and 37 Atlantic salmon smolts were tagged at Sona bridge, while 139 sea trout smolt and 105 Salmon smolt were tagged in the tributary Gråelva. Smolt were defined by *L*T < 23 cm. Four of the fish caught in the two smolt traps were defined as adult sea trout (*L*T = 27-29 cm).

A total of 450 fish were tagged with acoustic tags implanted into their abdominal cavity. After capture the adult fish were kept in holding nets in areas of the river with relatively low flow rate (<4 hours). The smolts were kept in a covered holding tank close to the riverbank (<24 hours), with continuous water flowthrough. Prior to tagging, the fish was anesthetized in a tub containing Benzoak VET (15-20 mL per 100 L water) for approximately four minutes. To be shielded from light, the tub was covered with a tarpaulin. The anesthetized fish was then measured for total body length and weight, before being placed in a half pipe with fresh water from the catch site. Wound opening and closure were performed with sutures, a 1,5-2,0 cm incision was made on the side of the *linea alba* and a sterilized acoustic tag was carefully inserted into the body cavity. Water was poured over the gills during the procedure to keep the fish wet and ensure normal breathing. The incision was closed using two or three individual sutures (suture; fish < 27 cm: Resolon 5/0, fish > 27 cm: Resolon 3/0). From adult fish, 5-10 scales were collected from above the lateral line for age determination, and a small piece of the adipose fin was collected for DNA analyses and sex determination. The fish were held in covered holding tanks for recovery after tagging for approximately 5-10 minutes. When consciousness and normal behavior was regained, the fish were released in a calm area of the river close to the capture and tagging site. The experimental procedures in the project were approved by the Food Safety department (permission number 20/113613) and the county governor in Trøndelag. All sampling and tagging of the fish were executed by approved personnel to maximize animal welfare.

Figur 6. Smolt traps **a)** at Sona bru, and **b) in** Gråelva, photo: Catrine Schulze.

Table 2. Year and time of tagging, number of fish tagged, sex, total body length (*LT*) and body mass (g). NA: ingen data.

Study group	Time of tagging	n	Male:Female (n)	Total length (mm) Mean	Total length (mm) Range	Body Mass (g) Mean	Body Mass (g) Range
Adult	Aug-Dec 2020		2:2				
S. Salar	April-May 2021		15:38	797	430- 1080	3142	420-8840
		57	NA = 4				
Adult	Aug-Dec 2020		21:23				
S. trutta	April-May 2021		35:16	389	272- 615	568	155- 2100
		97	NA = 2				
Smolt	April-May 2021						
S. Salar		142	59:72	141	125-188	21	15-34
Smolt	April-May 2021						
S. trutta		154	89:62	165	131-229	40	15-95

Salmon smolt had a shorter *LT* (Welch two-sample t-test, $P < 0.05$) and smaller body mass (Wilcoxon rank sum test, $P < 0.05$) than sea trout smolt. Adult salmon had a longer *LT* (Welch two-sample t-test, $P < 0.05$) and larger body mass (Wilcoxon rank sum test, $P < 0.05$) than adult sea trout.

2.2.2 Acoustic tags

The fish were tagged with a cylindric acoustic tags fit for their total body length. Tags from Thelma Biotel AS (Trondheim, Norway) and Vemco Inc. (Halifax, Canada) were used (Table 3), where the bigger tag models (9x28, 9x38, 9x31 mm) were used for fish *LT* > 27 cm, while smaller models (6x18mm and 6x23 mm) were used for for fish *LT* > 27 cm. The tags all transmitted a different acoustic signal, giving each tag a unique ID-code. To minimize the risk of signals colliding when several fish were in the range of on receiver, two different frequencies (69 and 71 kHz) were used and the tags transmitted an acoustic signal with a randomized interval between the signals, with a minimum of 40 seconds and a maximum of 80 seconds between each signal. Due to the expected battery life of the fish tags smolt may have been present in the estuary without being detected.

Table 3. Fish tag specifications from tagged sea trout and Atlantic salmon adults and smolt, in Aug-Dec 2020 and April-May 2021.

Tag model	Battery life (days)	Size of tag (Ø x length, mm)	Weight (g)	Output (dB re 1uPa @1m)
ADT-LP9-L	380	9 x 28	5.1	142
T-LP9-L	576	9 x 28	4.3	142
T2LP9L	1152	9 x 38	6.7	142
V9T-2L	410	9 x 31	4.6	146
ADT-LP6	70	6 x 18	1.3	137
T-LP6	90	6 x 23	1.6	137

2.2.3 Tracking of tagged fish

The migration patterns of the individual fish were tracked by arrays (Figure 2) of acoustic receivers deployed beneath the water surface in the estuary and fjord system. The acoustic receivers were tuned to the same frequency (69 and 71 kHz) as tag transmissions to be able to identify individual tags from detections when in range. The study area is of complex character, with a large variation in water conditions affecting registration range. Water temperature, salinity and current patterns are influenced by tidal levels and river flow. Registrations range within the estuary was approximately 50-200 meters, while it in the fjord were 200-400 m. Registration range within the estuary were the same as in similar studies done in areas with haloclines and thermoclines (Bordeleau *et al.*, 2018; Eldøy *et al.*, 2021). Data on registered fish by acoustic receivers were automatically stored, and the data was downloaded to a computer approximately every second month. The receivers were inspected regularly throughout the study period to ensure enough battery time and general function. A total of 50 acoustic receivers (ThelmaBiotel model TBR700 and Vemco Inc., Halifax Canada model VR2//VR2-AR) were deployed in the Trondheim fjord, the Stjørdal river and the Stjørdal estuary. These were either attached to poles placed at the estuary bed, attached to land or submerged to the sea floor with an acoustic release system (Sub sea sonic model AR60, Sub Sea Sonic inc., San Diego, USA or Vemco VR2-AR Acoustic Release, Vemco inc., Halifax, Canada).

2.3 AGE DETERMINATION BY SCALE ANALYSIS

The scales collected from the fish were stored in paper envelopes for drying prior to analysis. Using a light microscope, the 5-8 best readable scales were selected, and the scale patterns were imprinted onto a 1 mm polycarbonate Lexan plates using a pressing iron. The Lexan plates were photographed using a computer-stereoscope equipped with a camera (Leica M165C, camera: Leica MC170 HD, software: LAS V4.5, Leica systems, Sankt Gallen, Switzerland). Using the pictured scale structures, age and earlier sea migrations were analyzed for each individual fish. Due to replacement scales, age determination was not possible for all individuals. Continuous discussion and quality checks performed by an experienced technician during the analysis were done to avoid subjective results.

2.4 GENETIC SEX AND SPECIES DETERMINATION (DNA)

To avoid human errors in the sex and species determination, this was examined for and verified genetically using a small sample of the adipose fin from each fish. The DNA-analysis were all conducted at the NTNU University Museum DNA lab, Trondheim, according to methods described in Davidsen et al (2021).

2.5 ENVIRONMENTAL PARAMETERS

Measurements of water temperatures and salinity were taken at several locations of the estuary and fjord system. Data loggers (Star Oddi model DST centi-CT, Reykjavik, Iceland) were placed together with three of the acoustic receivers in the estuary. One data logger was placed in the shallow area inside Langøra by receiver H17, and two were placed between the beach area and Billedholmene in the exposed intertidal mudflats by receivers H8 and H10 (Figure 2). The data loggers were attached to poles together with acoustic receivers at the estuary bed at 0-5 meters depth, depending on the tides. A CTD (Conductivity, Temperature and Depth) apparatus was used to measure a transect of different areas in the estuary, presenting measurements of the momentary physical properties of the water (salinity, temperature, and depth).

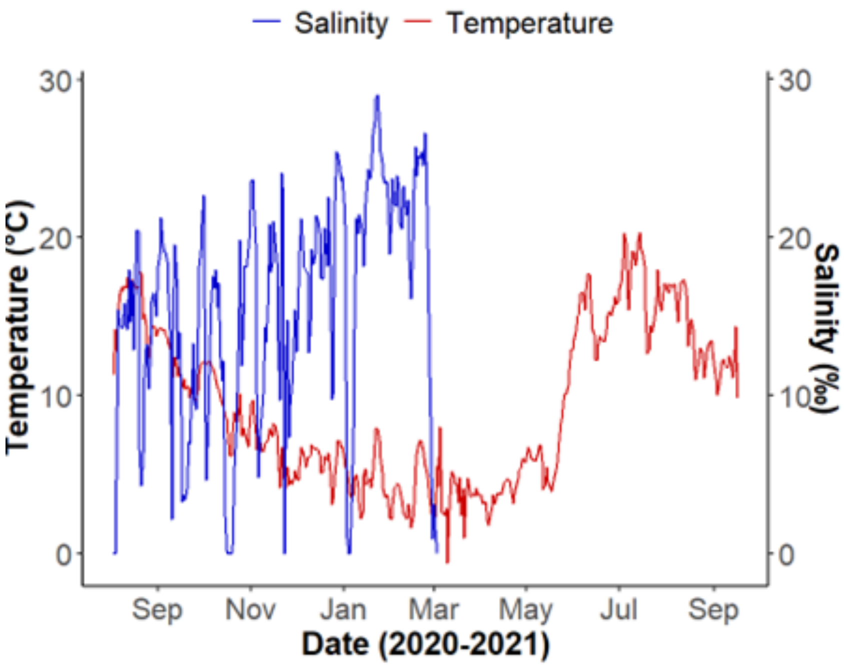


Figure 6 a. Temperature and salinity measured by dataloggers placed in the study area. Figure made by Signe Brekke Harbak, from the study area.

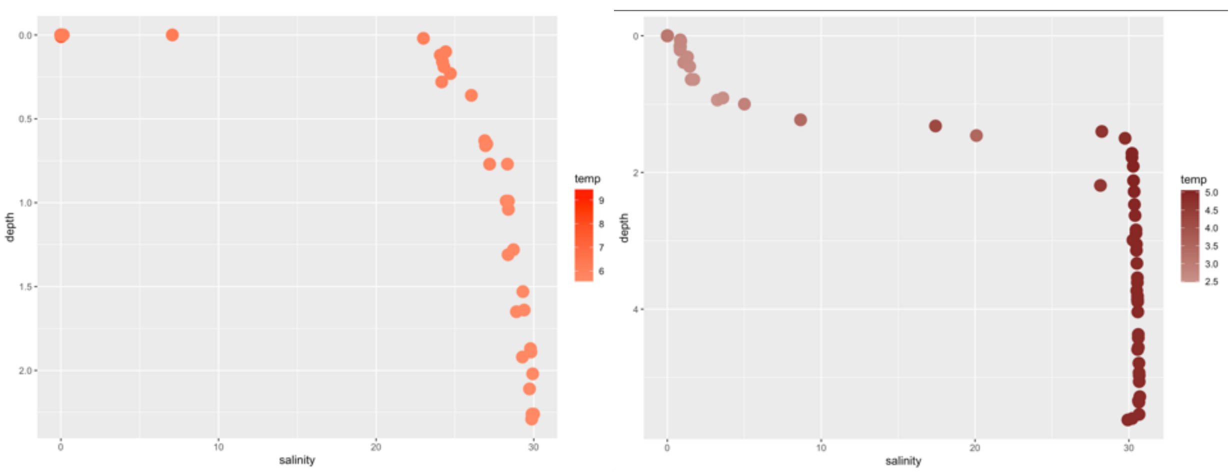


Figure 6 b. Salinity, temperature and depth measured **a)** by H17 in zone 3 **b)** by H11 in zone 2, on 19th of April 2021.

2.6 STATISTICAL ANALYSES

2.6.1 Data filtration

Collision of tag signals and sound pollution are two main sources of error to consider when practicing acoustic telemetry, where both may result in false registrations. Collision of tag signals occurs when sound signals from more than one fish tag reach an acoustic receiver at the same time. This signal collision may then be registered as an erroneous signal. Sound pollution may occur when there are other sources for sound that are interpreted as tag signals by an acoustic receiver. To minimize occurrence of false registrations in data analyses, the data were filtered so that an adult fish needed a minimum of two registrations on one receiver within 10 minutes to be approved for further analyses for the adult fish (Pincock 2012). A similar filter was not applied for data on smolt, as the smaller transmitters had a shorter range and fewer registrations. Visual inspection of individual plots was instead used to verify the smolt registrations.

2.6.2 Calculation of condition factor

Fulton's condition factor (K-factor) shows the relationship between the individual's weight and body length. The individual condition factor was calculated using the formula (Le Cren 1951):

$$K = 100\ x\ W\ x\ L^{-3}$$

W is body mass (g) and L is total body length (cm).

2.6.3 Data analyses

All data analyses were performed in RStudio Version 1.2.5033 (RStudio Team, 2020) and R version 3.6.2 (R Core Team, 2020). Wilcoxon rank sum tests were used to test for differences, when data did not meet normality. For hypothesis testing, observed differences between groups were considered significant when P-values were below 0.05. Six individuals (2 adult sea trout and 4 adult salmon) with unknown genetically tested sex were excluded from statistical analyses including sex as an explanatory variable. All mean values were calculated based on individual means to ensure independence of the data.

The temperature experienced by individual fish was investigated by mixed effects models with temperature as response variable and sex (S), species (SP), life stage (LS), total body length (L), date (D) and zone (Z) as explanatory variables and with fishID as random factor. The mixed effects models for experienced temperature were performed using the linear mixed effect model function "lme", from the "nlme" package in R. Due to missing values in the explanatory variables, some individuals were removed from the models. This resulted in n = 40 for adult Atlantic salmon, n = 69 for adult sea trout, n = 121 for Atlantic salmon smolt and n = 109 for sea trout smolt. Here, separate models were fitted for each species and life stage (adult/smolt).

Prior to modelling all individuals with missing values were removed, and all continuous explanatory variables (temperature, total body length and date) were standardized using the "scale" function in the R "base" package. Life stage replaced total body length as explanatory variable in models including two life stages, due to the two variables being highly correlated. The variance inflation factors (VIF) were investigated using the "check collinearity" function in the "performance" package in R. Model selection was performed with the "dredge" function in the "MuMIn" R-package (Bartoń, 2022) based on the second order of Akaike's information criterion (AICc). Due to a relatively high number of explanatory variables causing the sample size (n) to estimated parameter (K) ratio (n/K) to be lower than 40 for some of the models, the second order of Akaike's information criterion (AICc) rather than Akaike's information criterion (AIC) was chosen (Burnham *et al.*, 2011). When several alternative models were supported by the model selection (ΔAICc < 2, (Anderson *et al.*, 2001) conditional model averaging was applied, allowing inference from all models with AICc < 4 to calculating conditional average model parameter estimates and their standard errors.

3. RESULTS

3.1 CHARACTERISTICS OF TAGGED INDIVIDUALS

Mean Fulton's body condition factor at the time of capture was 1) 0.58 (SD = 0.12) for all tagged adult Atlantic salmon, 2) 0.88 (SD = 0.134) for all tagged adult sea trout, 3) 0.84 for all tagged Atlantic salmon smolt, and 4) 0.82 for all tagged sea trout smolt. For all adult fish tagged in the fall of 2020 and the spring of 2021 the condition factor was higher for the fish tagged in the fall of 2020, than for the fish tagged in the spring of 2021 (Welch's t-test, sea trout n = 97, $P < 0.001$; Atlantic salmon n = 97, $P = 0.014$, figure x). For all tagged smolt the condition factor was higher for sea trout smolt, than for Atlantic salmon smolt (Welch's t-test, n = xx, P < 0.01, figure x). The body condition did not differ between the sexes for any of the study groups (Wilcoxon rank sum test, $P > 0.05$).

Of the scales sampled from 57 tagged adult Atlantic salmon, 50 samples were suitable to analyze, while scale samples from 60 tagged adult sea trout were suitable for scale reading. Mean age for adult Atlantic salmon was 6.5 years (SD = 1.0; range 3-8 years). Mean age for adult sea trout was 4.7 years (SD = 1.0; range 2-5 years).

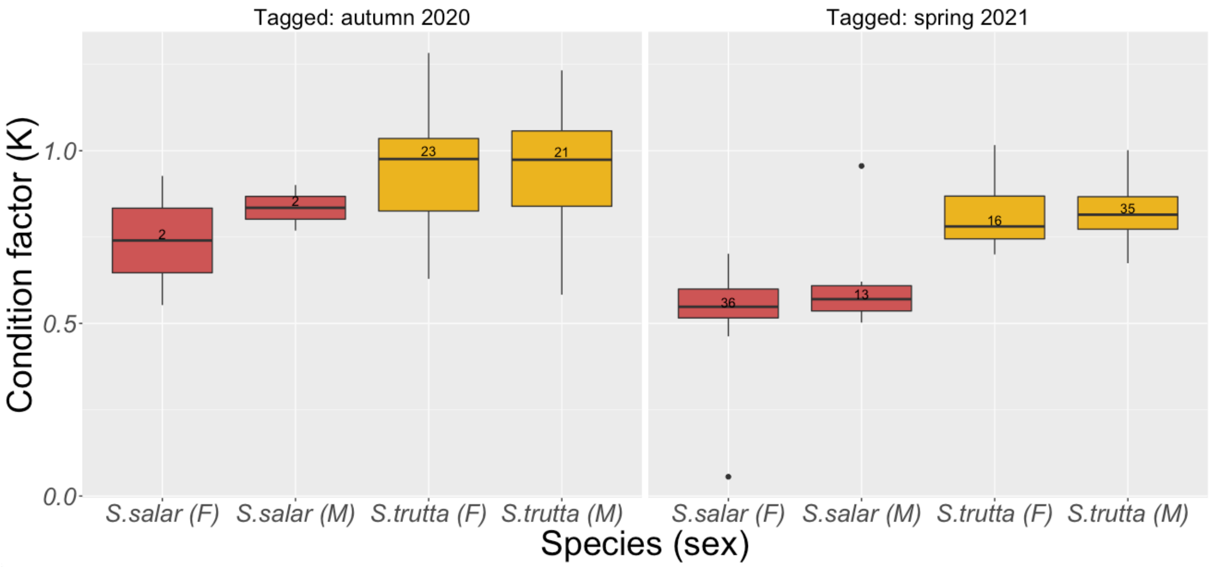


Figure 7 a : Fulton's condition factor (at the time of capture) for adult Atlantic salmon and sea trout, with fish tagged in the autumn of 2020 in the panel to the left and the fish tagged in the spring of 2021in the panel to the right. The box-plots shows 50% of the data points for each group within each box, the 5th and 95th percentiles (whiskers) and the median values (bold line). Sample size (*n*) of each tagging group is indicated by number within boxes. Sex is presented by M/F in parentheses.

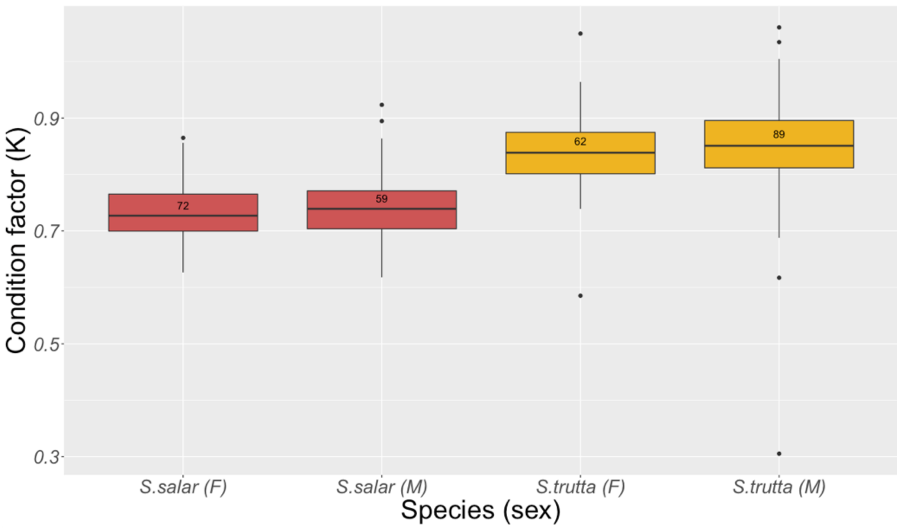


Figure 7 b: Fulton's condition factor (at the time of capture) for Atlantic salmon and sea trout smolt, tagged in the spring of 2021. The boxplots show 50% of the data points for each group within each box, the 5th and 95th percentiles (whiskers) and the median values (bold line). Sample size (*n*) of each tagging group is indicated by number within boxes. Sex is presented by M/F in parentheses.

3.2 HABITAT USE OF SEA TROUT AND SALMON

3.2.1 Overview of telemetry results

Of the total 450 fish tagged in the autumn of 2020 and spring of 2021, 396 (88 %) were detected by at least one receiver in the study area, the connected fjord system or upstream from 10.04.-15.09.2021. During the study period, the numbers of tagged fish detected in the estuary were 52 (91%) of 57 the tagged adult Atlantic salmon, 80 (83%) of 97 the tagged adult sea trout, 124 (88%) of 142 the tagged Atlantic salmon smolt and 120 (78%) of 154 the tagged sea trout smolt. As presented in "Figure 8", adult salmon were detected in the estuary from 15.04.-22.05, adult sea trout from 09.04.-14.09, Atlantic salmon smolt from 04.05.-27.07, and sea trout smolt from 21.04.-14.09.

Numbers of fish detected on one or more listening stations in the fjord/nearby marine areas were 51 adult Atlantic salmon, 61 adult sea trout, 121 Atlantic salmon smolt and 115 sea trout smolt, while the number of fish detected on one or more listening stations upstream were 42 adult Atlantic salmon, 59 adult sea trout, 75 Atlantic salmon smolt and 110 sea trout smolt. During the full study period, there were a total of 4 245 950 detections in the study area, and 1 141 081 detections by receivers outside the estuary (upstream or in the fjord).

3.2.2 Use of estuarine habitats use during spring and early summer

During the seaward spring migration (01.05.-30.06.2021), a total of 349 (78%) individuals of the 450 tagged fish, were detected by at least one receiver in the three estuarine habitats. With 98% of the total detected Atlantic salmon adults in this period, the river channel was visited by nearly all detected individuals, while 74% and 21% were observed in the exposed intertidal mudflats and the sheltered intertidal mudflats, respectively. In contrast, sea trout adults were observed with 77% of the total detected sea trout adults residing in the sheltered intertidal mudflats. The river channel was visited by 91% adult sea trout, and 79% in the exposed intertidal mudflats.

For smolts of both species, the river channel was observed used by nearly all individuals during this period, with 98% Atlantic salmon and 98% sea trout detected in this habitat. For Atlantic salmon smolt, 78% were observed utilizing the exposed intertidal mudflats, next to 92% of sea trout smolt. The sheltered intertidal mudflats were observed used by 51% of the sea trout smolt, while visited by 16% of the Atlantic salmon smolt. The total number of detections during this period were 2 058 088, with 438 090 in the exposed intertidal mudflats, 828 912 in the river channel and 791 086 in the sheltered intertidal mudflats.

Table 4: Number of fish (*n*) detected from each study group between 1 May and 30 June, distributed in the three estuarine habitats.

Date: 01.05.-30.06.2021	Exposed intertidal mudflats	River channel	Sheltered intertidal mudflats	Total
	n (% of total n)	n (% of total n)	n (% of total n)	*n*
Adult Atlantic salmon	32 (74%)	42 (98%)	9 (21%)	43 (100%)
Adult sea trout	55 (79%)	64 (91%)	54 (77%)	70 (100%)
Atlantic salmon smolt	96 (78%)	121 (98%)	20 (16%)	123 (100%)
Sea trout smolt	100 (91%)	107 (98%)	56 (51%)	109 (100%)

3.2.2 Residence time in different habitats within the estuary

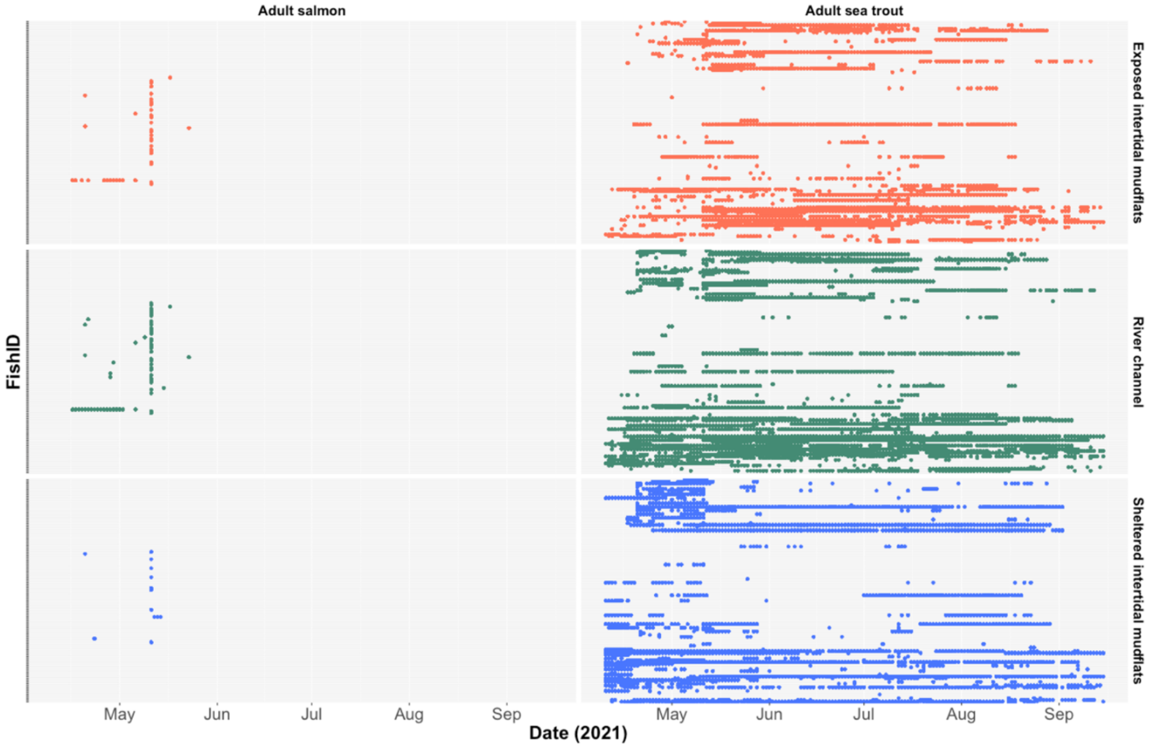
The number of detections (Figure 8, a) and b)), revealed that Atlantic salmon were detected in the estuary for a short period of time during the study period, compared to sea trout. A peak in numbers of adult Atlantic salmon (*n* = 38, Figure 9, a)) and for Atlantic salmon smolt (*n* = 82, Figure 9, b)), was evident between 8 May and 15 May. Atlantic salmon smolt had a second, less prominent peak (*n* = 19, Figure 9, b)) in number of detected individuals, between 22 May and 29 May. Atlantic salmon were shown to spend most of their time in the fjord throughout the study period (Figure 10, a) and b)). Atlantic salmon smolt were shown to spend 31% of their time in the estuarine habitats during the week of peak migration (Table 4). Many fish were shown to visit the exposed intertidal mudflats (Figure 9, a)) and b)), however little time was spent in this habitat (Figure 10, a) and b)). The sheltered intertidal mudflats were shown least important to Atlantic salmon, as only a few individuals were detected during their stay in the estuary (Figure 9, a) and b)). Salmon smolt spent at most 97 % of their time in the fjord between 15 May and 22 May. Atlantic salmon adults only spent 3% of their time in the estuary during the migration peak (Table 4). The last Atlantic salmon adults (*n* = 2) to exit the estuary were last observed between 15 May and 22 May, while smolt were detected in low numbers (*n* = 1-8) in the estuary through the second week of June. Some were however observed to spend time upstream through July. For all subsequential weeks, there were no detections of tagged Atlantic salmon in the estuary. Although, it was without certainty no smolt resided in the area after the second week of June, due to the expected battery life of the fish tags. Adult salmon detected outside the estuary spent time in the fjord until they exited the fjord system and remained undetected throughout the study period.

Sea trout on the other hand, were shown to spend time in the estuary throughout the study period (Figure 10, a) and b)) and are shown moving between the different habitats (Figure 8, a) and b)). During the peak migration, there seemed to be a shift from most adult sea trout residing in the sheltered intertidal mudflats, to the river channel (Figure 9 a). However, adult sea trout had approximately good portions of time spent in sheltered mudflats throughout the tracking period with the lowest residence time of 16% from 29 May to 5 of June. According to the data, the sheltered intertidal mudflats habitat was most important for adult sea trout than any other group throughout the study period (Figure 8-10). Here, their highest residence time of 75%, was spent during 4 April – 10 April, and the lowest residence time of 16% from 29 May to 5 of June. Between 1 May and 1 July, Adult sea trout spent at most, 15% of their time in the exposed intertidal mudflats and 29% in the fjord. For sea trout smolt, there was an evident reduction in fish detected in the estuarine habitats from Mid-June to July (Figure 9, a)), and more time was spent in the fjord (Figure 10, a)). Sea trout smolt spent 50% of their residence time in the fjord first week in June. They spent time in all three estuarine habitats throughout the study period, where the exposed intertidal mudflats were at the most used with 21% of their time during the second week of August.

Table 5: Number of fish (*n*) detected during the peak migration of Atlantic salmon between 8 May and 15 May, and percentage residence time (%) for the respective week in the three estuarine habitats and the total for all habitats, for each study group.

Date: 08.-15.05.2021	Exposed intertidal mudflats		River channel		Sheltered intertidal mudflats	
	(n)	Residence time (%)	(n)	Residence time (%)	(n)	Residence time (%)
Atlantic salmon adults	26	0.3%	37	2 %	9	1 %
Sea trout adults	39	9 %	46	29 %	39	35 %
Atlantic salmon smolt	67	8 %	84	22 %	9	1 %
Sea trout smolt	35	7%	41	21 %	13	8 %

a)



b)

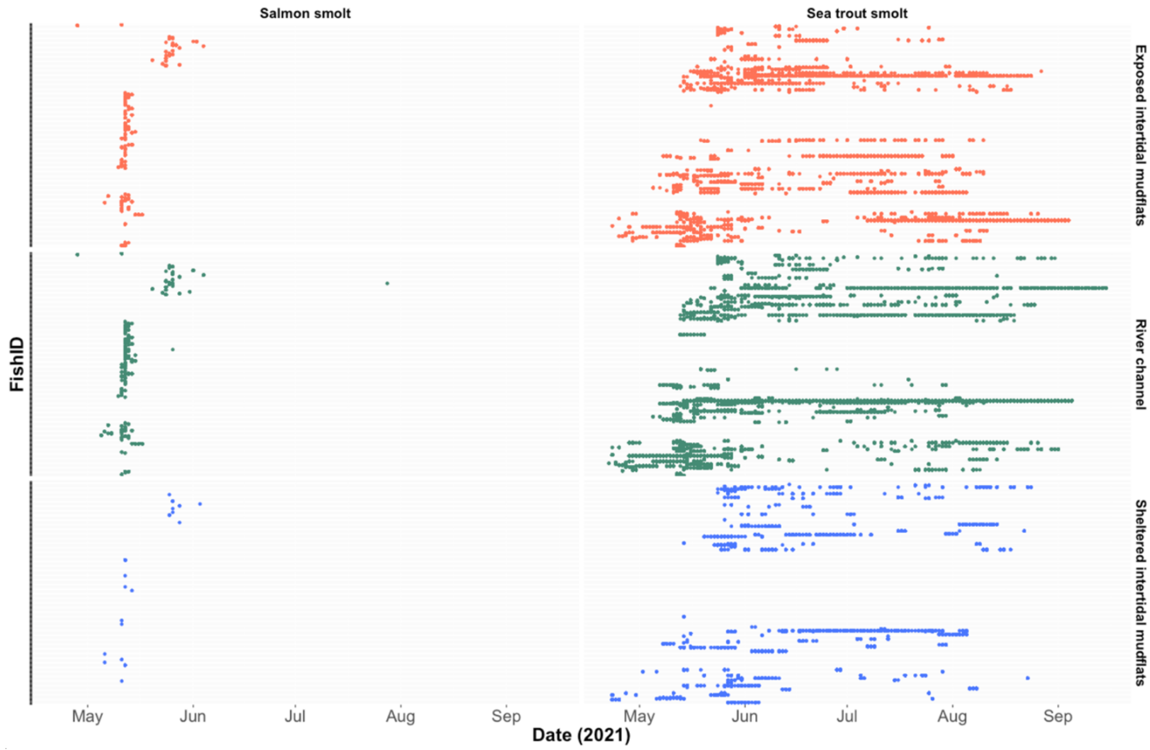
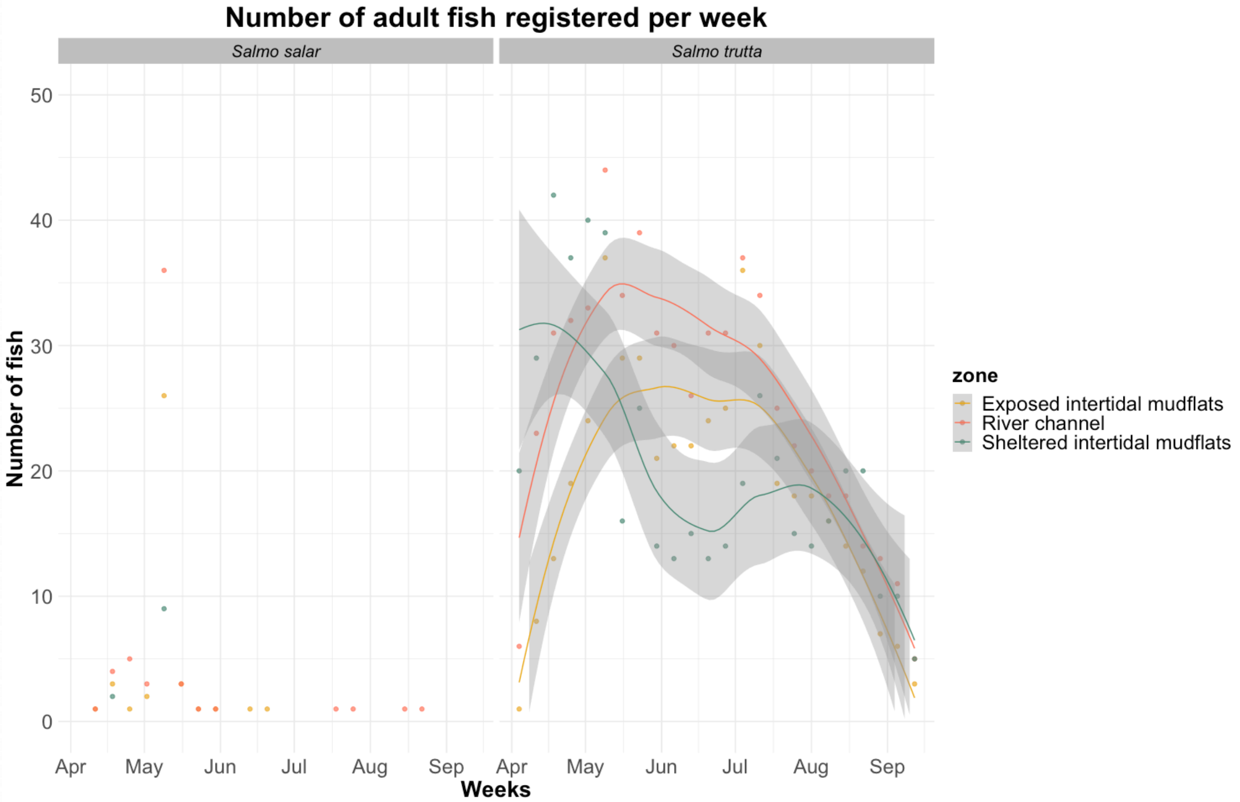


Figure 8: Habitat use in the estuary during the study period **a)** adult Atlantic salmon and sea trout, and **b)** Atlantic salmon and sea trout smolt. Each fish is represented by an individual line (y-axis) and its continuous registrations in the three estuarine habitats over time (x-axis).

a)



b)

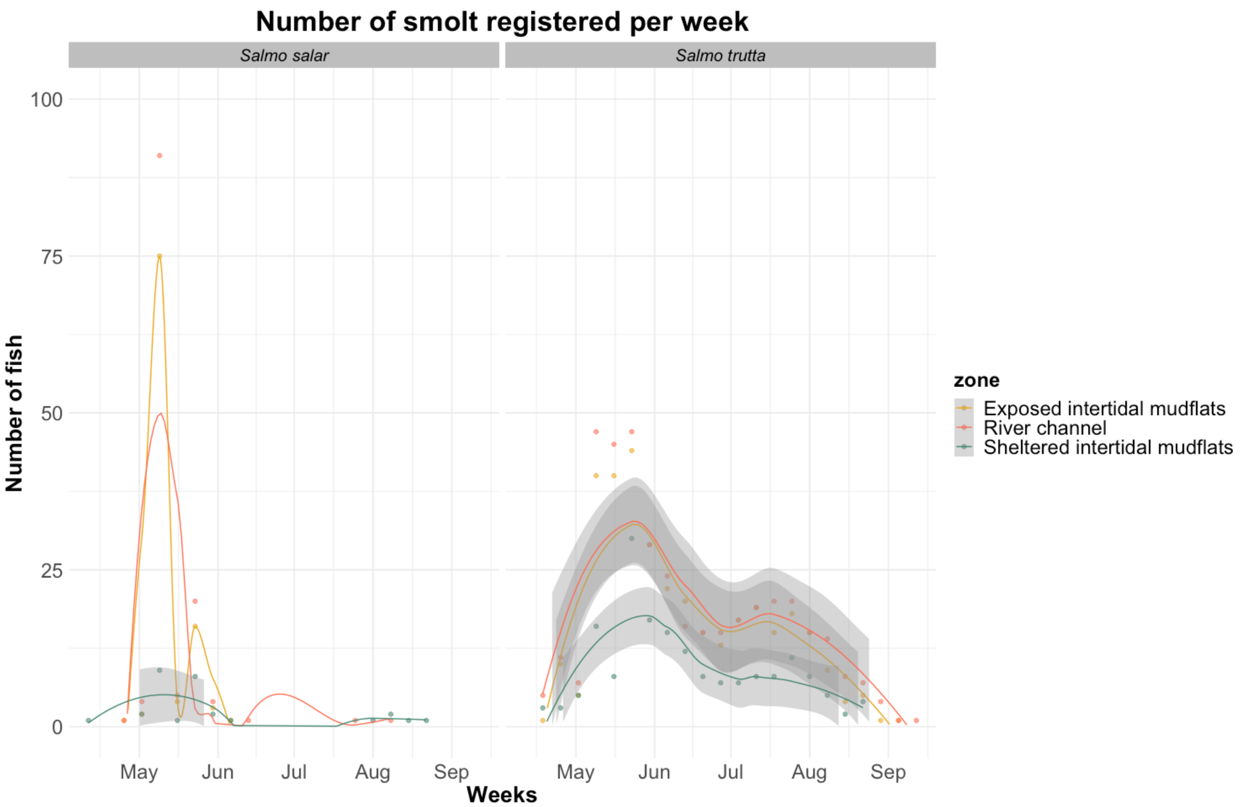


Figure 9: Number of fish registered per week in each zone **a)** adult Atlantic salmon and sea trout **b)** Atlantic salmon and sea trout smolt.

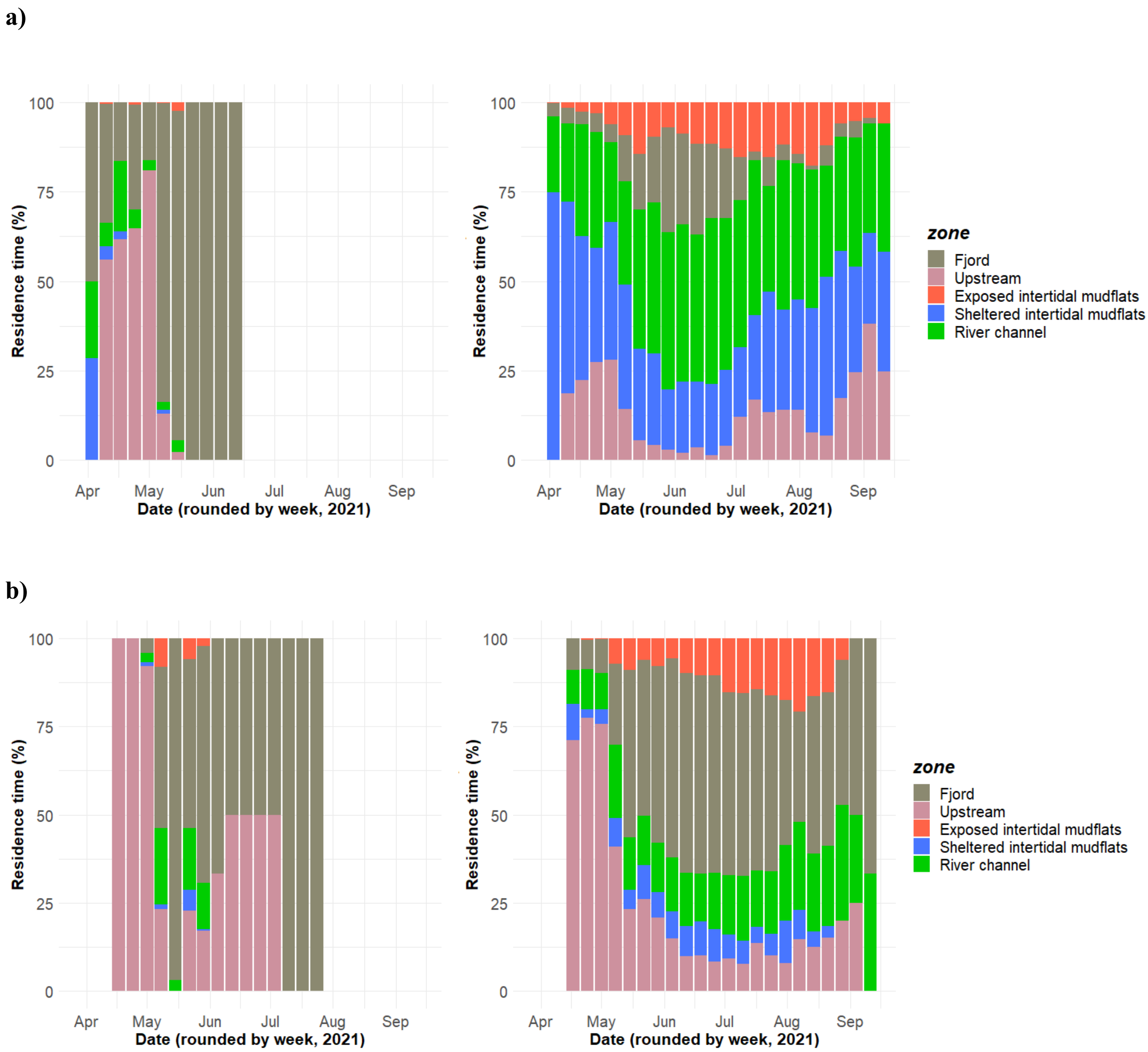


Figure 10: Percent residence time for Atlantic salmon and trout in; the fjord (beige), upstream (pink), exposed intertidal mudflats (red), sheltered intertidal mudflats (blue) and the river channel (green), during the study period, **a)** adult Atlantic salmon (left) and adult sea trout (right), and **b)** Atlantic salmon smolt (left) and sea trout smolt (right). Each bar represents one week and the average proportions of residence time in the different habitats by the fish. The number of fish may differ between weeks.

3.3 WATER TEMPERATURE EXPERIENCED BY SEA TROUT AND ATLANTIC SALMON

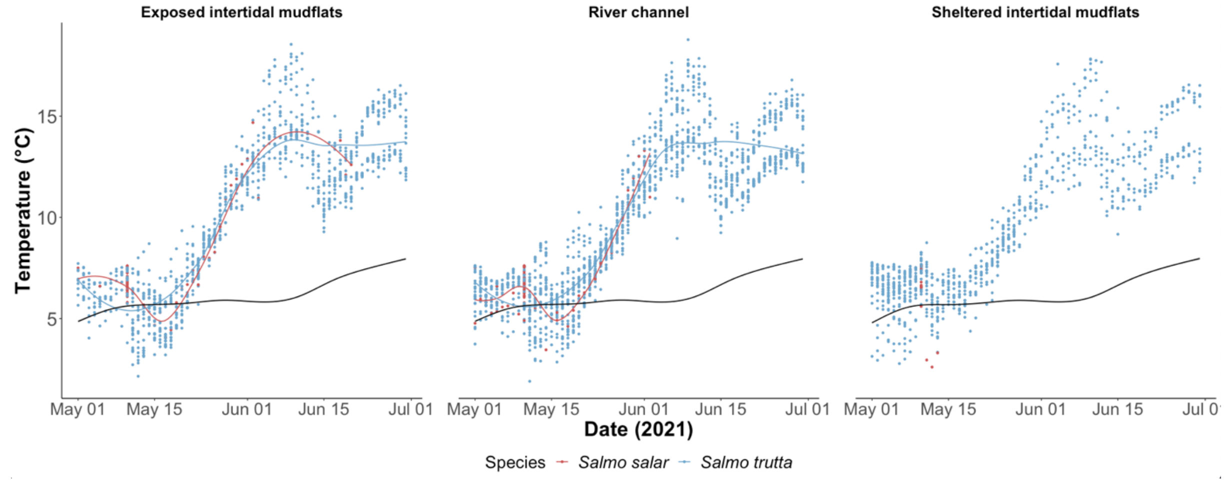
3.3.1 Temperature of the surrounding water masses

During spring and early summer, temperature was recorded for a total of 343 (76%) individuals of the 450 tagged fish, residing in at least one of the three zones in the estuary. This included $n = 43$ for adult Atlantic salmon, $n = 70$ for adult sea trout, $n = 123$ for Atlantic salmon smolt and $n = 109$ for sea trout smolt. From late May until 1 July all fish detected in the estuarine habitats experienced temperatures warmer (Figure 11) than the bottom marine water temperature at approximately 16 meters depth, measured by acoustic receiver H7, which was placed outside the river mouth between the pier and Billedholmene (Figure 2). During the peak migration, Atlantic salmon and sea trout experienced temperatures both warmer and colder than the marine water. Atlantic salmon experienced temperatures between 2.6-7.6°C for adults and between 2.2-16.8°C for smolt, while sea trout experienced temperatures between 1.5-19.9°C, and between of 2.2-20.6°C for smolt.

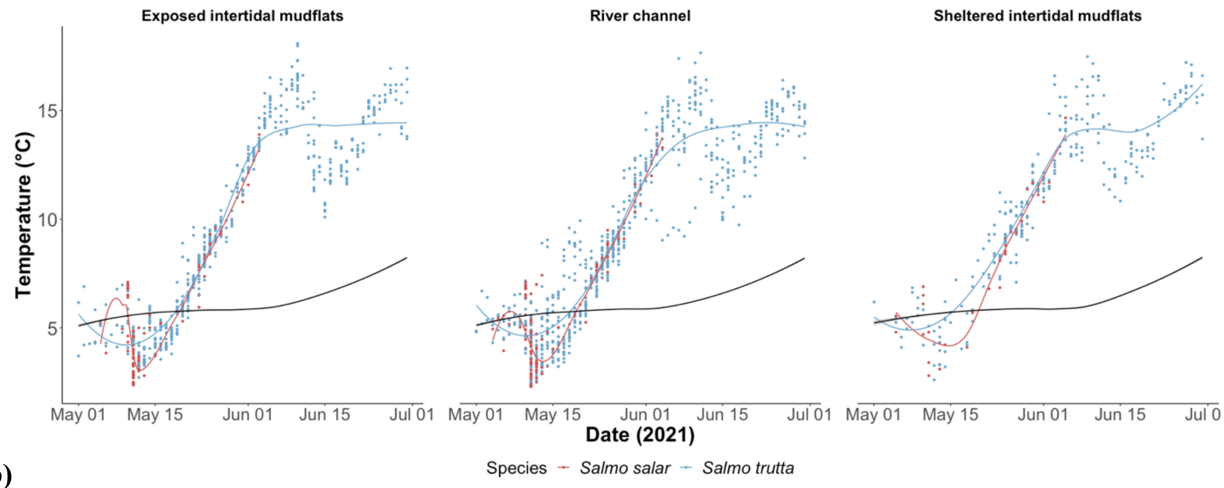
The daily averaged experienced water temperature during the peak migration (Table 6) ranged from approximately 5°C to 11°C. Atlantic salmon adults experienced temperatures around 6°C in all three habitats, while Atlantic salmon smolt experienced temperatures around 5°C in the exposed intertidal mudflats and the river channel, and around 7°C in the sheltered intertidal mudflats. Sea trout experienced temperatures around 9-10°C in all three habitats, although sea trout smolts experienced the highest daily average in the sheltered intertidal mudflats around 11°C. The daily averaged experienced water temperature differed between the two species, where sea trout smolts experienced a higher daily average than Atlantic salmon smolts (Wilcoxon rank sum test, $P < 0.01$), and adult sea trout experienced a higher daily average than adult Atlantic salmon (Wilcoxon rank sum test, $P < 0.05$).

Table 6: Daily averaged experienced temperatures for sea trout and Atlantic salmon in three estuarine habitats, during the peak migration from 08 May to 15 May (2021). The daily average is highlighted in **bold**, and range is included in parentheses.

	Exposed intertidal mudflats	River channel	Sheltered intertidal mudflats
Adult Atlantic salmon	**6.7 °C** (5.3-7.6°C)	**6.5 °C** (3.5-7.6°C)	**5.7 °C** (2.6-7.6°C)
Adult sea trout	**10.1 °C** (2.2-8.7°C)	**9.9 °C** (1.9-8.8°C)	**9.0 °C** (2.8-8.8°C)
Atlantic salmon smolt	**5.2 °C** (2.4-7.1°C)	**5.4 °C** (2.3-7.4°C)	**7.5 °C** (2.8-6.9°C)
Sea trout smolt	**9.6 °C** (2.4-6.9°C)	**9.3 °C** (2.3-9.0°C)	**11.0 °C** (2.6-6.9°C)



a)



b)

Figure 11: Daily average experienced temperatures (°C) recorded for **a)** adult Atlantic salmon (red) and adult sea trout (blue), and **b)** Atlantic salmon smolt (red) and sea trout smolts (blue), in the three estuarine habitats. The black line represents the daily average marine temperature measured by acoustic receiver H7 outside the river mouth, on approximately 16 meters depth. Each dot represents the daily average temperature of an individual fish.

3.3.2 Influence of individual characteristics on the experienced temperature of sea trout and Atlantic salmon

General Linear Models – mixed effects model

The influence of individual characteristics on the individual's temperature use were explored for Atlantic salmon and sea trout, using one generalized linear model for 1) adult individuals of salmon and sea trout, 2) salmon and sea trout smolts, 3) salmon adults and smolts, and 4) sea trout adults and smolts. Experienced temperature for individuals where all other necessary information/values for statistical modelling was also complete, was recorded for a total of 339 individuals of the tagged fish residing in at least one of the three zones of the estuary in the study period. Thus, the number of individuals (*n*) included in the models were 40 (93%) of 43 adult Atlantic salmon, 69 (98%) of 70 adult sea trout, 121 (98%) of 123 Atlantic salmon smolt and 109 (100%) of 109 sea trout smolt.

1) Adult salmon and sea trout

For adult individuals, model selection identified three equally well fitted models (table x), where combinations of date, species, total body length, and/or zone (Δ AIC < 2, table 7) were included as explanatory variables. Date and zone were included in all the best fitted models (table 7). Model averaging estimates (Δ AIC < 4, figure 12) revealed that adult Atlantic salmon had lower experienced temperature than adult sea trout, that the experienced temperature increased throughout the season and that experienced temperature increased with increasing body size. The estimates also showed that adult fish used water masses of warmer temperatures in zone 2 (the river channel) and zone 3 (sheltered intertidal mudflats) compared to zone 1 (exposed intertidal mudflats), and that they used water masses with warmer temperatures in zone 3 compared to zone 2. Sex seemed to have limited influence on the use of temperature for adult fish as the standard error exceeded the estimate (Figure 12).

Table 7. Model selection of mixed effects models for the influence of total body length (*L*), sex (S), date (D), zone (Z) and species (SP) on individual's experienced temperature in the period 01.05.-31.06.2021 for adult Atlantic Salmon and sea trout. The models are ranked by decreasing Δ AICc value, with supported models highlighted in bold (Δ AICc < 2).

Model	AICc	Δ AICc	AICc weights	d.f.
[D, SP, L, Z]	5240.4	0.00	0.258	8
[D, Z,]	5241.6	1.20	0.141	6
[D, L, Z]	5242.0	1.62	0.115	7
[D, S, SP, L, Z]	5242.4	2.00	0.095	9

[D, SP, L]	5242.9	2.56	0.072	6

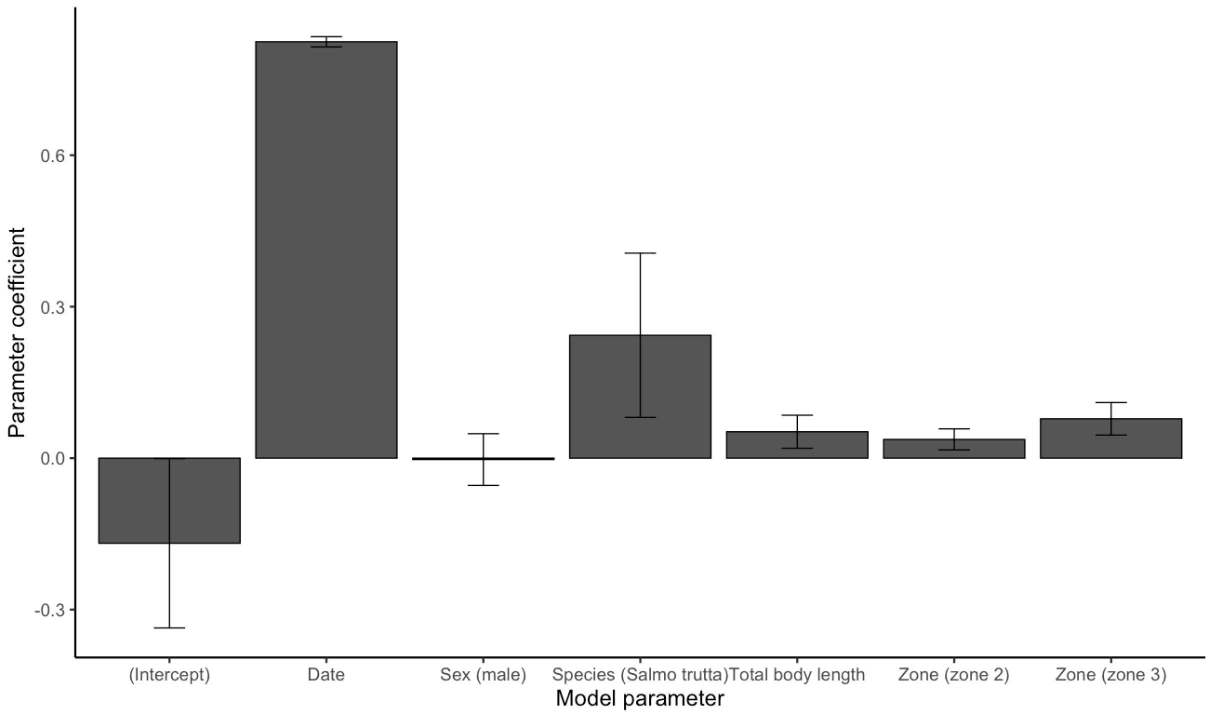


Figure 12. Conditional model averaging summary statistics for mixed effects models with Δ AIC < 4 for the effect of total body length (*L*), sex (S), date (D), zone (Z) and species (SP) on individual's experienced temperature in the period 01.05.-31.06.2021 for adult Atlantic Salmon and sea trout.

2) Sea trout and salmon smolts

For smolts, model selection identified four equally well fitted models (table w), where combinations of date, species, total body length, zone and/or sex (Δ AIC < 2, table 8) were included as explanatory variables. Date, species and zone were included in all of the best fitted models (Table 8). Model averaging estimates (Δ AIC < 4, figure 13) revealed that Atlantic salmon smolts had lower experienced temperature than sea trout smolts, males used warmer water than females, that the experienced temperature increased throughout the season (May-June), and that smaller smolt used colder water masses compared to larger smolt. The estimates also showed that compared to the temperature use in zone 1 (exposed intertidal mudflats), smolts used warmer water masses in zone 3 (sheltered intertidal mudflats), and slightly colder water masses in zone 2 (the river channel).

Body size seemed to have limited influence on the use of temperature for adult fish as the standard error exceeded the estimate (Figure 13).

Table 8. Model selection of mixed effects models for the influence of total body length (*L*), sex (S), date (D), zone (Z) and species (SP) on individual's experienced temperature in the period 01.05-31.06.2021 for Atlantic Salmon and sea trout smolt. The models are ranked by decreasing Δ AICc value, with supported models highlighted in bold (Δ AICc < 2).

Model	AICc	Δ AICc	AICc weights	d.f.
[D, S, SP, L, Z]	**1932.5**	**0.00**	**0.361**	**9**
[D, S, SP, Z]	**1932.6**	**0.16**	**0.333**	**8**
[D, SP, L, Z]	**1934.2**	**1.74**	**0.152**	**8**
[D, SP, Z]	**1934.2**	**1.74**	**0.151**	**7**
[D, S, Z]	1934.2	11.94	0.001	7

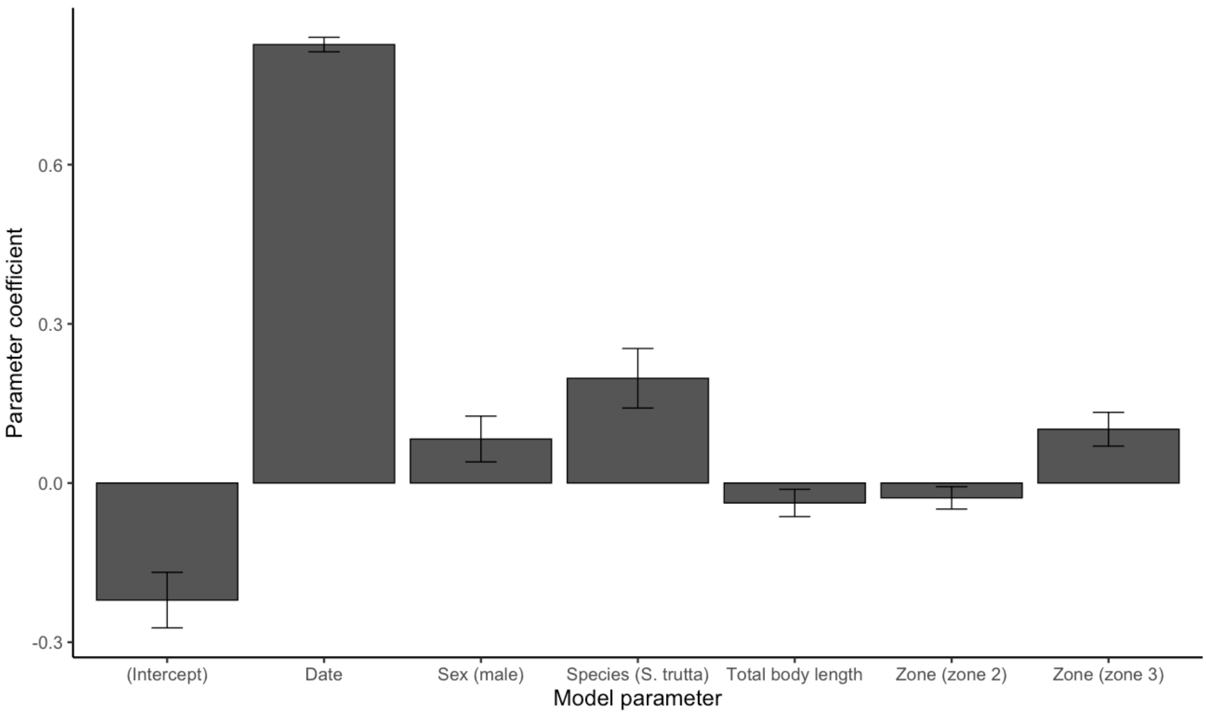


Figure 13. Conditional model averaging summary statistics for mixed effects models with Δ AICc < 4 for the effect of total body length (*L*), sex (S), date (D), zone (Z) and species (SP) on individual's experienced temperature in the period 01.05.-31.06.2021 for Atlantic Salmon and sea trout smolt.

3) Salmon adults and smolts

For all tagged Atlantic salmon (smolt and adult individuals), model selection identified four equally well fitted models including combinations of date, life stage, sex and/or zone as explanatory variables (Δ AICc < 2, table 9). The estimates presented by model averaging (Δ AIC < 4, Figure 14) suggested that the experienced temperature of Atlantic salmon increased through May-June, that they had warmer experienced temperatures when residing in in zone 2 (the river channel) compared to zone 1 (exposed intertidal mudflats), that males used warmer water compared to female individuals, and that salmon smolt had lower b experienced temperature than adult individuals. The estimates also revealed that zone 3 had limited influence on experienced temperature of the Atlantic salmon as the standard error exceeded the estimated estimates (Figure 14).

Table 9. Model selection of mixed effects models for the influence of sex (S), date (D), zone (Z) and life stage (LS) on individual's experienced temperature in the period 01.05-31.06.2021 for Atlantic Salmon. The models are ranked by decreasing Δ AICc value, with supported models highlighted in bold (Δ AICc < 2).

Model	AICc	Δ AICc	AICc weights	d.f.
[D, LS]	**645.1**	**0.00**	**0.318**	**5**
[D, LS, S]	**645.3**	**0.12**	**0.299**	**6**
[D, LF, Z]	**646.1**	**0.94**	**0.198**	**7**
[D, LS, S, Z]	**646.2**	**1.08**	**0.185**	**8**
[D]	711.8	66.65	0.000	4

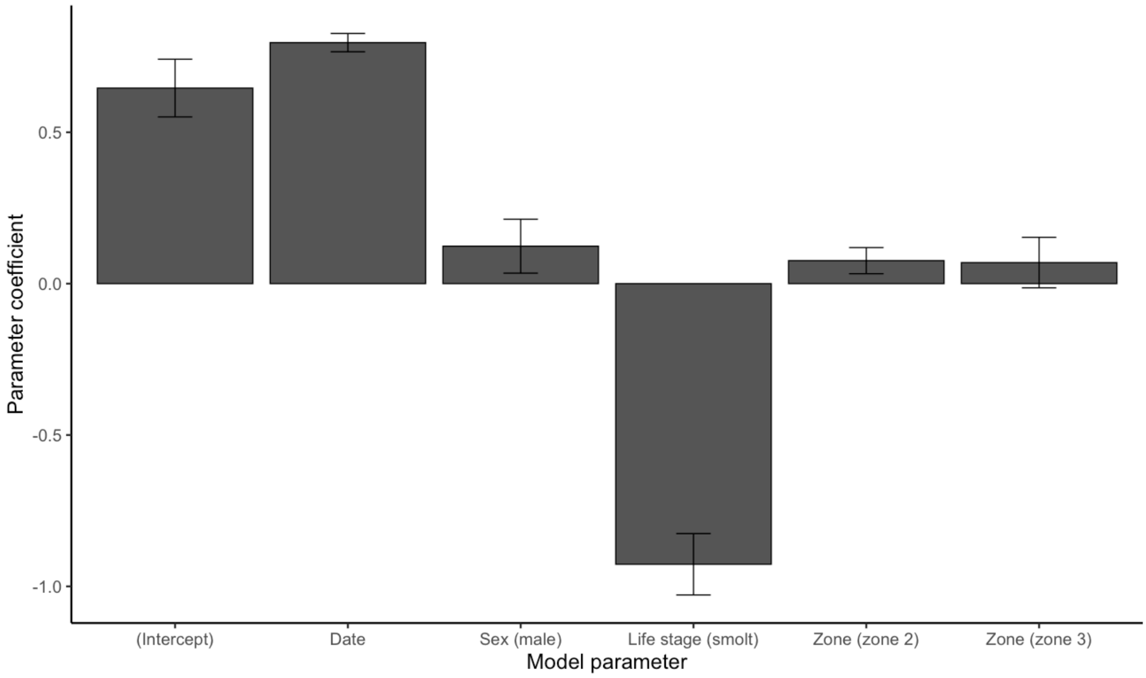


Figure 14.
Conditional model averaging summary statistics for mixed effects models with Δ AICc < 4 for the effect of total body length (*L*), sex (S), date (D), zone (Z) and species (SP) on individual's body temperature in the period 01.05-31.06.2021 for Atlantic Salmon smolts and adults.

4) Sea trout adults and smolts

For all tagged sea trout (smolt and adult individuals), model selection identified three equally well fitted models including combinations of date, life stage, sex and/or zone as explanatory variables (Δ AIC < 2, table 10). The estimates presented by model averaging (Δ AIC < 4, Figure 15) suggested that the experienced temperature of sea trout increased through May-June, that they had warmer experienced temperatures when residing in in zone 3 (exposed intertidal mudflats) compared to zone 1 (exposed intertidal mudflats), and that sea trout smolt had lower average experienced temperature than adult individuals. The estimates also revealed that zone 2 (the river channel) and sex had limited influence on experienced temperature of sea trout as the standard error exceeded the estimated estimates (Figure 15).

Table 10. Model selection of mixed effects models for the influence of sex (S), date (D), zone (Z) and life stage (LS) on individual's experienced temperature in the period 01.05-31.06.2021 for sea trout. The models are ranked by decreasing Δ AICc value, with supported models highlighted in bold (Δ AICc < 2).

Model	AICc	Δ AICc	AICc weights	d.f.
[D, LS, Z]	7035.2	0.00	0.433	7
[D, Z]	7036.1	0.84	0.284	6
[D, LS, S, Z]	7037.1	1.89	0.168	8

[D, S, Z]	7037.9	2.66	0.114	7
[D, LS]	7056.9	21.68	0.000	5

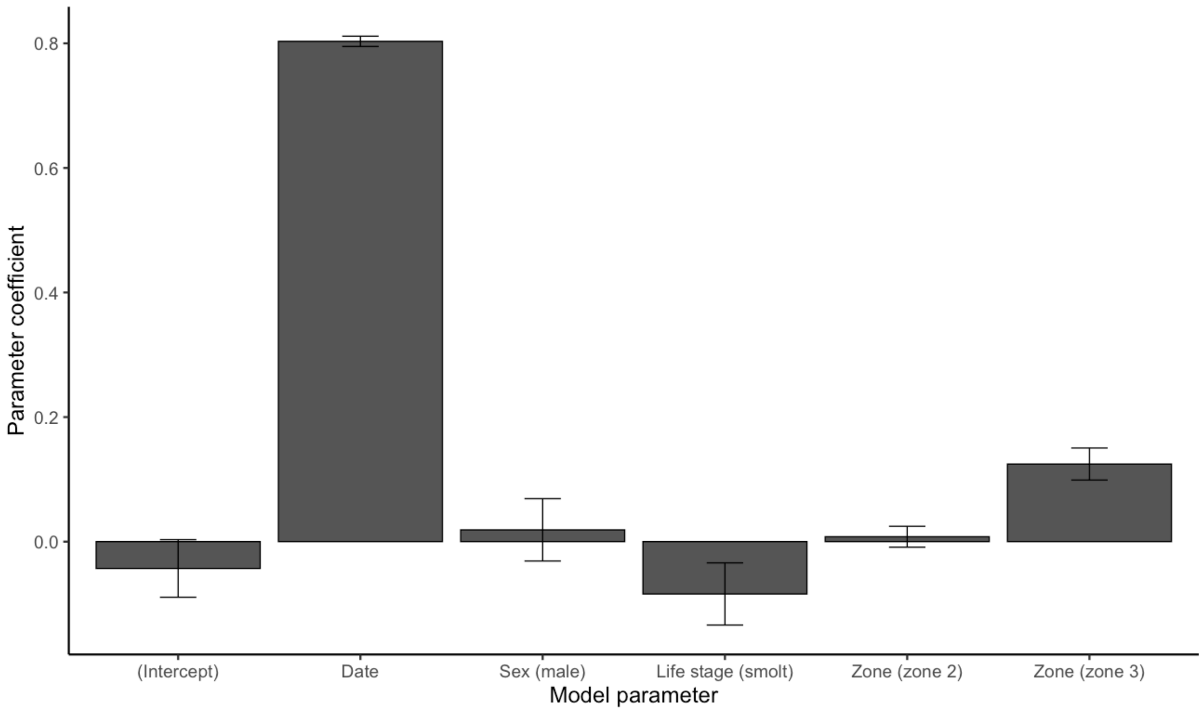


Table 15. Conditional model averaging summary statistics for mixed effects models with Δ AICc < 4 for the effect of total body length (*L*), sex (S), date (D), zone (Z) and species (SP) on individual's experienced temperature in the period 01.05.-31.06.2021 for Sea trout smolts and adults.

4. DISCUSSION

The estuarine habitat serves as a key part in the migration journey of seaward migrating sea trout and Atlantic salmon. The present thesis explored the utilization of three estuarine habitats, including recorded experienced temperature, for sea trout and Atlantic salmon adults and smolts in the Stjørdal river estuary in Middle Norway. The sea trout and Atlantic salmon were tracked for approximately 5 months, where the seaward spring migration was in focus. The results of this study indicated that residence time in the estuary varied between the four groups of fish, thus suggesting that species and life stage influenced the use/utilization of the estuarine area.

The seaward migration of Atlantic salmon was shown to occur collectively during essentially one week, from the Stjørdal river to the Trondheim fjord. Atlantic salmon adults spent only 3% of their time that week in the estuary, while not detected for most of the study period thereafter. On the contrary, adult sea trout arrived spread throughout the study period, and visited the estuarine habitats throughout the summer. The fact that Atlantic salmon in general had a short residency in the estuary during the seaward migration corresponds with previous studies from other watercourses including both adults (Halttunen *et al.*) and smolts (Thorstad *et al.*, 2004; Thorstad *et al.*, 2007; Davidsen *et al.*, 2009; Thorstad *et al.*, 2012). As environmental thresholds for triggering migration are considered genetically determined in anadromous individuals (Aarestrup *et al.*, 2002; Eldøy *et al.*, 2021), the collective migration timing for adult salmon indicate that Atlantic salmon were triggered simultaneously by these genetically determined thresholds. The present study also found that sea trout had a high residence time in the estuary throughout the season compared to the fjord. These findings are supported by studies showing that some sea trout are known to migrate short distances to their natal river estuary (Bordeleau *et al.*, 2018; Eldøy *et al.*, 2021), and in general many sea trout are likely to spend much time in near coastal areas in vicinity to their natal river, during their marine phase (Lyse *et al.*, 1998; Jensen *et al.*, 2014; Eldøy *et al.*, 2015; Thorstad *et al.*, 2016). The collective and quick migration found in Atlantic salmon, may be favorable to salmonids to avoid predation by large marine animals, such as the common harbour seal (*Phoca vitulina*) (Carter *et al.*, 2001; Middlemas *et al.*, 2006; Wright *et al.*, 2007). However, if salmonid predation in the Stjørdal estuary was prominent, it would be reasonable to expect a negative effect on the estuarine residence time for the sea trout population, who is shown to frequently visit all estuarine habitats in spring and early summer. This could possibly be explained by sea trout smolts needing more time than Atlantic salmon smolt to adapt to seawater. The high residence time by sea trout in all estuarine habitats might just as well indicate refuge from heavy predation in the marine areas. At the time of seaward migration, salmonid predators such as cod and pollock (Hvidsten & Lund, 1988; Jepsen *et al.*, 2006), gulls *(Larus spp.),* cormorants *(Phalacrocax carbo*) (Jepsen *et al.*, 2019) and the harbour seal, would likely be present outside the river mouth. An additional explanation could be that sea trout smolt resided in layers of water with lower salinities than the marine predators.

The habitat use of sea trout was observed with a shift in the end of May, where the number of adult sea trout residing in the sheltered intertidal mudflats decreased, while numbers increased in the river channel. This shift may suggest variation within the population, where some switched between different estuarine habitats, as well as the upstream river and nearby marine areas. Hence, the present findings support studies (Cucherousset *et al.*, 2005; del Villar-Guerra *et al.*, 2014) suggesting migratory behavior of sea trout should be considered as a continuum rather than a fixed choice between becoming a migrant or a freshwater resident. Furthermore, studies have shown individuals may assess their own needs through several environmental cues and physiological and fitness related factors, rather than relying on a fixed strategy (Cucherousset et al. 2005, Boel et al. 2014, del VillarGuerra et al. 2014).

The present thesis found that Atlantic salmon smolt had a longer residency than adults of their respective species, while sea trout smolt were found with a shorter estuarine residency than adult sea trout. Although residence time in the estuary was short for Atlantic salmon smolt compared to sea trout, the residence likely still represents an important phase, as the transition from freshwater to seawater is an energy-intensive and vulnerable phase for smolts (Thorstad *et al.*, 2012; Harvey *et al.*, 2020). The fact that Atlantic salmon smolt had a longer residence than adults, could be explained by an extension of estuary residence and nearby marine areas to forage, as found in many populations (Hubley *et al.*, 2008; Lacroix, 2013; Bordeleau *et al.*, 2019). As shown by Rikardsen *et al.* (2004), post-smolts in Northern Norwegian populations have been found to feed in areas nearby their natal river immediately after the seaward migration. Consequently, Atlantic salmon smolt could potentially achieve a better condition by foraging in the estuary and nearby marine areas, before migrating further.

2) The influence of individual characteristics on experienced temperature

Date had the overall strongest influence on the modelling of experienced temperature for all study groups, assumed to be a natural response due to the study period in spring being characterized by increasing temperatures. For all tagged adult individuals, Atlantic salmon adults had experienced lower temperatures than adult sea trout, and the highest experienced temperatures were registered in the sheltered intertidal mudflats habitat. Modelling shows that sea trout were more likely to reside in warmer water masses compared to Atlantic salmon, which could potentially be related to poor osmoregulatory capacity in cold water for sea trout. Tolerance for seawater in sea trout has been shown to change with temperature (Finstad *et al.*, 1988; Larsen *et al.*, 2008), meaning a possible explanation could be that sea trout would seek warmer temperatures to increase seawater tolerance when salinity levels were higher, while Atlantic salmon utilizing colder water masses may indicate they were well adjusted to seawater. During the event of a spring flow, the outgoing river flow may be of lower temperature than the marine tidal currents coming in, due to the cold meltwater. More dense marine water will follow the bottom when flowing into the estuary, and less dense brackish- and freshwater from the river flow will stay in the top layers, which could possibly explain some of the variance in temperature use.

Sex was suggested as having limited effect on the experienced temperature for adults. Although, results on percentage residence time and frequency of detections, showed more males utilized the sheltered intertidal mudflats, which was the habitat with the highest mean temperature during spring. The modelling of all tagged smolt revealed that Atlantic salmon smolts had a lower experienced temperature than sea trout smolts, that male smolt used warmer water than female smolt, and that smaller smolt experienced colder water masses compared to larger smolt. Physiological factors such as, sex (Pemberton 1976, Knutsen et al. 2004, Jensen et al. 2019) (Eldøy *et al.*, 2021) and body size (Jensen et al. 2014, Jonsson & Jonsson 2014) (Eldøy *et al.*, 2021) have been shown to strongly influence migratory patterns of sea trout. Atlantic salmon smolt experienced lower temperatures than adults of their respective species. With large variations in temperature and salinities creating haloclines and thermoclines in the estuarine habitats, there is likely an opportunity for the species to choose between water layers with the preferred conditions, such as direction of current, access to feed and salinity levels. Thus, findings may suggest Atlantic salmon utilized water depths slightly different than sea trout during their short estuarine stay. As the period in focus is during the collective migration of Atlantic salmon, likely accompanied by a spring flow coming down the river, this could potentially suggest Atlantic salmon smolt positioned themselves in water layers fit for their purpose of fast travel towards the fjord. Furthermore, as for many ectotherms (Martin & Huey, 2008), studies have shown sea trout may adjust their behavior and choice of depth, in search of preferred temperatures (Jonsson & Jonsson, 2009). Although, it is reasonable to believe that this plastic species has to tradeoff many factors in the use of water bodies and habitat. Temperature is well known to have an affect the metabolism and growth of ectotherm fish deriving heat from their environment (Elliott, 1975). Although, as pointed out by Jonsson and Jonsson (2011), it is important when investigating habitat use to take into consideration the complexity of fish behavior in the selection of habitat, as judging habitat suitability on merely one factor will be misleading.

Sea trout smolt had a longer residence time in the fjord compared to adult individuals. As seawater tolerance in sea trout is shown closely related to fish size, smaller fish are shown to have a lower tolerance for higher salinities than larger fish (Finstad & Ugedal, 1998). Thus, suggesting many sea trout smolt decided to migrate to more marine areas, despite a likely lower tolerance for seawater. Furthermore, sea trout of poor condition have been observed choosing migration behavior of higher risk (Eldøy *et al.*, 2021). The fact that adult sea trout were found to have a high residence time within the estuary rather than the fjord, could suggest that many sea trout adults actively made their residence choices due to linked rewards in the chosen habitat. Seeing as marine habitats are generally perceived to provide better feeding opportunities and higher growth, migration to sea may be outweighed by the benefits provided for adult sea trout in the Stjørdal river estuary. Sea trout of good condition have been shown more likely to remain close to the natal river (Eldøy *et al.*, 2021), probably to protect their reproductive opportunities until autumn, while fish of poorer fitness are motivated to seek more food in marine areas.

3) The function of estuarine habitats

Sea trout were frequently observed utilizing the sheltered intertidal mudflats, with their highest weekly percentage residence time spent in this habitat being 75%, indicating a substantial amount of time was spent in this habitat throughout the study period. The partly enclosed sheltered intertidal mudflats are positioned further upstream than the other estuarine habitats and is less affected by tides due to the rock threshold downstream, thus the physical characteristics of this habitat could indicate it is less accessible to marine salmonid predators. In addition, the area is not subjected to strong currents and is in general exposed to less extreme salinities than the river channel and the exposed intertidal mudflats. These traits may suggest a more stable area compared to the other estuarine habitats. Overall, this could indicate both satisfactory access to prey, based on samples by Kjærstad (2022), and less energy-intensive conditions for sea trout (Thorpe, 1994) compared to the river channel and exposed intertidal mudflats. Thus, suggesting this habitat could potentially meet the needed criteria for shelter and growth and consequently outweigh a migration to the more energy-intensive marine feeding habitats with higher risks of predation and intense salinity levels (Thorpe, 1994; Klemetsen *et al.*, 2003; Bordeleau *et al.*, 2018).

The river channel was used by sea trout during the spring migration and early summer, while the majority of Atlantic salmon adults overall short stay in the estuary was mainly being spent in the river channel. Atlantic salmon showed a relatively collective migration timing through the estuarine habitats, where 98% utilized the river channel during their residence in the estuary, before quickly leaving for more marine areas. Tides would have caused strong ingoing and outgoing currents in the river channel, while river flow is an outgoing current, and it is not clear whether the river channel is used as a feeding area, or if it mainly serves as a holding area until the richer exposed intertidal mudflats are within reach/available depth. With high current activity likely comes an abundance of benthic organisms/biotic communities, as oxygen is continuously supplied to the area. This could mean that the river channel offers a variety of possible prey for salmon and sea trout of both life stages. Although, strong currents are likely to make feeding less convenient than in more calm areas, where the fish may easily catch prey floating in calmer waters. A study by Levings et al. (1994) showed that the stomach contents of post-smolts caught in the Trondheim Fjord near the estuaries of Orkla and Gaula had recently eaten freshwater insects and estuary-living amphipods. Dietary studies of migrating salmon smolts have shown that the nutrient uptake in the first days after migration is important for survival (Hvidsten *et al.*, 2009).

The exposed intertidal mudflats were shown visited by sea trout throughout the season. Despite low residence time in this habitat compared to the other estuarine habitats, a large proportion of fish visited this habitat. As the receivers in this area were exposed to air twice a day during low tide, the habitat was inaccessible when the area was drained. Many fish still visited the area, indicating that this was an important habitat during their stay in the estuary. When the exposed intertidal mudflats are submerged in sufficient amounts of water, the habitat likely serves as a beneficial alternative for sea trout to forage rather than swimming to the fjord, without being exposed to as energy-intensive salinity levels (Davidsen *et al.*, 2014b). The habitat is highly influenced by waves from the fjord and changes in tidal levels, hence patches of macroalgae grow throughout the habitat floor, likely serving as important shelter for smaller fish and prey animals. Characterized by shallow water, fish may be at greater risk of predation by aviating predators, although sea trout have been shown to feed near the surface and close to shore (Klemetsen *et al.*, 2003; Eldøy *et al.*, 2017). Studies indicating smolts are often nocturnal migraters (Clark *et al.*, 2016; Furey *et al.*, 2016; Vollset *et al.*, 2017), could further indicate nocturnal activity between estuarine habitats would be beneficial to minimize predation. Although, in a highly tidal influenced habitat preferred water levels might not be consistent with the preferred time and light intensity. The likely abundance of small and easily caught prey, combined with a floor providing camouflage and shelter such as algae and rocks, the exposed habitat is likely a beneficial foraging area at higher tides. It can be speculated whether the exposed intertidal mudflat habitat would have been used for a longer amount of time if water levels were generally higher. Although, this would likely have resulted in a different overall environmental conditions and food accessibility, which might not have been as favorable. Here, shallow conditions provide good lighting conditions and growth opportunities for macroalgae, which constitute good hiding opportunities.

The great variety of habitat in the vicinity of the natal river allows individuals of different condition, and different life stage to not only use the most favorable habitat, but also to enjoy benefits of other close habitats by moving between them. As there are large daily, monthly and seasonal variations within each habitat, the recorded experienced temperatures were used to explore which water layers the species and different life stages utilized. Based on the known environmental characteristics of the respective habitats, as well as known preferences and behavior of the species through relevant literature it could be speculated that sea trout actively adjust their positioning to water bodies to warmer temperatures and less saline water masses than marine water masses. A recent master's study on temperature use in trout showed that they use different water layers (Risanger, 2021). Investigating the effect of individual characteristics on the use of temperature can help fill in details on the utilization of different coastal habitats by sea trout and Atlantic salmon, hence contribute to development of species- and population-specific management strategies.

Despite evident differences in habitat use and temperature preferences, Atlantic salmon and sea trout are often subjected to the same conservation strategies (innlandsfiskloven, 1993). Although, to implement species-specific management, extensive knowledge is required on the details on their use of estuaries and coastal areas and how their requirements ultimately differ. The present study pointed out prominent behavioral differences between two related salmonids from the same river during spring and early summer. The Atlantic salmon population of the Stjørdal river showed a trend to utilize marine habitats quickly during spring migration, rather than residing in brackish estuarine areas. Atlantic salmon smolt had a longer residence time in the estuary, and experienced lower temperatures than adults. Sea trout frequently resided within the estuary compared to salmon, likely due to an assessment of potential risks and rewards met within the chosen habitat, based on individual characteristics and their nutritional needs. Sea trout smolt were observed utilizing nearby marine areas and the fjord more frequently than sea trout adults, while Atlantic salmon smolt were observed with a frequent use of the three estuarine habitats, compared to Atlantic salmon adults. Hence, the study emphasized the importance of studying variation within a population, as results indicated behavior and habitat requirements may differ prominently between life stages. In addition, the study also highlighted how microhabitats may have different functions within an estuary, and how their value ultimately differs for different species and their life stages. One estuary may vary from serving as a simple migration corridor to provide microclimate refuges and temporary holding or foraging grounds.

The knowledge provided by this study is of value in a coastal management perspective, as there is a continuous pressure on coastal habitats and their inhabitants. Fully protecting the valuable estuarine habitats from anthropogenic stressors can be challenging when authorities must balance between urban development and nature conservation, as many estuaries are situated in areas that are already strongly urbanized. In order to mitigate the negative ecological effects of urban activities in estuaries, it is crucial to have more knowledge about the function of estuarine habitats for the species and life stages of concern.

5. References

Anderson, D. R., Link, W. A., Johnson, D. H. & Burnham, K. P. (2001). Suggestions for Presenting the Results of Data Analyses. *The Journal of wildlife management* **65**, 373-378.

Anon (2007). St.prp. nr. 32 (2006-2007). Om vern av villaksen og ferdigstilling av nasjonale laksevassdrag og laksefjorder. Del 2. Ferdigstilling av nasjonale laksevassdrag og laksefjorder.
p.

Anon (2021). Status for norske laksebestander i 2021. p.: Vitenskapelig råd for lakseforvaltning.

Bartoń, K. (2022). MuMIn: Multi-Model Inference. R package version 1.43.17. p.

Birnie-Gauvin, K., Thorstad, E. B. & Aarestrup, K. (2019). Overlooked aspects of the Salmo salar and Salmo trutta lifecycles. *Reviews in fish biology and fisheries* **29**, 749-766.

Bordeleau, X., Davidsen, J. G., Eldøy, S. H., Sjursen, 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.

Bordeleau, X., Hatcher, B. G., Denny, S., Whoriskey, F. G., Patterson, D. A. & Crossin, G. T. (2019). Nutritional correlates of the overwintering and seaward migratory decisions and long-term survival of post-spawning Atlantic salmon. *Conserv Physiol* **7**, coz107-coz107.

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.

Carter, T. J., Pierce, G. J., Hislop, J. R. G., Houseman, J. A. & Boyle, P. R. (2001). Predation by seals on salmonids in two Scottish estuaries. *Fisheries management and ecology* **8**, 207-225.

Clark, T. D., Furey, N. B., Rechisky, E. L., Gale, M. K., Jeffries, K. M., Porter, A. D., Casselman, M. T., Lotto, A. G., Patterson, D. A., Cooke, S. J., Farrell, A. P., Welch, D. W. & Hinch, S. G. (2016). Tracking wild sockeye salmon smolts to the ocean reveals distinct regions of nocturnal movement and high mortality. *Ecol Appl* **26**, 959-978.

Cucherousset, J., Ombredane, D., Charles, K., Marchand, F. & Bagliniere, J.-L. (2005). A continuum of life history tactics in a brown trout (Salmo trutta) population. *Canadian journal of fisheries and aquatic sciences* **62**, 1600-1610.

Davidsen, J. G., Rikardsen, A. H., Halttunen, E., Thorstad, E. B., ØKland, F., Letcher, B. H., Skarðhamar, J. & Næsje, T. F. (2009). Migratory behaviour and survival rates of wild northern Atlantic salmon Salmo salar post-smolts: effects of environmental factors. *J Fish Biol* **75**, 1700-1718.

Davidsen, J. G., Daverdin, M., Arnekleiv, J. V., Rønning, L., Sjursen, A. D. & Koksvik, J. I. (2014a). Riverine and near coastal migration performance of hatchery brown trout Salmo trutta. *J Fish Biol* **85**, 586-596.

Davidsen, J. G., Daverdin, M., Sjursen, A. D., Rønning, L., Arnekleiv, J. V. & Koksvik, J. I. (2014b). Does reduced feeding prior to release improve the marine migration of hatchery brown trout Salmo trutta smolts? *J Fish Biol* **85**, 1992-2002.

Davidsen, J. G., Bordeleau, X., Eldøy, S. H., Whoriskey, F., Power, M., Crossin, G. T., Buhariwalla, C. & Gaudin, P. (2021). Marine habitat use and feeding ecology of introduced anadromous brown trout at the colonization front of the sub-Antarctic Kerguelen archipelago. *Scientific reports* **11**, 11917-11917.

del Villar-Guerra, D., Aarestrup, K., Skov, C. & Koed, A. (2014). Marine migrations in anadromous brown trout (Salmo trutta). Fjord residency as a possible alternative in the continuum of migration to the open sea. *Ecol Freshw Fish* **23**, 594-603.

Eldøy, S. H., Davidsen, J. G., Thorstad, E. B., Whoriskey, F., Aarestrup, K., Næsje, T. F., Rønning, L., Sjursen, 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., Sjursen, 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., Sjursen, 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 (Halstenbek)* **665**, 185.

Elliott, J. M. (1975). The Growth Rate of Brown Trout (Salmo trutta L.) Fed on Reduced Rations. *The Journal of animal ecology* **44**, 823-842.

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.

Elliott, M. & Whitfield, A. K. (2011). Challenging paradigms in estuarine ecology and management. *Estuarine, coastal and shelf science* **94**, 306-314.

Erikstad, L., Husteli, B., Dahl, R. og Heldal, T. (2018). Delta, Landform. Norsk rødliste for naturtyper. Artsdatabanken, Trondheim. p. Artsdatabanken, Trondheim.

Finstad, B., Staurnes, M. & Reite, O. B. (1988). Effect of low temperature on sea-water tolerance in rainbow trout, Salmo gairdneri. *Aquaculture* **72**, 319-328.

Finstad, B. & Ugedal, O. (1998). Smolting of sea trout (Salmotrutta L.) in northern Norway. *Aquaculture* **168**, 341-349.

Forseth, T., Barlaup, B. T., Finstad, B., Fiske, P., Gjøsæter, H., Falkegård, M., Hindar, A., Mo, T. A., Rikardsen, A. H., Thorstad, E. B., Vøllestad, L. A. & Wennevik, V. (2017). The major threats to Atlantic salmon in Norway. *ICES Journal of Marine Science* **74**, 1496-1513.

Furey, N. B., Hinch, S. G., Bass, A. L., Middleton, C. T., Minke-Martin, V. & Lotto, A. G. (2016). Predator swamping reduces predation risk during nocturnal migration of juvenile salmon in a high-mortality landscape. *J Anim Ecol* **85**, 948-959.

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., Rikardsen, A. H., Davidsen, J. G., Thorstad, E. B. & Dempson, J. B. Survival, Migration Speed and Swimming Depth of Atlantic Salmon Kelts During Sea Entry and Fjord Migration. pp. 35-49. Dordrecht: Dordrecht: Springer Netherlands.

Harvey, A. C., Glover, K. A., Wennevik, V. & Skaala, Ø. (2020). Atlantic salmon and sea trout display synchronised smolt migration relative to linked environmental cues. *Sci Rep* **10**, 3529-3529.

Hubley, Amiro, Gibson, Lacroix & Redden (2008). Survival and behaviour of migrating Atlantic salmon (Salmo salar L.) kelts in river, estuarine, and coastal habitat. *ICES Journal of Marine Science* **65**, 1626-1634.

Hvidsten, N. A. & Lund, R. A. (1988). Predation on hatchery-reared and wild smolts of Atlantic salmon, Salmo salar L., in the estuary of River Orkla, Norway. *Journal of fish biology* **33**, 121-126.

Hvidsten, N. A., Jensen, A. J., Rikardsen, A. H., Finstad, B., Aure, J., Stefansson, S., Fiske, P. & Johnsen, B. O. (2009). Influence of sea temperature and initial marine feeding on survival

of Atlantic salmon Salmo salar post-smolts from the Rivers Orkla and Hals, Norway. *J Fish Biol* **74**, 1532-1548.
innlandsfiskloven, L.-o. (1993). Lov om laksefisk og innlandsfisk mv. (lakse- og innlandsfiskloven). LOV-2021-05-07-34 fra 01.06.2021. p.
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.
Jepsen, N., Holthe, E. & ØKland, F. (2006). Observations of predation on salmon and trout smolts in a river mouth. *Fisheries management and ecology* **13**, 341-343.
Jepsen, N., Flávio, H. & Koed, A. (2019). The impact of Cormorant predation on Atlantic salmon and Sea trout smolt survival. *Fisheries management and ecology* **26**, 183-186.
Jonsson, B. & Jonsson, N. (2009). A review of the likely effects of climate change on anadromous Atlantic salmon Salmo salar and brown trout Salmo trutta, with particular reference to water temperature and flow. *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. p. Dordrecht: Springer Netherlands : Imprint: Springer.
Jonsson, N. & Finstad, B. (1995). *Sjøørret : økologi, fysiologi og atferd*.p. Trondheim: Norsk institutt for naturforskning.
Kennish, M. J. (2002). Environmental threats and environmental future of estuaries. *Envir. Conserv* **29**, 78-107.
Kjærstad, G. (2022). «Innsamling med sparkeprøver i mars, mai, jui og november 2021». Unpublished data.
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.
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.
Larsen, P. F., Nielsen, E. E., Koed, A., Thomsen, D. S., Olsvik, P. A. & Loeschcke, V. (2008). Interpopulation differences in expression of candidate genes for salinity tolerance in winter migrating anadromous brown trout (Salmo trutta L.). *BMC Genet* **9**, 12-12.
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**.
Lyse, A. A., Stefansson, S. O. & Fernö, A. (1998). Behaviour and diet of sea trout post-smolts in a Norwegian fjord system. *Journal of fish biology* **52**, 923-936.
Martin, T. L. & Huey, R. B. (2008). Why "Suboptimal" Is Optimal: Jensen's Inequality and Ectotherm Thermal Preferences. *Am Nat* **171**, E102-E118.
Middlemas, S. J., Barton, T. R., Armstrong, J. D. & Thompson, P. M. (2006). Functional and aggregative responses of harbour seals to changes in salmonid abundance. *PROC R SOC B* **273**, 193-198.
Nefedova, Z. A., Murzina, S. A., Pekkoeva, S. N. & Nemova, N. N. (2018). Comparative Analysis of the Fatty Acid Profiles of Smolts of the Brown Trout Salmo trutta L. and Atlantic Salmon Salmo salar L. during Smoltification (Indera River, White Sea Basin). *Biology bulletin of the Russian Academy of Sciences* **45**, 126-131.
Nemova, N. N., Murzina, S. A., Lysenko, L. A., Meshcheryakova, O. V., Churova, M. V., Kantserova, N. P., Nefedova, Z. A., Krupnova, M. Y., Pekkoeva, S. N., Ruokolainen, T. R., Veselov, A. E. & Efremov, D. A. (2020). Ecological and Biochemical Status of the Atlantic Salmon Salmo salar L. and the Brown Trout Salmo trutta L. at Early Stages of Development. *Biology bulletin reviews* **10**, 239-249.

O'Higgins, T. G., Lago, M. & DeWitt, T. H. (2020). Ecosystem-based management, ecosystem services and aquatic biodiversity : theory, tools and applications. p. Cham, Switzerland: Springer International Publishing : Imprint: Springer.
Olsson, I. C., Greenberg, L. A., Bergman, E. & Wysujack, K. (2006). Environmentally induced migration: the importance of food. *Ecol Lett* **9**, 645-651.
Quigley, D., Harvey, M., Hayden, T., Dowling, C. & O'Keane, M. (2006). A Comparative Study of Smoltification in Sea Trout(Salmo trutta L.) and Atlantic Salmon (Salmo salar L.): Seawater Tolerance and Thyroid Hormone Titres. *Biology and Environment-proceedings of The Royal Irish Academy - BIOLOGY ENVIRONMENT* **106**, 35-47.
Rikardsen, A. H., Haugland, M., Bjørn, P. A., Finstad, B., Knudsen, R., Dempson, J. B., Holst, J. C., Hvidsten, N. A. & Holm, M. (2004). Geographical differences in marine feeding of Atlantic salmon post-smolts in Norwegian fjords. *Journal of fish biology* **64**, 1655-1679.
Strand, J. E. T., Davidsen, J. G., Jørgensen, E. H. & Rikardsen, A. H. (2010). Seaward migrating Atlantic salmon smolts with low levels of gill Na+, K+ -ATPase activity; is sea entry delayed? *Environmental biology of fishes* **90**, 317-321.
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.
Thorpe, J. E. (1994). Salmonid Fishes and the Estuarine Environment. *Estuaries* **17**, 76-93.
Thorpe, J. E., Mangel, M., Metcalfe, N. B. & Huntingford, F. A. (1998). Modelling the proximate basis of salmonid life-history variation, with application to Atlantic salmon, Salmo salar L. *Evolutionary ecology* **12**, 581-599.
Thorstad, E. B., Økland, F., Finstad, B., Sivertsgård, R., Bjørn, P. A. & McKinley, R. S. (2004). Migration speeds and orientation of Atlantic salmon and sea trout post-smolts in a Norwegian fjord system. *Environmental biology of fishes* **71**, 305-311.
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., Whoriskey, F., Uglem, I., Moore, A., Rikardsen, A. H. & Finstad, B. (2012). A critical life stage of the Atlantic salmon Salmo salar: behaviour and survival during the smolt and initial post-smolt migration. *J Fish Biol* **81**, 500-542.
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.
Vainikka, A., Huusko, R., Hyvärinen, P., Korhonen, P. K., Laaksonen, T., Koskela, J., Vielma, J., Hirvonen, H. & Salminen, M. (2012). Food restriction prior to release reduces precocious maturity and improves migration tendency of Atlantic salmon (Salmo salar) smolts. *Canadian journal of fisheries and aquatic sciences* **69**, 1981-1993.
Vollset, K. W., Barlaup, B. T. & Normann, E. S. (2017). Release during night enhances survival of wild Atlantic salmon smolts. *Fisheries management and ecology* **24**, 256-264.
Wright, B. E., Riemer, S. D., Brown, R. F., Ougzin, A. M. & Bucklin, K. A. (2007). Assessment of Harbor Seal Predation on Adult Salmonids in a Pacific Northwest Estuary. *Ecol Appl* **17**, 338-351.
Wysujack, K., Greenberg, L. A., Bergman, E. & Olsson, I. C. (2009). The role of the environment in partial migration: food availability affects the adoption of a migratory tactic in brown trout Salmo trutta. *Ecology of freshwater fish* **18**, 52-59.
Aarestrup, K., Nielsen, C. & Koed, A. (2002). Net ground speed of downstream migrating radio-tagged Atlantic salmon (Salmo salar L.) and brown trout (Salmo trutta L.) smolts in relation to environmental factors. *Hydrobiologia* **483**, 95-102.

s6. APPENDIX

1) Adult salmon and sea trout

Table A. Conditional model averaging summary statistics for mixed effects models with Δ AIC ≤ 4 for the effect of total body length (*L*), sex (S), date (D), zone (Z) and species (SP) on individual's body temperature in the period 01.05-31.06.2021 for adult Atlantic Salmon and sea trout. Significant values (P ≤ 0.05) are highlighted by the asterisk mark (*).

Effect	**Estimate**	**Std.Error**	**z value**	***P***
(Intercept)	-0.208989	0.168033	1.244	0.2137
Date	0.824915	0.010132	81.388	<2e-16 ***
Species (Salmo trutta)	0.276001	0.140188	1.946	0.0516
Total body length	0.054972	0.032189	1.695	0.0900
Zone (zone 2)	0.037052	0.020874	1.774	0.0760
Zone (zone 3)	0.078036	0.032205	2.422	0.0154 *
Sex (male)	0.005006	0.049795	0.099	0.9208

2) Salmon and sea trout smolt

Table B. Conditional model averaging summary statistics for mixed effects models with Δ AICc ≤ 4 for the effect of total body length (*L*), sex (S), date (D), zone (Z) and species (SP) on individual's body temperature in the period 01.05-31.06.2021 for Atlantic Salmon and sea trout smolt. Significant values (P ≤ 0.05) are highlighted by the asterisk mark (*).

Effect	**Estimate**	**Std.Error**	**z value**	***P***
(Intercept)	-0.22064	0.05233	4.214	2.51e-05 ***
Date	0.82642	0.01367	60.404	< 2e-16 ***
Sex (male)	0.08297	0.04313	1.913	0.055705
Species (Salmo trutta)	0.19744	0.05613	3.502	0.000461 ***
Total body length	-0.03754	0.02573	1.451	0.146751
Zone (zone 2)	-0.02795	0.02114	1.321	0.186380
Zone (zone 3)	0.10142	0.03182	3.185	0.001449 **

3) Salmon adults and smolts

Table C. Conditional model averaging summary statistics for mixed effects models with Δ AICc ≤ 4 for the effect of total body length (*L*), sex (S), date (D), zone (Z) and species (SP) on individual's body temperature in the period 01.05-31.06.2021 for Atlantic Salmon smolts and adults. Significant values (P ≤ 0.05) are highlighted by the asterisk mark (*).

Effect	**Estimate**	**Std.Error**	**z value**	***P***
(Intercept)	0.64605	0.09532	6.749	<2e-16 ***
Date	0.79623	0.03024	26.205	<2e-16 ***
Life stage (smolt)	-0.92693	0.10144	9.068	<2e-16 ***
Sex (male)	0.12376	0.08904	1.379	0.1678
Zone (zone 2)	0.07603	0.04315	1.754	0.0795
Zone (zone 3)	0.06957	0.08339	0.830	0.4064

4) Sea trout adults and smolts

Table D. Conditional model averaging summary statistics for mixed effects models with Δ AICc ≤ 4 for the effect of total body length (*L*), sex (S), date (D), zone (Z) and species (SP) on individual's body temperature in the period 01.05-31.06.2021 for Sea trout smolts and adults. Significant values (P ≤ 0.05) are highlighted by the asterisk mark (*).

Effect	**Estimate**	**Std.Error**	**z value**	***P***
(Intercept)	-0.043047	0.046221	0.931	0.3518
Date	0.803277	0.008242	97.432	< 2e-16 ***
Life stage (smolt)	-0.084008	0.049922	1.671	0.0947
Zone (zone 2)	0.007878	0.016775	0.470	0.6387
Zone (zone 3)	0.124611	0.025691	4.849	1.2e-06 ***
Sex (male)	0.018953	0.050044	0.376	0.7068

NTNU

Kunnskap for en bedre verden