Master's thesis

NTNU
Norwegian University of Science and Technology
Faculty of Natural Sciences
Department of Biology

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Individual habitat use of sea trout (*Salmo trutta*) in the estuary of river Stjørdalselva

Master's thesis in Ocean Resources
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ACKNOWLEDGEMENTS

First, I would like to thank my main supervisor Jan Grimsrud Davidsen for giving me this unique opportunity to work with such an interesting field, sharing his valuable knowledge on salmonids and field work related to it, and giving me important guidance along the way. Jan is genuinely interested that me and my fellow students shall succeed, which I am forever grateful for. I am also grateful for all the help that my co-supervisor Sindre Håvarstein Eldøy has given me during my work with the master thesis. There has been a steep learning curve related to the data analysis in r-studio, and guidance from Sindre has been crucial for the success of this.

A special thanks goes to the amazing people working at NTNU university museum, and especially the staff in Freshwater Ecology Group. They have been welcoming and pleasant from my very first meeting with them, and their positive work environment is inspirational. Thanks to; Lars Rønning for not retiring before I got the chance to meet him, where he could share his long-earned knowledge with field work, Aslak Darre Sjursen for training me in fish scale analysis and giving me good fishing advice, Marc Daverdin for creating the map of the study area, and Gaute Kjærstad for valuable data on the benthic communities in the estuary. The present thesis was a part of a larger project at Hellstranda, funded by Nye veier, via Acciona Construction and Rambøll. Also, thanks to Avinor and Forsvarsbygg for allowing deployment and maintenance of receivers in their areas.

Lastly, I wish to express my great appreciation to my supportive family and girlfriend, for making this study less stressful, and my fellow students for making the study more enjoyable.

ABSTRACT

Brackish estuaries are important habitats for some sea trout (*Salmo trutta*) throughout the year. Anthropogenic activities affecting estuaries will have a negative effect on these sea trout. Hence, a better ecological understanding of the species and how it utilizes the estuary in time and space could be helpful for future management. The present thesis investigated the habitat use of the sea trout based on activity level and depth use within the estuary of river Stjørdalselva, from 20 December 2020 to 15 April 2022. In total, 30 sea trout were captured and tagged with acoustic transmitters, and the fish were detected by acoustic receivers that were placed strategically within the estuary, upstream river and in the innermost part of the fjord, next to the estuary.

Based on their different abiotic characteristics, the exposed intertidal mudflats, river channel, and sheltered intertidal mudflats were defined as three different habitats within the estuary of river Stjørdalselva. Habitat use differed for the individual sea trout, with 65% being registered in the exposed habitat, 96% in the river channel, and 85% in the sheltered habitat. Spring was the season with the highest abundance of tagged sea trout within the estuary. Mean activity level was highest in the river channel, possibly because the habitat provided good feeding opportunities, but also was affected by the river flow, which could force the fish to accelerate more when hunting prey or escaping predators. Second highest level of activity was found in the fish using the exposed intertidal mudflat, possibly because it is shallower and a calmer habitat, while the lowest mean activity level was found in sea trout using the sheltered intertidal mudflats. The latter could be explained by being a habitat that has lower currents and is safer, thus, more energy-conserving for the sea trout. There was a seasonal difference in activity with higher levels during summer and spring than winter and autumn. This may be linked to the water temperature, with warmer temperatures having a positive effect on the metabolism of the fish, which affects the feeding behavior. There was no correlation between total body length and the level of activity. Males had a higher activity level than females overall, with all habitats and seasons combined. The depth use was in general deeper in spring and summer, and shallower in autumn and winter, which could be linked to sea trout avoiding environments that have a combination of cold temperatures and high salinities. The river channel had a deeper mean swimming depth compared to exposed- and sheltered intertidal

mudflats, which could be explained by being a deeper habitat, but also potentially better feeding opportunities in the thicker marine layer within this habitat.

The present study shows for the first time that sea trout activity and depth use differ within season and within different habitats inside the same estuary. Further, the findings support previous studies showing that estuaries are important habitats for sea trout. Knowledge on habitat use, and how the estuary is utilized in time and space, is crucial for decision-makers and management when implementing mitigated or compensatory measures in connection with projects that affect the habitat of the sea trout.

SAMMENDRAG

Brakkvannsestuarier er viktige habitat for noen sjøørret (*Salmo trutta*) gjennom hele året. Menneskelige aktiviteter som påvirker estuarier, vil ha en negativ effekt på disse sjøørretene. Derfor vil en bedre økologisk forståelse av arten, og hvordan den benytter seg av estuariet i tid og rom, være til hjelp for fremtidig forvaltning. I denne studien ble habitatbruken til sjøørreten undersøkt basert på aktvitetsnivået og dybdebruken i estuariet til Stjørdalselva, fra 20 desember 2020 til 15 april 2022. Det ble totalt fanget og merket 30 sjøørret med akustiske merker, og fisken ble oppdaget av lyttestasjoner som var plassert strategisk i estuariet, oppstrøms i elven og innerst i fjorden, i nærheten av estuariet.

Det eksponerte område, elvekanalen og beskyttede område ble definert som tre ulike habitat i estuariet til Stjørdalselva, basert på deres ulike abiotiske egenskaper. Habitatbruken var forskjellig for den individuelle sjøørreten, hvor 65% ble registrert i det eksponerte habitatet, 96% i elvekanelen og 85% i det beskyttede habitatet. Den var høyest tetthet av sjøørreter i estuariet på våren. Aktivitetsnivået var høyest i elvekanalen, muligens fordi habitatet hadde rikelig med tilgang på mat, men også fordi påvirkning fra strømmen i elva kunne tvinge sjøørreten til å måtte akselerere mer når den jaktet etter byttedyr eller flyktet fra predatorer. Det nest høyeste aktivitetsnivået ble funnet i fisk som brukte det eksponerte området, kanskje fordi dette habitatet er roligere og grunnere enn elvekanalen, mens det beskyttede habitatet viste det laveste aktivitetsnivået. Sistnevnte kan forklares ved at det er lite vannstrømmer, og er et tryggere habitat, som er energibesparende for sjøørreten. Det var en sesongmessig forskjell i aktiviteten, med høyere nivå på sommeren og våren enn om vinteren og høsten. Dette er muligens knyttet til vanntemperaturen, hvor varmere vanntemperaturer har en positiv effekt på metabolismen til fisken, som igjen påvirker fôringsatferden. Det var ingen korrelasjon mellom kroppslengde og aktivitetsnivå. Totalt sett hadde hannfisk et høyere aktivitetsnivå enn hunnfisk, når en kombinerte alle habitater og sesonger. Dybdebruken var generelt dypere på våren og sommeren, og grunnere på høsten og vinteren, muligens knyttet til at sjøørret unngår miljø som har en kombinasjon av kald temperatur og høy salinitet. Elvekanalen hadde en dypere gjennomsnittlig svømmedybde sammenlignet med det eksponerte- og beskyttede området, som kan forklares ved at elvekanelen er dypere, men også potensielt bedre mattilgang i det tykkere marine laget i dette habitatet.

Dette studiet viser for første gang at aktiviteten og dybdebruken til sjøørreten er forskjellig innen sesong og mellom ulike habitater i samme estuariet. Videre støtter funnene tidligere studier som viser til at estuarier er viktige habitat for sjøørreten. Kunnskap om habitatbruken, og hvordan estuariet blir brukt i tid og rom, kan være til nytte for beslutningstakere og forvaltning når avbøtende eller kompenserende tiltak skal implementeres i forbindelse med prosjekter som påvirker estuarier og sjøørreten.

1. INTRODUCTION

The brown trout (*Salmo trutta*) is an important and highly-priced species for anglers due to its fighting abilities and value as food. Consequently, the species has been introduced to countries outside the natural distribution and has a worldwide distribution today (Klemetsen et al., 2003; Thorstad et al., 2016). Brown trout is a freshwater fish, but their life strategies may differ on an individual level. The balance of costs and benefits makes individuals either freshwater residents throughout their life or become anadromous (hereinafter referred to as sea trout), where they undertake marine migration (Thorstad et al., 2016). The migration of the sea trout between freshwater and marine water is viewed as a life history strategy of adaptive value, where they seek to utilize the optimal habitat in different stages of their life cycle to maximize individual fitness (Gross et al., 1988; Lucas & Baras, 2008). The advantage of marine migration includes better feeding opportunities, which will result in enhanced growth, fitness, and fecundity. The cost of migration is physiological demands related to the salinity adjustment, higher risk of predation, and the energy investment needed in the migration itself (Ferguson, 2006; Jonsson & Jonsson, 2006; Thorstad et al., 2016).

Sea trout typically enter the marine environment for the first time as smolts in spring or early summer (Gargan et al., 2006; Jensen, 1968; Jonsson & Jonsson, 2009). They normally spend the summer at sea but display variations in the timing and duration of their marine migration. The sea trout typically remain in coastal areas close to their river of origin (<80km), where they can spawn after just one summer at sea, but some individuals will delay their first reproduction until having spent several summers at sea (Thorstad et al., 2016). Spawning season usually starts in the beginning of autumn (Jensen & Rikardsen, 2008). A study done in central Norway (Eldøy et al., 2021), found that female sea trout were more likely to undergo longer marine migrations than males, instead of remaining in the brackish and freshwater areas where they were tagged. This is probably due to better feeding opportunities at sea, and the strong correlation between body size and the number of eggs the female can produce (Elliott, 1995). The sea trout that return to freshwater after a few months in sea during summer, are often over-wintering in the river or estuary after the spawning season (Berg & Berg, 1989; Jonsson & Jonsson, 2009; Skaala et al., 2014). The reason for this could be that the combination of high salinity and low marine temperatures may be physiologically stressful for the sea trout (Larsen et al., 2008; Thorstad et al., 2016). However, as an alternative to the strategy to overwintering in the freshwater habitat, some sea trout migrate only to estuarine areas or will undertake repeated and relatively brief movements between freshwater and marine environments (Chernitsky et al., 1995; Koksvik & Steinnes, 2005; Pratten & Shearer, 1983). This could indicate that saltwater tolerance differs between sea trout populations (Thorstad et al., 2016) or individuals, or that different estuaries are better suited for over-wintering. As an example, frequent movements between freshwater, estuary, and marine environments have been observed in a north Norwegian river (Jensen & Rikardsen, 2012). One component of a population can feed in the brackish estuary, while another undertakes a longer coastal migration. The advantage of staying in the estuary relates to the attendant feeding opportunities, less exposure to marine predators and the reduced adjustment need to salinity changes (Thorstad et al., 2016). The duration and distance of the migration, and the habitat the sea trout resides in during winter, are likely governed by trade-offs between the cost and benefits related to those different habitats (Thorstad et al., 2016).

Sea trout are opportunistic predators that will feed in different habitats, such as in freshwater, brackish estuaries, or more marine pelagic open waters (Thorstad et al., 2016). The prey will vary depending on the body length of the sea trout. Larger sea trout (>25 cm) will mainly feed on different fish species, whereas smaller sea trout feed on species such as crustaceans and insects (Davidsen et al., 2017; Pemberton, 1976; Rikardsen et al., 2007). The season is also a variable that will affect the feeding of the sea trout. The consumption rate is highest in early summer to early autumn (April-September), and lowest during late autumn and winter (October-December) (Rikardsen et al., 2006). A study showed that prey will vary with season, where sea trout feed on crustaceans during wintertime and fish from spring to autumn (Rikardsen et al., 2006). Sea trout is not an apex predator, meaning it is also vulnerable to predation. This is especially during the earlier life stages since size will have a strong correlation to predation vulnerability. Predators that could prey on sea trout are animals such as birds, larger fish, and marine mammals (Thorstad et al., 2016).

Like most fish species, sea trout is ectothermic, thus, abiotic factors like temperature will have a big impact on the spatial distribution of the species. This also means that the metabolism, which correlates with growth, is affected by the water temperature (Elliott, 1975). The preferred temperature for sea trout growth is ranging from 4-19 °C, with an optimum temperature of around 16 °C (Elliott & Elliott, 2010; Elliott, 1994). In a study done by Kristensen et al. (2018) it was observed that sea trout tend to move to deeper layers in the water column when the surface temperature exceeds 17 °C. These observations could indicate that sea trout are regulating their body temperature by actively moving to areas with preferred temperature (Jensen et al., 2014; Risanger, 2021). Salinity is also a major abiotic factor that affects the spatial and temporal habitat use for sea trout. Although sea trout are expected to tolerate a wide range of salinities, moving from freshwater to seawater is energy-demanding because of the increased metabolic activity that comes from osmoregulation (Bœuf & Payan, 2001; Risanger, 2021). The salinity tolerance is also heavily linked to the size of the fish, where larger sea trout have a higher salinity tolerance (Finstad & Ugedal, 1998; Parry, 1960). Water masses with a combination of low temperatures and high salinity could therefore be areas that the sea trout avoids since the osmoregulatory is poor in cold water (Larsen et al., 2008) and the osmoregulation is energy demanding. Such abiotic factors could affect the swimming depth of the sea trout, where it was found in a study that swimming depth was influenced by habitat and season (Eldøy et al., 2017), which could have different abiotic characteristics. Consequently, the brackish water layers typically found in estuaries may be attractive for some sea trout populations or individuals.

An estuary is defined as a partially enclosed body of water and is a transition zone between freshwater rivers and marine waters. The surrounding land will also create a transition between land and sea. Freshwater from rivers will flow into the estuary and get mixed with seawater from the ocean. Both abiotic and biotic conditions in an estuary will differ from these two environments. Temperature, salinity, and turbidity fluctuate daily due to tides and changes in the water flow in the river causing a constantly changing mixture of salt and freshwater. Estuaries are among the most productive ecosystems in the world, where both sea and rivers will carry fine sediments, that will accumulate in the estuary to form mudflats (McLusky & Elliott, 2004). Due to variations of abiotic factors within an estuary, several smaller and different habitats may be created within the estuary, and these may be utilized differently in time and space by the inhabitants.

River estuaries in urban areas are constantly under pressure from anthropogenic activities, e.g., due to urban and industrial development, creating a potential conflict regarding land use between humans and sea trout (Davidsen et al., 2021; McLusky & Elliott, 2004; Thorstad et al., 2019). Because of the strong impact of different anthropogenic activities affecting most or all important habitats for the sea trout, there has been a decline in the Norwegian populations of sea trout over the years. In a recent review, it was found that there were less than 25% of the populations from 1251 investigated watercourses that were in a good or very good state (Forseth & Fiske, 2022).

The present thesis was part of a bigger project, where both sea trout and Atlantic salmon (*Salmo salar*) were monitored in the estuary of river Stjørdalselva due to a planned construction of a new highway (E-6 from Trondheim to Stjørdal). As part of the road construction, the plans included landreclamation of parts of the estuary (Davidsen et al., 2021). Because the estuary has three different habitats, defined by different abiotic characteristics, it is important to get detailed knowledge on individual sea trout behavior in all of them. Proper management of sea trout and other species is critical to keep a sustainable population in Norway, but also on a global perspective. Both mitigated and compensatory measures that are related to coastal development depend on a better ecological understanding of the affected fish species. To my knowledge, this is the first study that has focused on the individual activity level of sea trout within an estuary in a period that expands one year. This study could therefore provide important knowledge on the individual behavior within a sea trout population, which is crucial for the decision-makers when it comes to coastal development affecting the sea trout and the habitat they live in.

The aim of this study was to investigate how individual sea trout used different habitats within an estuary, and the importance of these habitats based on the spatiotemporal area use, individual activity level, and swimming depth over one year. Further, it was examined how individual characteristics (sex and total body length) influenced activity level. It was hypothesized that - 1) sea trout in the estuary had different level of activity between the different estuarine habitats and seasons, 2) swimming depth within the estuary varied with season and the different habitats used, and 3) that individual characteristics (sex & total body length) influenced the activity level.

2. MATERIALS AND METHODS

2.1 STUDY AREA

The study took place in the estuary of river Stjørdalselva (63.44899 °N, 10.88527 °E), located in Stjørdal municipality, Trøndelag county (Figure 1). River Stjørdal flows out in the Trondheim fjord and creates a brackish estuary at the river mouth and the areas in the immediate vicinity. The Trondheim fjord has been given status as a national salmon fjord (Anon, 2007), and the river of Stjørdal is a national salmon river. The main study site was zone 1-3 in the estuary, which were defined as three different habitats within the estuary. By definition, an estuary consists of the tidal mouth of the river, which includes parts of the river further upstream that is influenced by the tidal waters. In this study, the term estuary refers to the lower and more marine parts of the estuarine (Figure 1). The study site was divided into five different zones, (1) exposed intertidal mudflats, (2) river channel, (3) sheltered intertidal mudflats, (4) fjord (adjacent & Muruvika), and (5) upstream river. The adjacent marine area was the marine water that is in close proximity to the estuary (<2 km), whereas Muruvika was the line of acoustic receivers deployed in the marine water 2-4 km from the estuary.

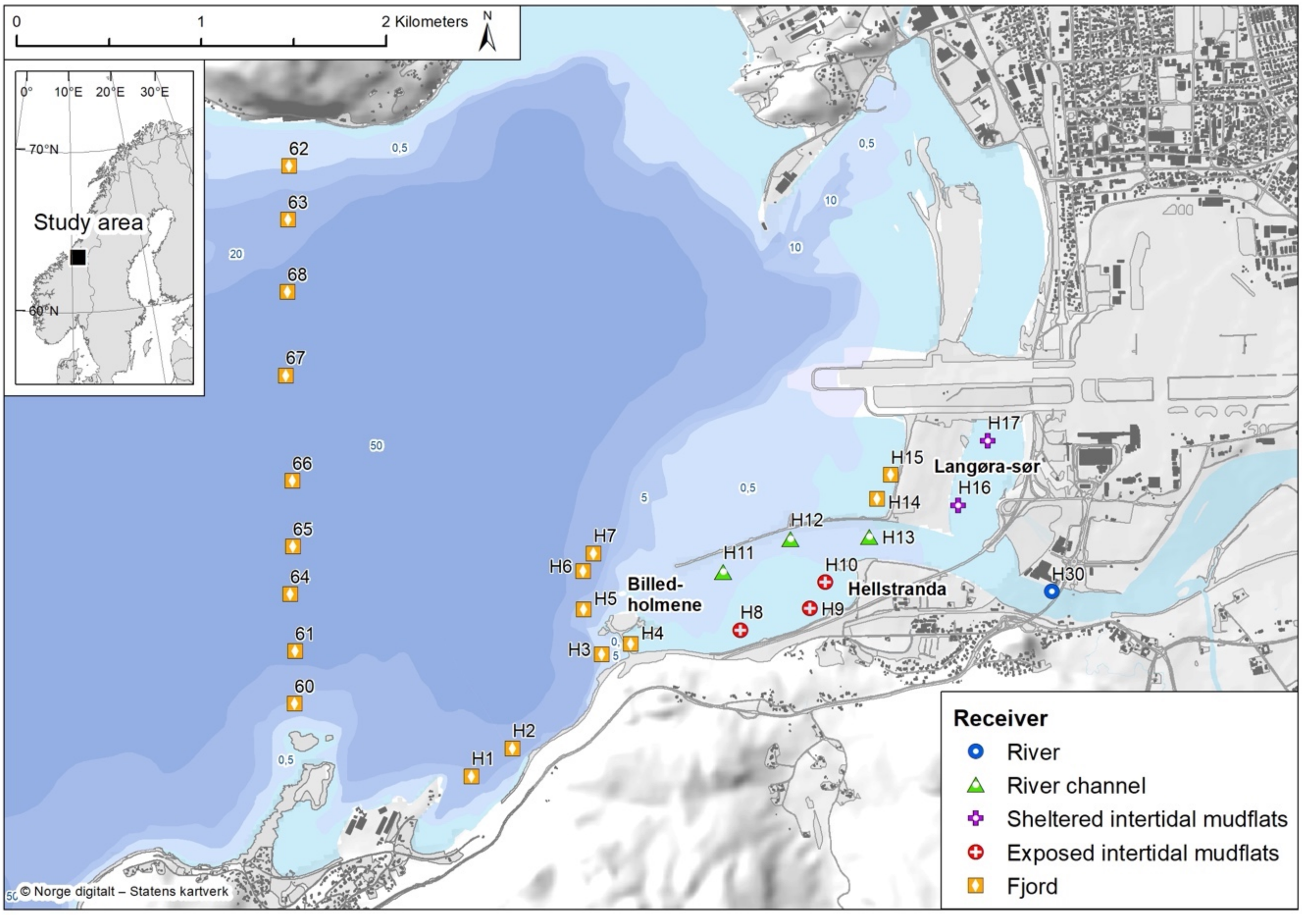

Figure 1:Map of the study area. Acoustic receivers are marked with different shape and color representing the habitat (blue= upstream river, green= the river channel, purple= sheltered intertidal mudflats, red=exposed intertidal mudflats, yellow= fjord, with 60-68 being Muruvika & H1-H7 + H14-15 being the adjacent marine area).

2.1.1 Description of estuarine habitats

The three different habitats within the estuary were characterized by different environmental conditions. The old river channel was closed due to the development of Trondheim Airport (Værnes) around 1954. The remains of the old river channel still exist and are located at Langøra-sør (Figure 1). This shallow area with brackish water is slightly impacted by tidal water but sheltered from the waves coming from the fjord. The new river channel flows out next to Billedholmen. Due to the change in river outlet from the airport development, a stone pier was created north from the new river channel, as a compensatory measure to maintain brackish water at the river mouth. This created a shallow brackish area between Hellstranda and Billedholmen, that is heavily impacted by the tides.

Exposed intertidal mudflats

This part of the estuarine area is characterized by a high influence from the tidal water, waves, and water flow. The result of these characteristics is a change in both temperature and salinity during the tidal water cycle each day for the whole season. This shallow pool is exposed to air twice a day due to changes in water level from the tides. The size of the area that is exposed to air will change during the season in correlation with the moon phase. The area has a gradient in salinity levels, where the water becomes more marine closer to Billedholmen, and more brackish at Hellstranda beach. The input of freshwater from the river likely comes in at the tip of Hellstanda, where it is mixed with the marine water in the area. There is an occurrence of some seaweed in the area, with a higher abundance in the more marine area of the habitat. Large parts of this habitat will freeze in wintertime, with regular breaks in the ice flakes, likely due to the flow from the river and the tidal water. Previous samples done on benthic species in this habitat Kjærstad (2022)- included Nematodes (roundworms), Gammarus (amphipod) and earthworms in the more brackish area close to the beach, and earthworms, Janiridae (isopod), and Gammarus in the more marine water close to Billedholmen. Sand and small rocks constitute the floor in this habitat.

Figure 2: *The exposed intertidal mudflats during low tide at different seasons. Photo, top: Catrine Schulze, photo, left: Jan Grimsrud Davidsen.*

River channel

When the tide is at the highest level in this habitat, the maximum depth is 5-6 meters in the river channel. Since this area is located directly where the freshwater flows out and the marine water from the fjord comes in, the lower layers of the water column consist of dense marine water, while the top layer will have a variation between brackish and fresh water. Abiotic variables like temperature and salinity will vary by factors such as river flow, tidal phase, and season. The area does not freeze in the winter season cause of the strong currents and water masses from both the river and the fjord. The floor in this habitat consists of rocks and river gravel.

Figure 3: *The river channel at winter (left, February 2021) and spring (right, April 2021), photo: Catrine Schulze.*

Sheltered intertidal mudflats

This habitat is located where the old river channel used to be, at Langøra-sør. The development of the airport runway has made this area enclosed from the original river outlet. This area is characterized as relatively shallow, and is sheltered from waves coming from the fjord, and has no strong current. There is a human-made threshold downstream in the river (Figure 4), just before the sheltered intertidal mudflats. This works as a barrier and reduces the amount of marine water that enters the area. The marine water is also controlled by the tidal levels and lunar phase, while the amount of incoming freshwater is dependent on the river flow. The lower layer of the water column consists of marine water and the top layers vary between brackish and fresh water. The main factors for change in temperature and salinity are time of the day, lunar phase, and season. This habitat will have a relatively solid layer of ice during wintertime. In the winter, the marine water layer is warmer than the fresh, this relationship is reversed when the spring flow occurs. Benthic species samples done previously in this area showed that this habitat had the highest abundance of benthic animals. This includes earthworms, Corophiidae (amphipods), Mysida (Crustacean), and Gammarus (Kjærstad, 2022). The sediment in this habitat consists mainly of fine particles and sand.

Figure 4: *The sheltered intertidal mudflat at different seasons (top) and human made threshold (bottom, sheltered habitat left, upstream river right). Photo, top: Jan Grimsrud Davidsen, photo, bottom: Joakim Endresen.*

2.2 COLLECTION OF DATA BY ACOUSTIC TELEMETRY

2.2.1 Fish capture and tagging

The fish for this study were captured and tagged in the winter of 2020 and spring of 2021. Eleven of the 30 fish were captured on 20.12.2020, while the rest were captured during spring 2021 (26.03-16.04.2021). The sea trout (n=30) were caught with rods from both land and boat from the lower parts of the river and in the brackish estuary at the river mouth. Other data from the tagged fish than those analyzed in this thesis, have previously been described in other projects in the same area (Davidsen et al., 2021; Harbak, 2022; Schulze, 2022). After capture, the fish were held in holding nets in low currents areas of the river for up to 4 hours before the tagging.

Each fish was tagged with an individually coded acoustic transmitter that was placed into the abdominal cavity. Prior to tagging, the fish was anesthetized in a tank that contained diluted Benzoak VET (20 mL per 100 L water). To keep the stress level of the fish at the lowest possible level and shield it from light, the tank was covered with a tarpaulin. The body length and weight of each fish were measured before the procedure. The anesthetized fish were placed in an open tube with fresh water from the river. To ensure normal breathing and to keep the fish wet during the procedure, the gills were continuously flushed with new water. On the side of the *linea alba*, a 1-3 cm incision was made, where a sterilized acoustic transmitter was carefully inserted in the abdominal cavity. The wound was closed using sutures (Resolon 3/0). A small piece of the adipose fin was collected and stored in alcohol using a sterile scissor, to use for later genetic analysis on sex determination. After the surgical procedure and tissue sampling, the fish were kept in covered holding tanks until they regained consciousness and showed normal swimming behavior (5-10 minutes). The fish were released in a calm part over the river close to the capture site. The experimental procedures were approved by the Food Safety Department (permission number 20/113613) and the county governor of Trøndelag. The surgical procedures were executed by approved and experienced personnel to maintain good fish welfare.

2.2.2 Acoustic tags

The tags used in this study were cylindric acoustic tags (ThelmaBiotel; Tag family: ADT-LP9-L) fit for the total body length of the fish. The tag size was 9x28 millimeters. Each tag transmitted a unique ID code (fish ID), giving them different acoustic signals. They also had sensors for temperature, depth, and acceleration, which give unique useful information on the fish's behavior along with where it is located in time and space. These tags had a signal frequency of 71 kHz, and the tags transmitted randomized intervals between the signals, 40-80 seconds between each signal. The weight of the tags was 5.1 g in air, they had a battery life expectancy of 380 days and a signal strength of 142 dB re 1uPA@1m).

2.2.3 Tracking of tagged fish

The study area had an array (Figure 1) of acoustic receivers that were deployed beneath the water's surface. This made it possible to track the migration pattern of each tagged fish. Since the main study took place in an estuary, large fluctuations in water conditions affected the registration range. Salinity, water temperature, and current patterns are influenced by tides and river flow. The detection range in the fjord was 200-400 meters, while in the estuary was 50-200 meters. The signal range was the same as similar studies that have taken place in areas with different layers of salinity (haloclines) and temperature (thermoclines) in the water masses (Bordeleau et al., 2018; Eldøy et al., 2015). Fish data registered by acoustic receivers were automatically stored, and the data was downloaded to a computer every second month. The acoustic receivers were regularly inspected to make sure of good condition and enough battery lifetime. A total of 27 Receivers (ThelmaBiotel model TBR700) were placed in the river Stjørdalselva, the estuary of river Stjørdalselva, and Trondheim fjord. In the estuary of river Stjørdalselva, eight receivers were operating during the study period (Figure 1). There were nine receivers further out in the Trondheim fjord, eight in the adjacent marine area (proximity to the estuary), and one placed upstream of the river mouth. The receivers were either attached to poles stuck at the estuary bed or attached to land using ropes with a floating element at the top and anchor at the bottom. In the deeper parts of the study area, the receivers were submerged to the sea floor using a rope with a floating element at the top and 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) and anchor at the bottom.

2.3 SEX DETERMINATION BY GENETIC ANALYSIS

The small sample of the adipose fin taken from each fish during the surgical procedure was used for further genetic analysis. This is to avoid human errors when determining both sex and species for the tagged fish. All DNA-analysis were conducted at the NTNU University Museum DNA lab, from methods described in Eldøy et al. (2021).

2.4 ENVIRONMENTAL PARAMETERS

Both temperature and salinity were measured in the study area during parts of the study period, to get a better understanding of the environment the fish stayed in. Data loggers (Star Oddi model DST centi-CT, Reykjavik, Iceland) were attached on poles together with two different acoustic receivers in the estuary. Depending on the habitat and the tides, the data loggers were on a depth between 0-5 meters. One was placed in the sheltered intertidal mudflats together with receiver H17, and the other was placed in the exposed intertidal mudflats by receiver H8 (Figure 1). The data loggers were measuring every 30 minutes during their active period, which ranged from autumn 2020 to autumn 2021. To get a better sense of the relationship that both temperature and salinity have with different depths in the estuary, a CTD (Conductivity, Temperature, and Depth) device was used within each habitat in the estuary. The measurements were taken during high tide, where these measurements gave a momentary representation of the physical properties of the water masses.

2.5 STATISTICAL ANALYSIS

2.5.1 Data filtration

One of the biggest challenges when working with acoustic telemetry is false detections. These may occur as a cause of sound pollution in the sea, or when the signal from two transmitters are colliding, making the receiver detect an ID code that is not present (Pincock, 2012). These colliding signals are either detected as an unknown transmitter ID code, or identical to another transmitter in the study, making the last one harder to filter out of the dataset (Simpfendorfer et al., 2015). False registrations are more likely when several fish stay in the vicinity of the same acoustic receiver, thus increasing the chance for false registrations for receivers in an estuary (Pincock, 2012). It is not possible to eliminate all false detections, but identification and removal of these will make for a more realistic dataset, although there is a risk of removing real data.

To minimize false registrations in the dataset, each fish needed at least two registrations from the same receiver within 10 minutes, to be approved for the filtered dataset. The receivers deployed in the zones connected to the river Stjørdalselva had a total of 1 076 063 registrations in the time period between December 2020 to April 2022. After the dataset filtration (removal of false registrations), there was a total of 912 101 registrations, where 471 341 were from the sea trout tagged in the winter of 2020, and the remaining registrations (440 760) were from the sea trout tagged in the spring of 2021. There was a different distribution of registrations within the different zones in the study area for both tagging groups. The exposed intertidal mudflats had 94 241 registrations, while there were 216 566 registrations in the river channel, and the sheltered intertidal mudflats had 515 377 registrations throughout the study period. The receivers within the zone categorized as fjord (adjacent marine) areas had 43 202 registrations, the fjord (Muruvika) zone had 3141 registrations and the upstream river zone had 39 574 registrations. Detections were sectioned into 5-minute bins in order to have corresponding temperature- acceleration and depth data linked to an observation. Bins with missing values were removed, resulting in a total of 81 293 observations.

2.5.2 Data analyses

The data analysis was conducted in RStudio version 2022.07.1 + 544 (Rstudio team, 2022), using R version 4.2.1 (R Core Team, 2022). Welch two sample t-test and one-way/two-way ANOVA were used for hypothesis testing, where the observed difference between groups were considered significant when the p-values were below 0.05. Tukey HSD post hoc test was used to find which sub-variables within a variable that had significant differences between each other. The package "ggplot2" (version 3.3.6) in R studio was used to make the different plots in this thesis. Four sea trout were excluded for further statistical analysis based on a short tracking period, few registrations, or only zero values from the acceleration sensor.

The individual mean activity level and swimming depth were estimated by calculating the mean for each individual fish (fish ID) within each of the three estuarine habitats in all four seasons. The ANOVA test that was used calculated the mean on the different seasons and habitats based on the individual mean for each fish, to observe the difference between groups. The same was done for the mean activity level between the sexes. The daily mean temperature, activity level, and swimming depth were estimated by calculating the daily mean for each individual fish (fish ID).

The individual activity level and depth use were also investigated by mixed effect models with both acceleration and depth as a response variable in their respective model. Season (S), habitat (H), sex (s), and total body length (L) were the explanatory variables for the activity level, with fish ID as random factor for both models. The mixed effect models for activity level and depth use were performed using the linear mixed effect model function “lmer” from the “lme4” package in R. The function “check_collinearity” was used to investigate variance inflation factors (VIF) from the “Performance package in R, where all explanatory variables had a VIF value of 1.

Model selection was performed with the use of the “Dredge” function in the “MuMIn” package in R (Bartoń, 2023) based on the second order of Akaike’s information criterion (AICc). Since the sample size (n) to estimated parameter (K) ratio (n/K) was lower than 40 in some models, the second order was used rather than Akaike’s information criterion (AIC) (Burnham et al., 2011). When models have ΔAICc<2, they are considered equally good. After several models were supported by the model selection (ΔAICc<2) (Anderson et al., 2001), conditional model averaging was used. This allowed inference from all the models (ΔAICc<2) to calculate the conditional average model parameter estimates and their standard error.

2.6 Activity level as an indicator

The activity level was one of the main characteristics that were investigated in this study. This characteristic is based on the data received from the acceleration sensors on the acoustic tag, where the final data that is filtered and formatted will provide an estimate of the total activity during the tracking period of the tagged fish. Approximately 80% of the acceleration data on four sea trout were removed as a result of zero values from a specific date till the last registration. Through analysis of these four fish, the zero-values did not look like a natural behavior and were probably some sort of source of error on the acceleration sensor. These four fish were not the same four fish that were excluded from further statistical analysis.

2.7 Season as an explanatory variable

The season was one of the main explanatory variables that were used to investigate which factors that affected the activity level and depth use. It helped answer the temporal aspect of habitat use and was defined as normal seasons in a sub-polar region. Winter was from 1. December to 28. February, spring from 1. March to 31. May, summer from 1. June to 31. August, and autumn from 1. September to 30. November. Both winter and spring appeared two times (winter 2020 and 2021, spring 2021 and 2022) during the study period (2020.12.20-2022.04.15) and were therefore merged as “Winter” and “Spring”.

3. RESULTS

3.1 Environmental parameters

Temperature and salinity were measured by dataloggers in the exposed and sheltered intertidal mudflats. The mean daily temperature in the exposed intertidal mudflats (receiver H8, Figure 1) ranged from 1.7-17.9 °C in the period from August 2020 to March 2021, with an average of 8.2 °C (SD= 4.2 °C). The water temperature peaked at the start of the measurements and had a steady decline towards winter (Figure 5). In the sheltered intertidal mudflats, the mean daily temperature (receiver H17, Figure 1) ranged from 5.3- 20.6 °C in the time period from April- September 2021, with an average of 12.9 °C (SD= 4.3 °C). The water temperature was at the lowest in mid-spring, peaked in July, and declined when autumn came (Figure 6).

The salinity in both habitats was influenced by tides, resulting in daily fluctuations. However, the estimations of the daily mean salinity hide the daily variation in salinity. In the exposed intertidal mudflats, the mean daily salinity ranged from 0- 29 ‰ from August 2020 to March 2021, while in the sheltered intertidal mudflats, the mean daily salinity ranged from 0- 27 ‰ from April- September 2021.

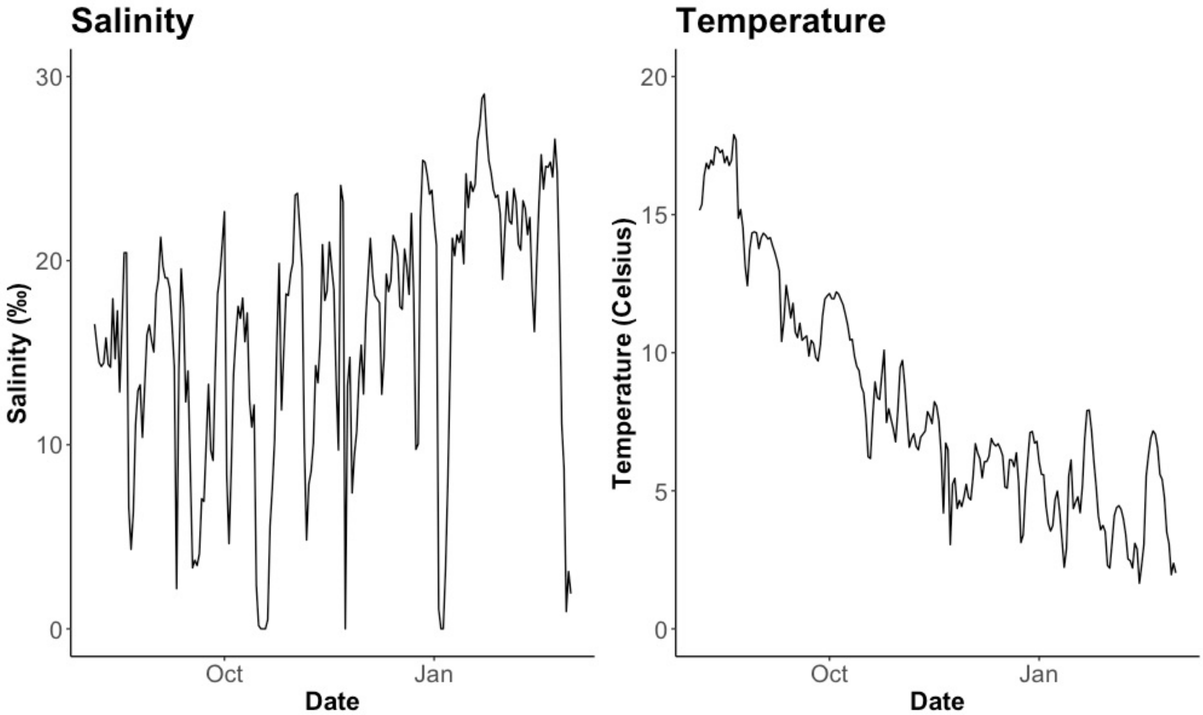

Figure 5: *Mean daily salinity (‰) and* water temperature (°C) *measured from 2020.08.05- 2021.03.02 in the exposed intertidal mudflats (Figure 1, H8) from data logger attached to a pole 5 cm above the sea bottom.*

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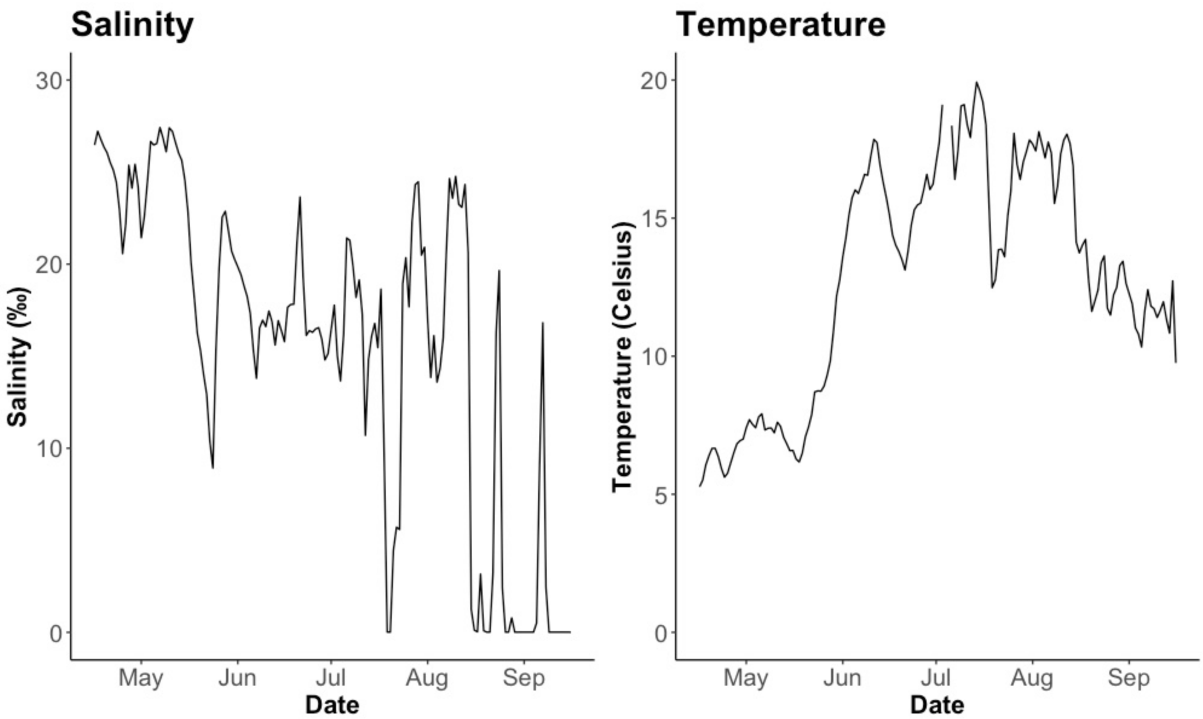

Figure 6: *Mean daily salinity (‰) and water temperature (℃) measured from 2021.04.16-2021.09.16 in the sheltered intertidal mudflats (Figure 1, H17) from data logger attached to a pole 5 cm above the sea bottom.*

Measuring of water temperature and salinity vertically in the water column in the estuary of river Stjørdalselva, revealed a halocline and thermocline (Figure 7). It is important to note that the measurements were done in spring during high tide. The depth of both halocline and thermocline will change with the season, tidal water, and river flow. In the exposed intertidal mudflats, there was a distinct layering of the water column at approximately 0.5 meters depth, with a temperature range between 3-4 °C in the upper freshwater layer, where the salinity exceeded 30 ‰ at 6 °C in the marine layer (Figure 7 a). In both river channel and sheltered intertidal mudflats, the change in layer from freshwater to marine water happened at approximately 1-1.5 meters depth. The freshwater layers were around 2.5- 3.5 °C and 3- 4 °C in their respective habitats, with marine water masses (30 ‰) at 5 °C and 6 °C (Figure 7 b, c).

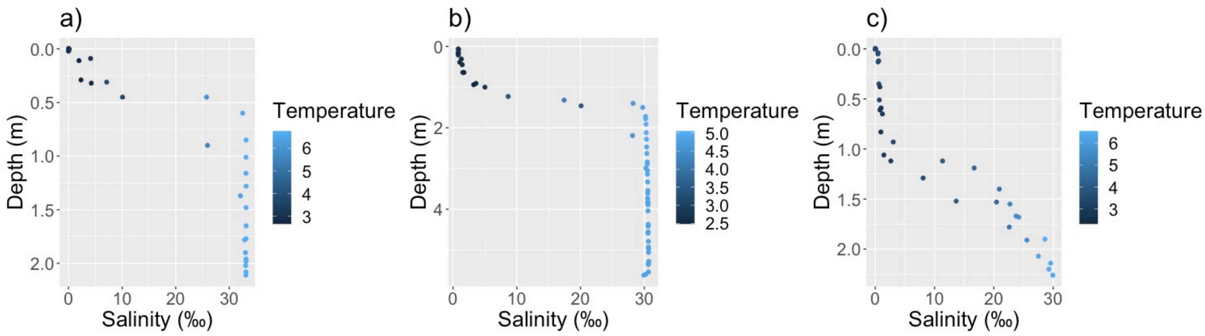

Figure 7: *Water temperature (℃) and salinity (‰) in the estuary of river Stjørdalselva measured at different depths (m) in a) exposed intertidal mudflats (2023.04.24), b) river channel (receiver H11, 2021.19.04), c) sheltered intertidal mudflats (2023.04.24). The temperature graded from dark blue (colder temperature) to light blue (warmer temperature). NB! The scale of the y-axis differs between the panels (a, b, c).*

3.2 Total body length

Body length was smaller for the spring group (mean 402 mm, range 290-615 mm; SD= 96, *n*= 17), compared to the winter group (mean 412 mm, range 290-615 mm; SD= 67, *n*= 9), although not significant (Welch two-sample t-test; $p>0.05$). Body length for males was smaller (mean 384, range 300-615 mm; SD= 86, *n*= 14) than for females (mean 430 mm, range 290-580 mm; SD= 83, *n*= 12), although not significant (Welch two-sample t-test; $p>0.05$) (Figure 8).

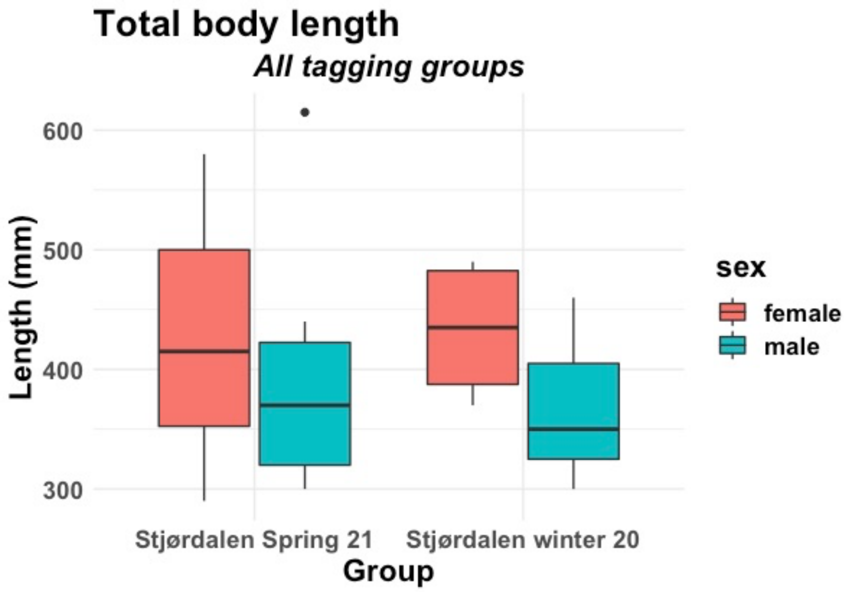

Figure 8: *The total body for two tagging groups tagged in river Stjørdalselva. The boxplot shows 50% of the data points for each group within each box, the 5th and 95th percentiles (whiskers), the median values (bold line) and outliers (dot).*

3.3 Individual migration of the sea trout

A total of 30 sea trout were tracked during the study period, where information on migration and habitat use were covered. Four sea trout (13%) were removed from the dataset due to few registrations and/or a short tracking period (< 1 week). Out of the 26 sea trout, 14 were males (three from winter 2020 group and 11 from spring 2021 group) and 12 were females (six from winter 2020 group and six from spring 2021 group). The individual fish had a different behavior regarding the migration and preference of habitat during different seasons. The sea trout migration pattern of moving from the estuary to marine water in summer, returning to the river in autumn for potential breeding, and stay in the estuary for the rest of the period (until next spring/summer) was found in 11 out of 26 sea trout's (42%). There was a special case, where one of the fish only stayed in the sheltered estuary and upper river during the whole study period. After some filtering of the data from the receivers, a total of 17 fish (65%, 10697 registrations) were registered in the exposed estuary, 25 (96%, 21433 registrations) in the river channel, 22 (85%, 49163 registrations) in the sheltered estuary, 17 (65%, 6392 registrations) in the adjacent marine area, 13 (50%, 400 registrations) in the Muruvika area and 14 (54%, 6207 registrations) in the upper river. These numbers indicate that the sea trout utilized the zones in the study area differently. The tracking period where different for each fish, which resulted in more data on some of the fish (Figure 8).

Three of the 13 sea trout (23%) detected in the Muruvika area (fjord) did not return to the estuary during the study period. Of the ones that migrated to the fjord, 54% of them were males. There were six sea trout (23%) that did not return from the upper river, linked to the spawning migration up the river. The abundance of the tagged sea trout differed between the three estuarine habitats at different times of the year (Figure 9). Spring was the season that had the highest abundance of sea trout within the estuary, with 24 sea trout present during the season (92%). Out of the 14 sea trout that were present in the estuary during summer, male sea trout had a higher abundance (62%) compared to female (38%). In winter, 12 sea trout were present in the estuary (46%), where females had a higher abundance (66%) compared to males (34%) (Figure 9).

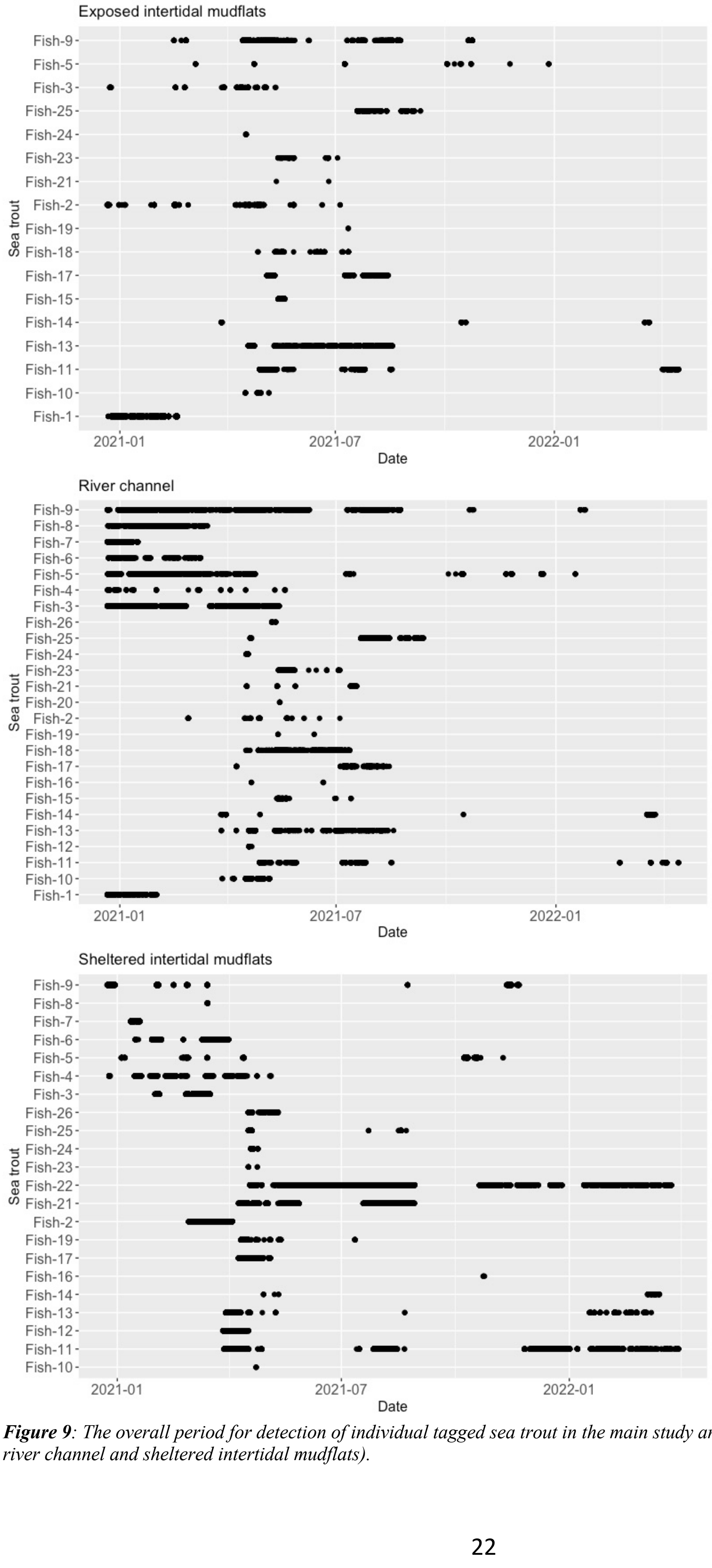

Figure 9*: The overall period for detection of individual tagged sea trout in the main study area (exposed intertidal mudflats, river channel and sheltered intertidal mudflats).*

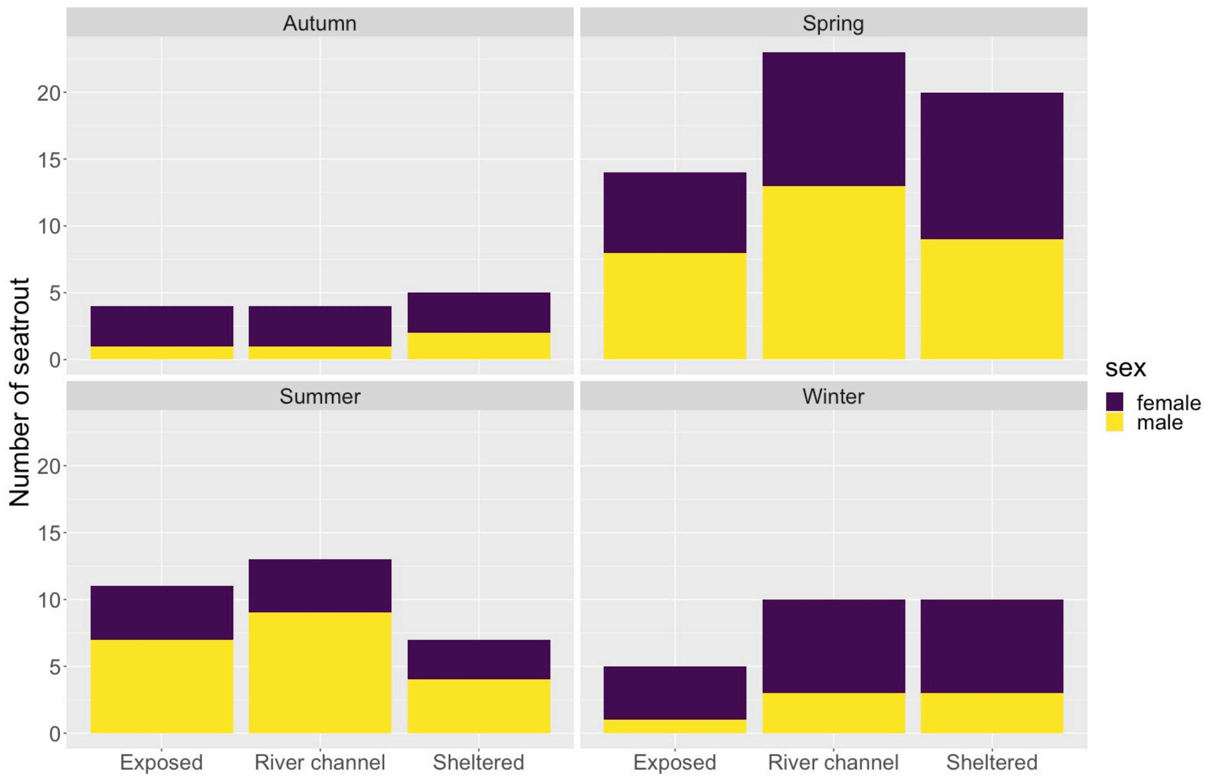

Figure 10: *The number of seatrout in the three estuarine habitats at different seasons with the distribution of male & female.*

3.4 Temperature use by the sea trout

The temperature surrounding the sea trout had a steady incline towards summer, with the highest peak during the summer in all three habitats (Figure 11). In contrast, the mean daily temperature had a decline towards the winter, with the lowest experienced temperature in winter. There was a difference (ANOVA-test, $p<0,05$) in temperature between the habitats, although the experienced temperature and pattern were similar within the three estuarine habitats (Figure 11). Exposed intertidal mudflats had the highest experienced mean temperature during the study period as a whole (mean= 9.6 °C; SD=5.3), based on the mean from the daily mean experienced temperature for each individual fish within this habitat. The river channel had the second highest (mean= 7.8 °C; SD=4.9), followed by sheltered intertidal mudflats (mean= 6.6 °C; SD=5.0). July was the month with the highest experienced mean temperature in all three habitats (exposed: 16.4; SD=1.9, river channel: 16.8; SD=1.5, and sheltered: 15.8 °C; SD=1.7). The coldest month in both exposed intertidal mudflats and river channel was November (2.4 °C; SD=0, only one fish present & 2.7 °C; SD=1.2, only one fish present), with February being the month with the lowest experienced mean temperature (3.6 °C; SD=1.4) in the sheltered intertidal mudflats (Figure A3, appendix).

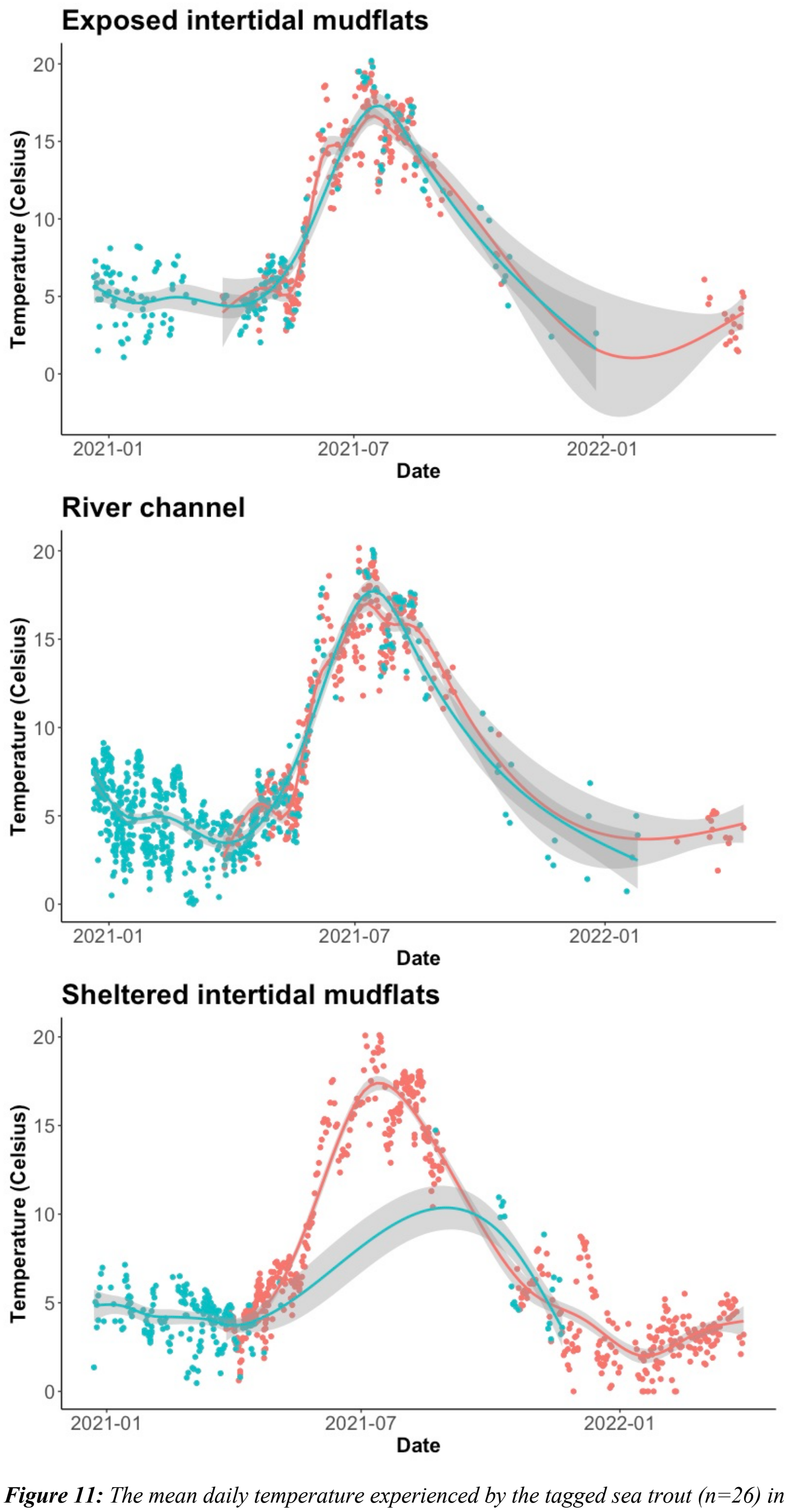

Figure 11: *The mean daily temperature experienced by the tagged sea trout (n=26) in the three habitats within the estuary. The blue dots are the group tagged at winter 2020 and red are the group tagged at spring 2021, with the mean 95% confidence interval indicated by the grey band.*

3.5 Activity level

3.5.1 Individual difference in the activity level between different habitats and seasons

Seasonal mean activity level within each habitat differed between the three estuarine habitats in the estuary and between the four seasons (ANOVA-test, $p<0.05$, $n=26$; Figure 12). The significance was between sheltered and exposed, sheltered and river channel, and summer and winter (Post hoc test, $p<0.05$). The highest activity level was in the river channel (mean= 0.35 m/s^2; SD= 0.13), which was the habitat that had the biggest variance within the activity level. The exposed intertidal mudflats showed the second highest activity level (mean= 0.33 m/s^2; SD= 0.1), while the sea trout using the sheltered intertidal mudflats had the lowest level of activity (mean= 0.23 m/s^2; SD= 0.01). Summer was the season with the highest activity level (mean= 0.36 m/s^2; SD= 0.16), with spring being the second highest (mean= 0.31 m/s^2; SD= 0.1), followed by autumn (mean= 0.26 m/s^2; SD= 0.16), and with winter having the lowest activity level (mean= 0.24 m/s^2; SD= 0.06). Both season and habitat influenced the activity level in different ways, thus, the mean activity level differed within the habitats at different seasons (Table 1).

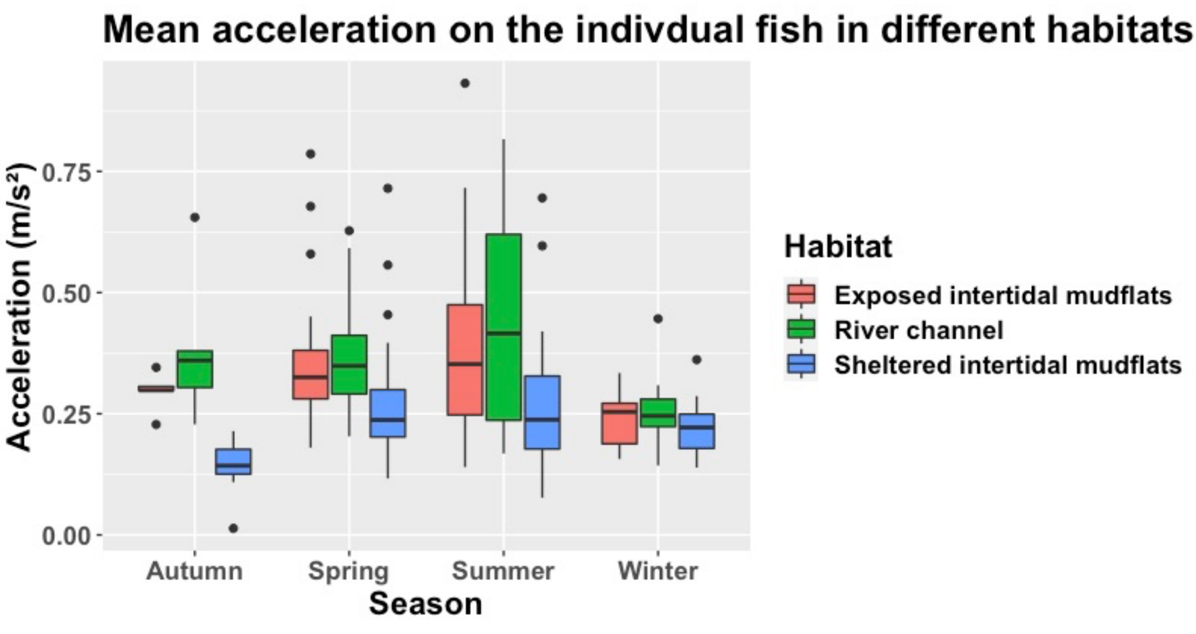

Figure 12: *Mean acceleration on the individual sea trout (n=26) within the three estuarine habitats in the main study area and different seasons during the study period. The boxplot shows 50% of the data points for each group within each box, the 5th and 95th percentiles (whiskers), the median values (bold line) and outliers (dots).*

Table 1: *The mean and standard deviation (SD) of the activity level on the individual sea trout (n=26) within the three estuarine habitats at each season.*

Season	**Habitat**	**Mean**	**SD**
Winter	Exposed	0.25	0.05
Winter	River channel	0.27	0.07
Winter	Sheltered	0.21	0.04
Spring	Exposed	0.35	0.09
Spring	River channel	0.34	0.08
Spring	Sheltered	0.25	0.08
Summer	Exposed	0.35	0.11
Summer	River channel	0.42	0.18
Summer	Sheltered	0.27	0.16
Autumn	Exposed	0.28	0.04
Autumn	River channel	0.39	0.18
Autumn	Sheltered	0.13	0.07

Daily mean activity level differed both between the seasons and the three habitats (ANOVA-test, $p<0.05$, $n=26$; Figure 13). The significant difference was between sheltered and exposed habitats and between sheltered and river channel habitats (Post hoc test, $p<0.05$). Between seasons, there was no significant difference between winter and autumn (Post hoc test, $p>0.05$). The sea trout detected in the exposed intertidal mudflat had the highest mean daily activity level (mean= 0.34; SD= 0.20), the river channel showed the second highest (mean= 0.33; SD= 0.18), and sheltered intertidal mudflats had the lowest (mean= 0.29; SD= 0.19). The exposed intertidal mudflats were more used by the sea trout in summer compared to the rest of the year, where summer had the most detections and highest mean daily activity level within the habitat. The sea trout were more active in the sheltered estuary during winter 2021/2022 compared to the two other habitats (more registrations), whereas the river channel showed a more active sea trout throughout the year. Data from the summer season was affected by some sea trout migrating out in the marine areas (fjord zone), which reduced the abundance of sea trout within the estuary. The same happened during late autumn/ early winter, when the sea trout migrated up the river for potential spawning. June was the month that had the highest mean activity level for all three estuarine habitats, where the mean was highest within the sheltered habitat (0.69 m/s^2; SD=0.42) followed by the river channel (0.62 m/s^2; SD=0.18), then exposed intertidal mudflats (0.57 m/s^2; SD=0.22). It should be noted that the number of tagged sea trout detected during June was one in the sheltered habitat, eight in the river channel, and six in the exposed habitat, which explains why the sheltered intertidal mudflats had the highest mean activity level in June. The month with the lowest mean activity level was January (0.23 m/s^2; SD=0.05) for the exposed habitat, December for the river channel (0.21 m/s^2; SD=0.04), and October for the sheltered habitat (0.13 m/s^2; SD=0.1) (Figure A4, appendix). It should be noted that different tracking period for each individual fish, number of detections and number of different sea trout detected within the three estuarine habitats in different seasons could have an impact on the results on the level of activity within the three different habitats and different seasons.

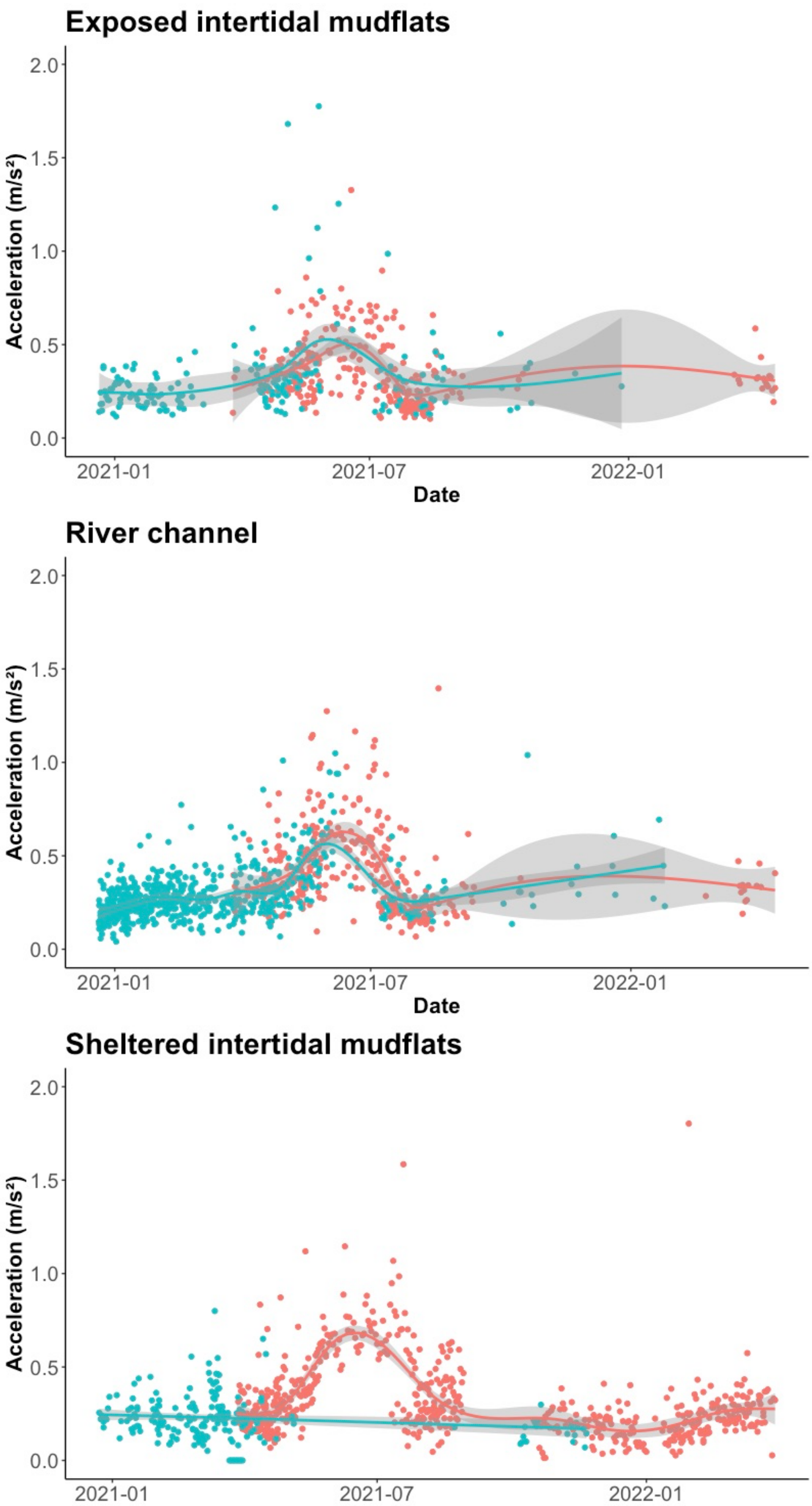

Figure 13: *The mean daily activity level on the tagged sea trout (n=26) in the three habitats within the estuary. The blue dots are the group tagged at winter 2020 and red are the group tagged at spring 2021, with the mean 95% confidence interval indicated by the grey band.*

3.5.2 The effect of total body length on the individual mean activity level

There was no correlation between the total body length and mean activity level (ANOVA-test, $p>0.05$, $n=26$) (Table 2) (Figure 14 & 15). Sea trout with body lengths between 300-450 mm had the highest mean activity level during the study period (Figure 14 & 15). Sea trout having the highest mean within a habitat during a season was 365 mm in total length (mean= 0.81 m/s^2, habitat= river channel, season= Summer), and the sea trout with the lowest mean was 615 mm (mean= 0.014 m/s^2, habitat= sheltered, season= Autumn). It could be argued that there was a difference in activity level between sea trout with different body lengths in the sheltered intertidal mudflats during spring (Table C, appendix).

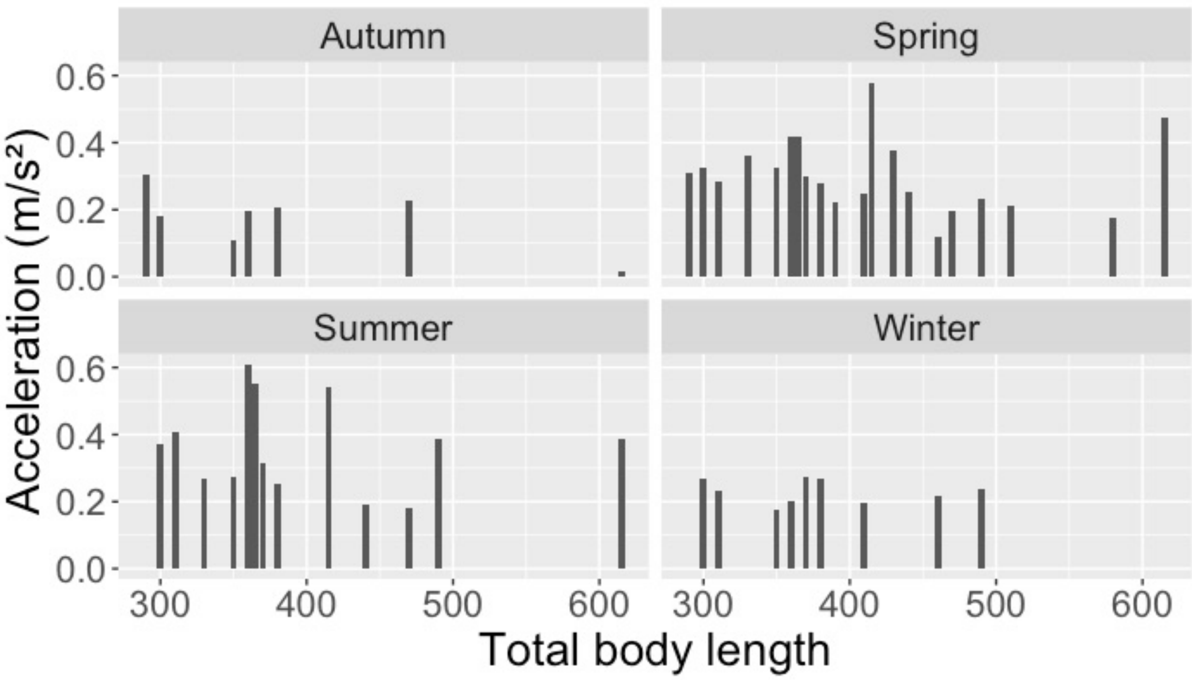

Figure 14: *The mean daily activity level on the tagged sea trout (n=26) at different body lengths (mm) in different seasons.*

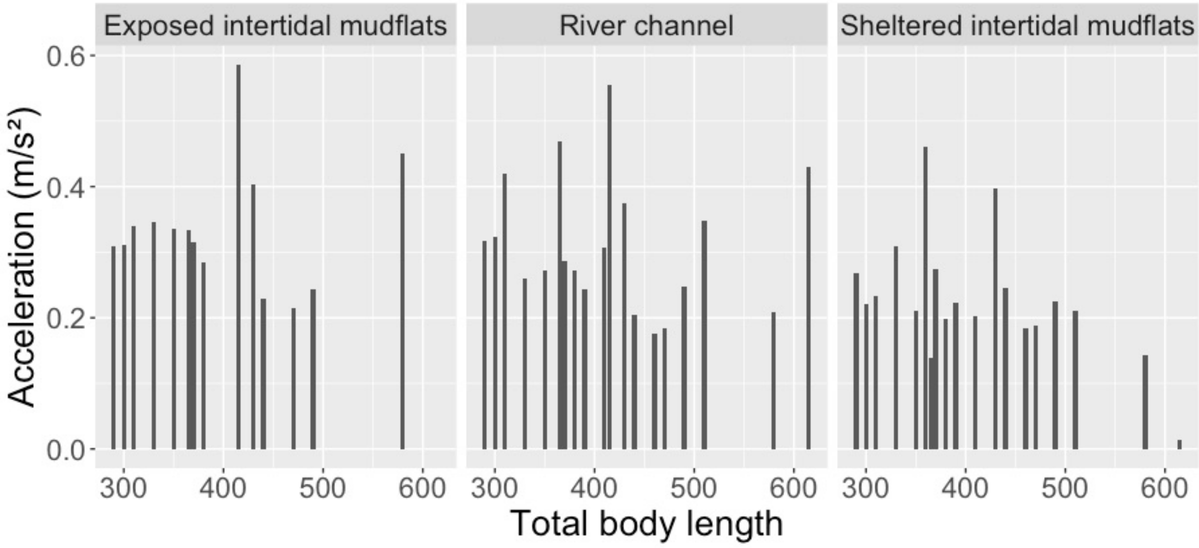

Figure 15: *The mean daily activity level on the tagged sea trout (n=26) at different body lengths (mm) within the three estuarine habitats.*

3.5.3 The effect of sex on the individual mean activity level

The tagged sea trout had an even distribution between the different sexes, with 14 males and 12 females from the 26 fish that were used for the analyses. The overall activity level, all seasons and habitats together, differed between males and females (welch two-sample t-test, $p<0.05$; Figure 16), with males having a higher (0.32 m/s^2; SD=0.1) mean activity level than females (0.25 m/s^2; SD=0.08).

During winter, activity level was similar between the sexes in all three habitats (Figure 16). However, during spring and summer (Figure 16) males had a higher activity in all habitats. In the autumn, male sea trout had a higher mean activity level in the exposed habitat, but lower than females in the river channel and sheltered habitat (Figure 16), although there were few registrations in the river channel during autumn for male sea trout. When comparing activity level between the three estuarine habitats in different seasons, females and males only differed in the river channel during spring and autumn (one-way ANOVA; Table 2).

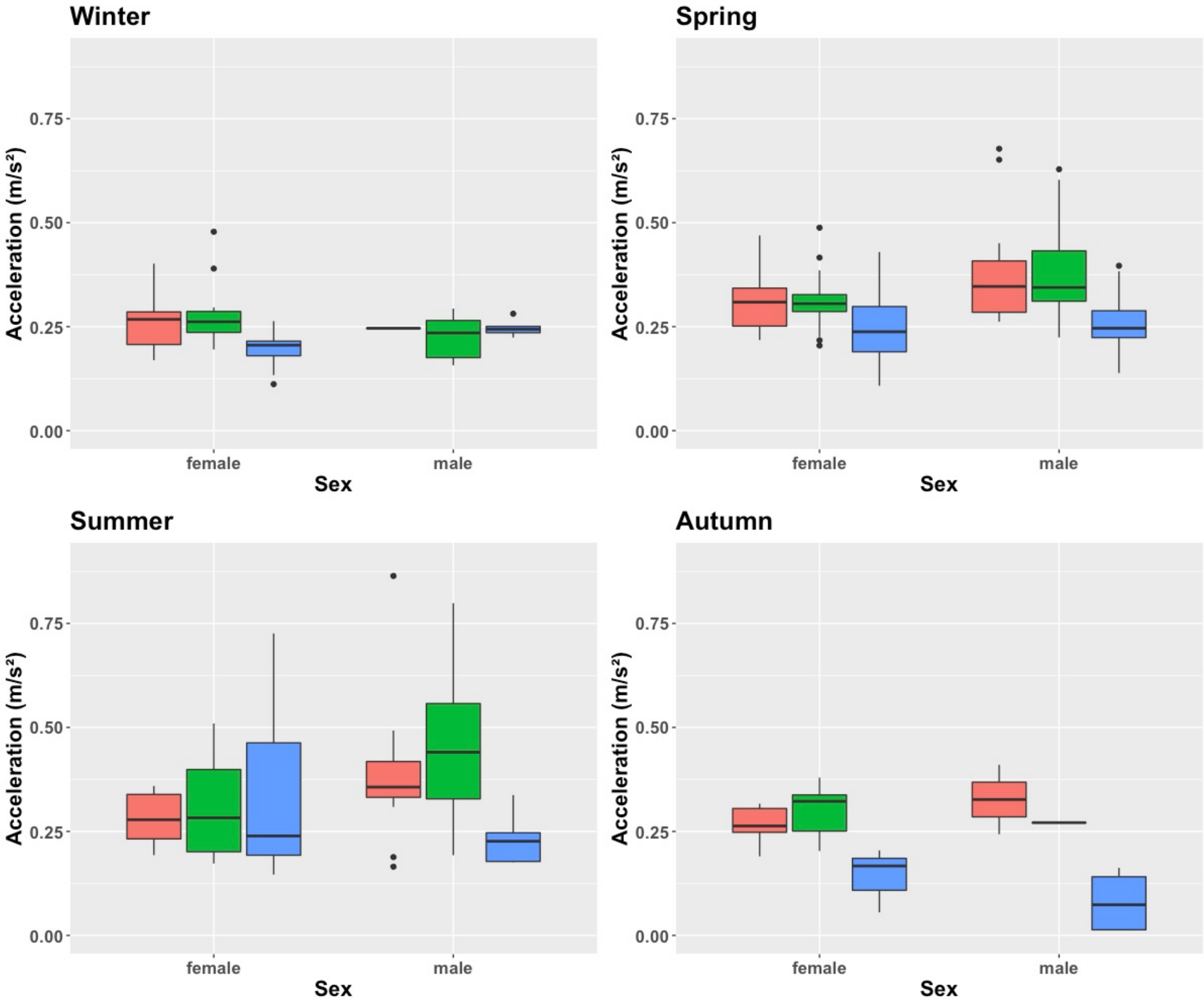

Figure 16: *The mean activity level of each individual tagged sea trout (n=26) on both sex during all season. The boxplot shows 50% of the data points for each group within each box, the 5th and 95th percentiles (whiskers), the median values (bold line) and outliers (dots). The red boxes are the exposed intertidal mudflats, the green is the river channel, and the blue are the sheltered intertidal mudflats.*

Table 2: *The P-value from a one-way ANOVA test with acceleration as output and sex as a variable within different seasons and habitats. The number of fish (n) represented in each habitat at different seasons. Significant values (P ≤ 0.05) are highlighted by the asterisk mark (*).*

Season	Habitat	n	P-value
Winter	Exposed	5	0.92
Winter	River channel	10	0.28
Winter	Sheltered	10	0.09
Spring	Exposed	14	0.34
Spring	River channel	23	0.05*
Spring	Sheltered	20	0.73
Summer	Exposed	11	0.19
Summer	River channel	13	0.19
Summer	Sheltered	7	0.36
Autumn	Exposed	4	0.72
Autumn	River channel	4	0.05*
Autumn	Sheltered	5	0.40

3.5.4 Influence of individual variables on the activity level of the sea trout

The influence of habitat, season, sex, and total body length on the individual mean activity level of the tagged sea trout were explored using a generalized linear model. The number of sea trout included in this model were 26, where each fish residing in at least one of the three habitats within estuary.

Three equally well-fitted models were identified by the use of model selection (Δ AICc<2, Table 3), where season, habitat, total body length, and sex were the explanatory variables in the models. Both habitat and season were included in all models, indicating that these variables had the biggest effect on the activity level. The estimates from the model averaging (Δ AICc<2, Figure 17) showed that both summer and spring were seasons when the sea trout had a higher activity level, especially summer, meaning these sub-variables were significant for the activity level. The river channel was the habitat that had the biggest influence on the level of activity. The standard error exceeded the estimate for winter and total body length, indicating that these variables had limited influence on the activity level (Figure 17). Sex had an impact on the activity level, where males had a higher mean activity level than females.

Table 3: *Model selection of mixed effects models for the influence of season (S), habitat (H), total body length (L) and sex (s) on the mean activity level of the individual sea trout during the study period. The models are ranked by decreasing ΔAICc value, with supported models highlighted in bold (Δ AICc<2).*

Model	AICc	ΔAICc	AICc weights	d.f.
[S,L,H]	**-203.7**	**0.00**	**0.308**	**9**
[S,H]	**-203.2**	**0.53**	**0.236**	**8**
[S,s,,H]	**-202.8**	**0.91**	**0.195**	**10**
[S,s,L,H]	-202.5	1.25	0.165	9

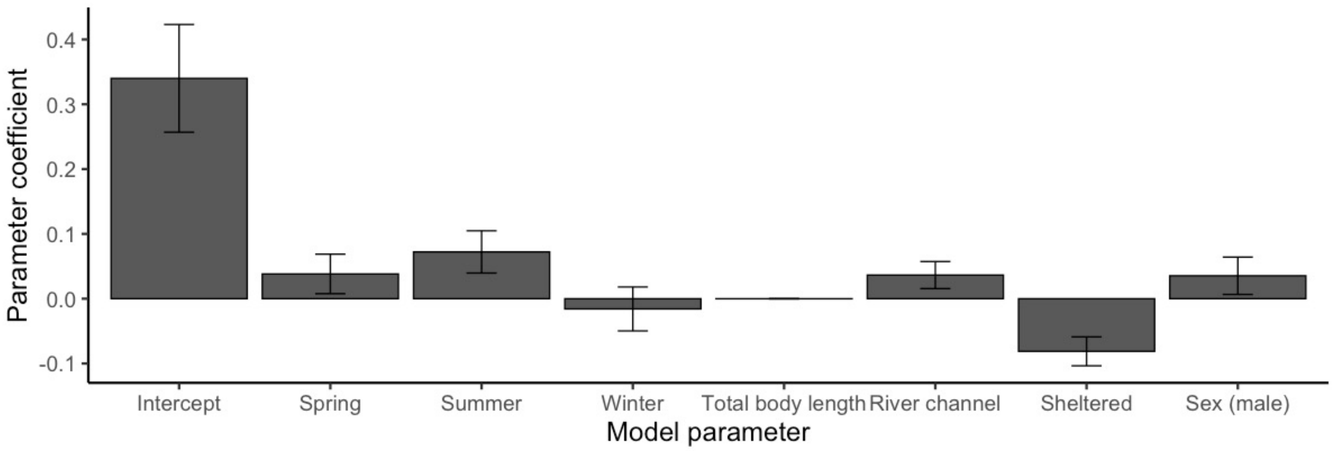

Figure 17: *Model averaging summary statistics for mixed effects models with ΔAICc <2 for the effect of season (S), habitat (H), total body length (L) and sex (s) on the activity level of the individual sea trout during the study period.*

3.6 Depth use

3.6.1 Depth use varies between seasons

Seasonal mean swimming depth within each habitat differed between the three estuarine habitats in the estuary and between the four seasons (ANOVA-test, $p<0.05$, $n=26$; Figure 18). The difference was significant between spring and autumn, and spring and winter (Post hoc test, $p<0.05$). Between the habitats, the significant difference was between river channel and exposed, and river channel and sheltered (Post hoc test, $p<0.05$). Within each habitat, there was only a significant difference in the mean activity level between spring and summer in the exposed habitat (Post hoc test, $p<0.05$). In the exposed intertidal mudflats, the sea trout stayed closer to the surface in summer and winter, while it went closer to the bottom during spring. In the river channel, spring and summer were the seasons with the deepest mean swimming depth, while in the sheltered intertidal mudflats, autumn was the season when the sea trout stayed closest to the surface. In general, within the estuary, the sea trout stayed deeper in summer (mean= 2.16 m; SD= 0.93) and spring (mean= 2.31 m; SD= 0.72), and closer to the surface during autumn (mean= 1.82 m, SD= 0.94) and winter (mean= 1.90 m; SD= 0.51). In the three different habitats throughout the year, the sea trout stayed deepest in the river channel (mean= 2.8 m; SD=0.8), followed by sheltered intertidal mudflats (mean= 1.8 m; SD=0.3), then exposed intertidal mudflats (mean=1.7; SD=0.5).

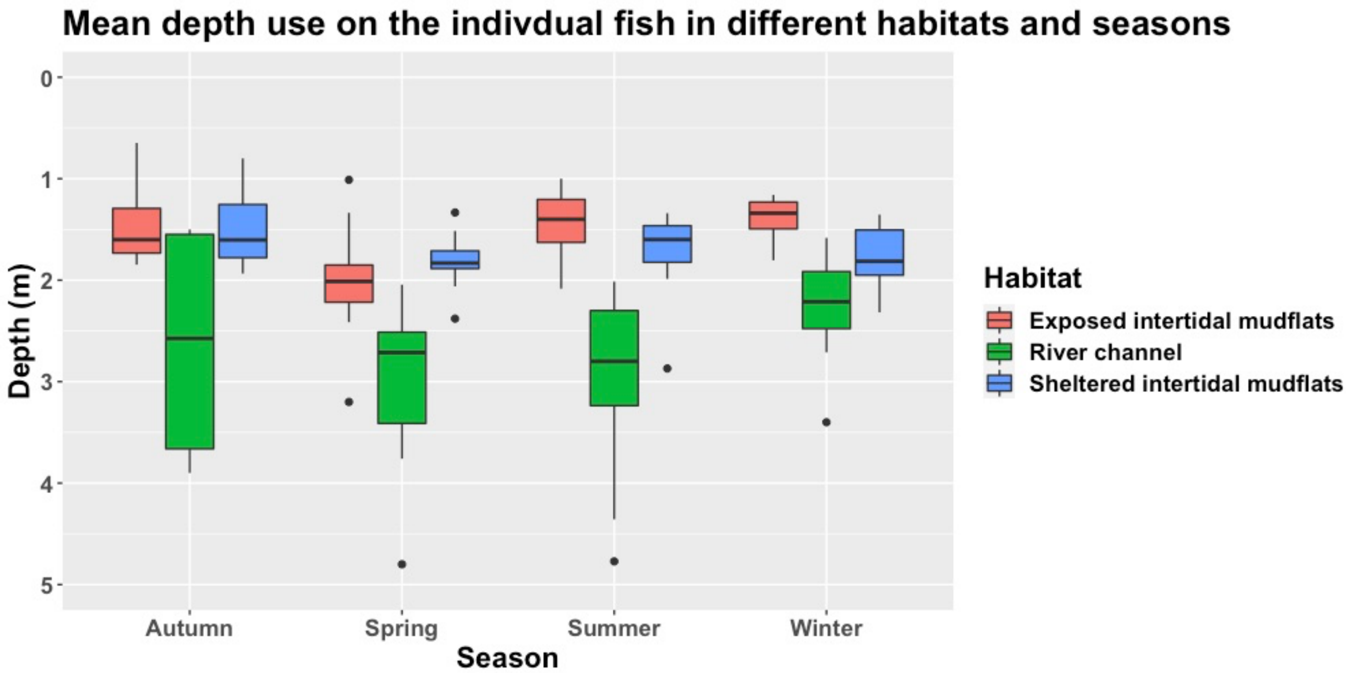

Figure 18: *Mean depth use on the individual sea trout (n=26) within the different habitats in the main study area and different seasons during the study period. The boxplot shows 50% of the data points for each group within each box, the 5th and 95th percentiles (whiskers), the median values (bold line) and outliers (dots).*

Spring and summer were the seasons where the deeper layers of the river channel and exposed intertidal mudflats were more frequently used by the sea trout, based on the daily mean depth use from each individual fish (Figure 19), giving a significant difference in the depth use between seasons (ANOVA-test, $p<0.05$, $n=26$). In the exposed habitat, winter and autumn were the only two seasons with no difference between them (Post hoc test, $p>0.05$, $n=17$). In the river channel, there was only a significant difference (Post hoc test, $p<0.05$, $n=25$) between spring and winter, and summer and winter. The sheltered intertidal mudflats had a significant difference in the depth use between spring and autumn, summer and spring, and winter and spring (Post hoc test, $p<0.05$, $n=22$). In the exposed habitat, spring was the season with the deepest daily mean depth use, followed by summer then winter, with autumn being the season where the fish were staying closest to the surface. For the river channel, summer was the season where the fish stayed the deepest, followed by spring and autumn, with winter being the season where the fish used the upper water layers more frequently. The sheltered intertidal mudflats had the deepest swimming depth in spring, followed by winter then summer, with autumn being the season when the sea trout stayed closer to the surface. There was a difference in the daily mean swimming depth between the habitats as well (ANOVA-test, $p<0.05$, $n=26$). The river channel had the deepest daily mean swimming depth throughout the year (mean= 2.5 m; SD=0.9), followed by the sheltered intertidal mudflats (mean= 1.8 m; SD=0.4), then the exposed intertidal mudflats (mean= 1.7 m; SD=0.6). March was the month with the deepest mean swimming depth in the exposed estuary (2.4 m; SD=0.4) and sheltered intertidal mudflats (1.9 m; SD=0.3), while September was the month with the deepest mean swimming depth (3.6 m; SD=1.15, only one fish present) in the river channel (Figure A5, appendix). It should be noted that different tracking period for each individual fish, number of detections and number of different sea trout detected within the three estuarine habitats in different seasons could have an impact on the results on depth use within the three different habitats and different seasons.

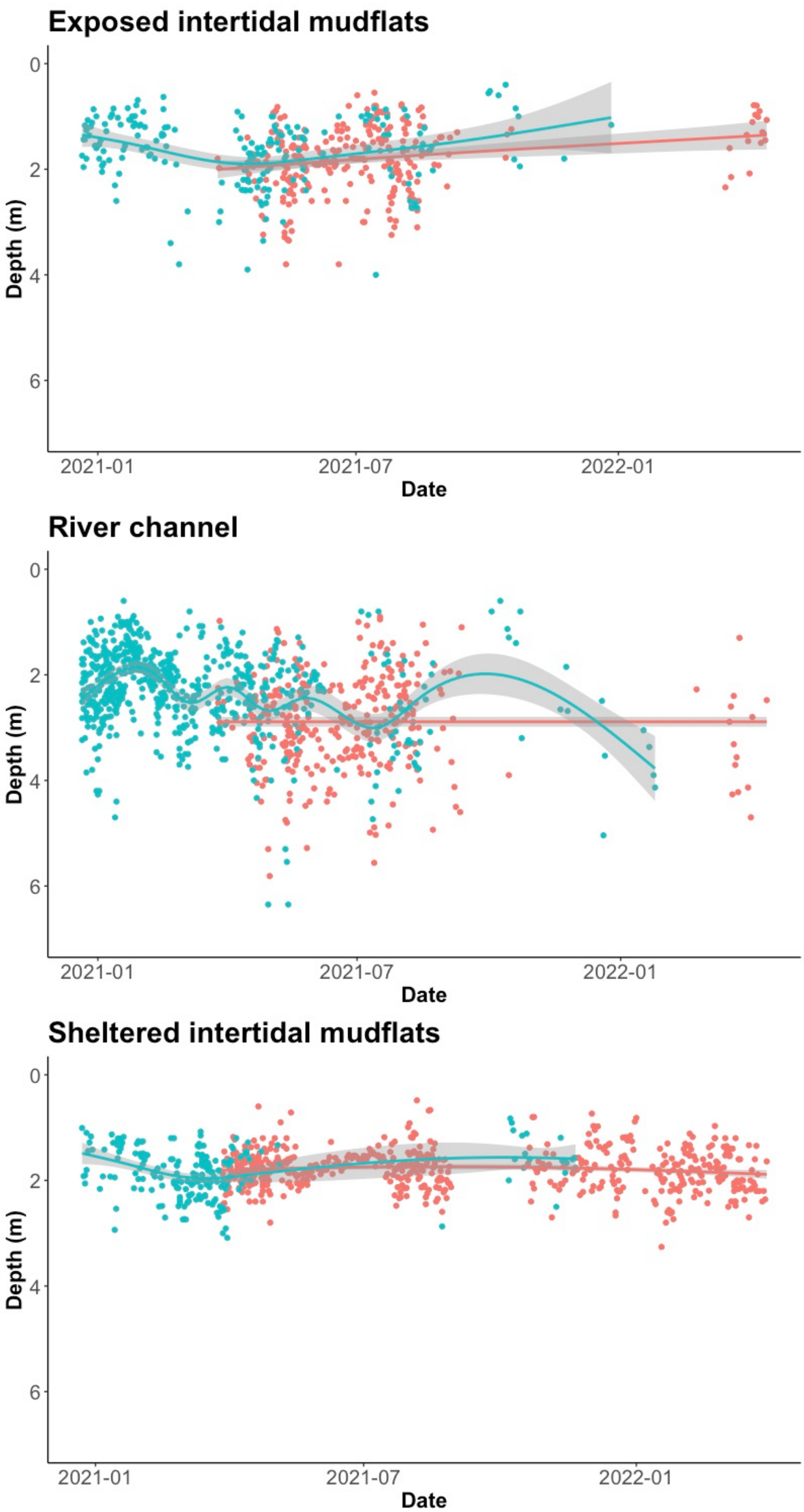

Figure 19: *The mean daily depth use on the tagged sea trout (n=26) in the three habitats within the estuary. The blue dots are the group tagged at winter 2020 and red are the group tagged at spring 2021. Each dot is the mean daily depth for an individual sea trout, with the mean 95% confidence interval indicated by the grey band.*

3.6.2 Influence of individual variables on the depth use of the sea trout

The influence of season, sex, total body length, and habitat on the individual depth use of the tagged sea trout were explored using a generalized linear model. The number of sea trout included in this model were 26, where each fish residing in at least one of the three habitats within the estuary.

Three equally well-fitted models were identified with the use of model selection (Δ AICc<2, Table 4), where season, total body length, sex, and season were the explanatory variables in the models. Season and habitat were included in all four models, indicating that these variables had the biggest effect on depth use. The estimates from the model averaging (Δ AICc<2, Figure 20) showed that both summer and spring, and especially the latter, were seasons when the sea trout had a deeper depth use, meaning these sub-variables were significant for the depth use. The standard error exceeded the estimate for winter, total body length, and sheltered habitat, indicating that these variables had limited influence on the depth use (Figure 20). The figure also shows that males tended to stay at deeper layers than females, although this was not investigated further.

Table 4: *Model averaging summary statistics for mixed effects models with ΔAICc <2 for the effect of season (S), total body length (L), sex (s), and habitat (H) on the depth use of the individual sea trout during the study period. The models are ranked by decreasing ΔAICc value, with supported models highlighted in bold (Δ AICc<2).*

Model	AICc	ΔAICc	AICc weights	d.f.
[S, L ,H]	**223.2**	**0.00**	**0.254**	**9**
[S, H]	**223.2**	**0.02**	**0.251**	**8**
[S, s, H]	**223.4**	**0.20**	**0.230**	**9**
[S, s, L, H]	224.4	1.20	0.139	10

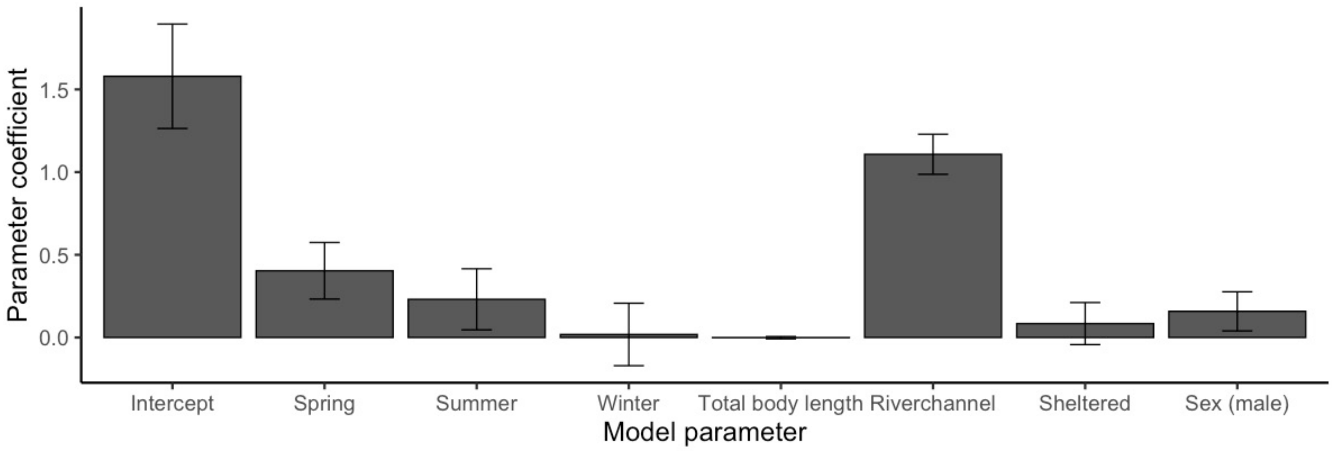

***Figure 20**: Model averaging summary statistics for mixed effects models with ΔAICc <2 for the effect of season, total body length, sex, and habitat on the depth use of the individual sea trout during the study period.*

4. DISCUSSION

The sea trout from river Stjørdalselva extensively utilized both the river channel and the exposed- and sheltered intertidal mudflats, indicating that these three habitats all were important for the species. This thesis explored the sea trout's individual spatiotemporal use of the three habitats with focus on activity level and swimming depth. The results indicated that there were individual differences in habitat use based on the individual variation in spatial and temporal level of activity and depth use.

Individual migration and habitat use

The three estuarine habitats were frequently used throughout the year. The river channel was used by most individuals (96%), with sheltered intertidal mudflats (85%) being the second most used, and exposed intertidal mudflats (65%) being the habitat that was less used within the estuary. Although the river channel was the habitat that was used by most individuals, the sheltered intertidal mudflats had the highest residence time (Figure A1, appendix). In summer, some individuals migrated out to the inner parts of the fjord (50%), contrary to other individuals that chose to stay in the estuary/ river throughout the study period (50%). Of the individuals that migrated out in the fjord, 23% did not get registered during the rest of the study period. This could be because they either died due to predation or other factors, or chose to stay longer than the battery life of the fish tags in the fjord, for the beneficial feeding opportunities that the marine waters can provide (Eldøy et al., 2015). The ones that remained in the estuary throughout the study period probably took advantage of the benefits here, such as good feeding opportunities, reduced need for physiological adjustment to salinity, avoidance of predators, and saving energy from a longer migration to the fjord or open coast (Thorstad et al., 2016). Thus, for some individuals, the benefit of residing in the estuary outweighed the marine migration, indicating that the estuary provides the necessary biotic and abiotic factors for the growth of these individuals, while other individuals took a higher risk for better feeding opportunities in the fjord. During the spawning migration up the river in autumn (54%), six individuals did not get registered in the estuary for the rest of the study period (23%). Reasons could be that they died due to different factors, chose to stay in the river longer than the battery life of the acoustic tags, or it could be a source of error linked to the acoustic transmitter, although the latter is unlikely.

Influence of habitat and season on the activity level

There was an individual spatial and temporal variation in the level of activity for the sea trout in the estuary of river Stjørdalselva. The activity level shown in the different habitats is an indication of how the fish utilized the different habitats in time and space, and a suggestion of what these habitats were used for, and thus, the importance of these different areas within the estuary.

The river channel was the habitat with the highest mean activity level, and there could be several explanations for this phenomenon. The food availability here is unknown, but the high activity level could indicate an active feeding behavior. If so, the results suggest that the river channel could be an important foraging area for the sea trout. Within the river channel, tides will cause both in- and outgoing currents in this habitat, while the river flow that goes directly through the area will cause a strong outgoing current. In total, these currents provide constant nutrient and oxygen flow through the habitat and hence make the river channel a suitable habitat for many species that the sea trout potentially can prey on. Another reason for the river channel showing the highest level of activity could be the periodically strong currents. Since the habitat potentially is an important feeding area, catching prey could demand a higher acceleration because of the variable pattern of flow. A third reason could be that the river channel is a passage to the marine waters; thus, the habitat could have visitors from the marine waters during the high tidal water. Marine predators could be a factor that stimulates the activity level, where the sea trout accelerates to escape and/or avoid the predator in this area, where the currents could demand a higher acceleration during the escape compared to the other habitats in the estuary. The river channel was the deepest of the three habitats studied and had a larger layer of marine water underneath the brackish water, compared to the two other habitats. Consequently, there was more space for both marine prey and marine predators, which could have affected the activity level.

The exposed intertidal mudflat was the habitat that had the second highest mean activity level. This habitat had the highest mean from the daily mean activity level overall, although the daily mean will “remove” some data from the actual mean. This habitat, which was especially popular during spring and summer could have a similar function as the river channel. Both habitats are next to each other, indicating that they share some similarities. The river channel is a deeper area, whereas the exposed habitat is shallower and is heavily affected by the tidal waters. The high activity level suggests that this habitat could also be used as a foraging area. The tidal water could be a factor that decides if the sea trout is the dominant predator in the area or becomes a potential prey for larger marine fish and mammals. At low tide, some parts of the habitat are exposed to air, making the use of this habitat limited at different times of the day. Since this habitat is calmer, compared to the river channel, catching prey could demand less acceleration, thus, explaining why this habitat has a lower mean activity level than the river channel. Both exposed intertidal mudflats and river channel were habitats that were important for the sea trout and could be a better alternative than marine waters for some individuals. This habitat had the warmest experienced mean temperature in general, which helps explain the high activity level, though this habitat had a lower abundance and was less used compared to the river channel. There were most likely good feeding opportunities in these habitats, and they also save energy by being less exposed to marine predators and the reduced need for physiological adjustment to higher salinity levels compared to the fjord and sea (Thorstad et al., 2016).

The sheltered intertidal mudflats showed the lowest activity level among the fish that utilized this habitat and had the least influence on the activity level out of the three habitats. The habitat is placed further upstream, compared to the other two, where the impact from the marine water through tidal water and waves are lower, as a result of a stone threshold in the estuary. Lower ingoing currents from the marine water and outgoing currents from the river in this habitat suggest that the fish could save energy in this habitat when it stands still. Less impact from the marine water probably makes the sheltered intertidal mudflats less favorable for marine predators, but also for marine prey, because of lower salinity levels. Thus, suggests that this habitat had the lowest activity level as a cause of a potentially lower abundance of marine predators and prey, hence, reducing the activity level. The sheltered intertidal mudflats was the habitat with the highest residence time (Figure A1, appendix), indicating that this was an important area for the “estuary resident” sea trout. It was especially used during winter, after the spawning season that takes place in late autumn, and hence suggests that the sheltered area was an important habitat for overwintering. In winter, there is a solid and stable layer of ice that covers the habitat, which could prevent both sea mammals and birds from hunting in this area. These factors make this habitat safer and an area where the fish can conserve energy. Lower currents and less exposure to predators could be one of the main reasons it was used for overwintering. In general, this habitat had the coldest experienced temperature by the sea trout, where temperature is linked to activity level, which also could explain the low activity level within this habitat.

The seasons (spring, summer, autumn, winter) had a big impact on the activity level of the sea trout. Both summer and spring had a higher impact on the activity level compared to winter and autumn. In a previous study on sea trout in northern Norway, it was found that consumption rate was highest in spring and summer, and lowest in autumn and winter, because of the seasonal variation in somatic conditions (Rikardsen et al., 2006). Warmer water temperatures will affect the metabolism of the fish, thus increasing the food intake, digestion, and swimming ability (Watz & Piccolo, 2011), giving the fish more energy in the warmer seasons. A previous study showed that at colder water temperatures, the probability of catching prey will reduce below 8°C (Watz & Piccolo, 2011). That study supports the results from the present thesis, where the activity level is highest in seasons with the highest experienced temperature. The lower activity level showed during autumn and winter could be that the catching probability is reduced, and so is the swimming ability and digestion. Also, the reduced swimming ability and energetic demand could be factors that make the fish forage less actively at colder temperatures to reduce the predator risk (Metcalfe et al., 1998; Watz & Piccolo, 2011). Thus, both predation risk and foraging were increased during the summer, making both catching prey and avoiding predators as potential indicators of why the activity level was highest at this season.

The influence of individual characteristics on the activity level

Sex dependent activity level

The difference in mean activity level between males and females were significant, with males having a higher mean compared to females. Female sea trout tend to have a higher need for food, because of the correlation between body length and fecundity (Elliott, 1995). Eldøy et al. (2021) found that female sea trout were more likely to migrate to the sea, although other studies have reported an equal sex ratio for sea trout migrants (Elliott, 1993). Only slightly more males (54%), than females (46%) were registered in the inner fjord, outside the estuary. This supports the previous reports of equal sex ratio, although 26 tagged sea trout will not necessarily be enough to answer if it is a coincidence or not. In general, males tend to mature earlier than females, whereas females are often larger than males (Jonsson, 1989). They grow at the same rate under the same conditions, though, males exploit less risky habitats, but there is little difference in diet by sex for fish living in the same habitat (Jonsson, 1989). In the present thesis, there was a higher abundance of males in the estuary during the summer season, when the activity level was highest. This suggests that female sea trout spend a longer time out in the fjord compared to male sea trout, where the males likely had briefer movements between the estuary and the fjord. This indicates that the estuary was more used by the males during the summer, and it could be speculated that intraspecific interactions between males could cause a higher activity level for this sex. The consumption rate is highest during the summer, and hunting could be a decisive factor for the intraspecific interaction, where males could be more aggressive towards each other due to competition.

Relationship between body length and activity level

Total body length was not correlated to the level of activity. Courses for a size related activity level could be that presence of a larger sized and more dominant trout affects activity level of smaller sea trout (Holliday et al., 1974), causing them to accelerate to avoid or escape the more dominant trout. Marine predators will also have the same effect, especially on the smaller sea trout.

Feeding behavior may also have an impact on sea trout activity levels. Due to high abundance of different invertebrates within the three estuarine habitats (Kjærstad, 2022), it might be expected that the sea trout prey intensively on these when residing in the estuary. However, it is also likely that different prey species of fish are either visitors in the estuary due to tidal waters or reside as residents. This could suggest that the diet of the sea trout in the estuary of river Stjørdalselva could be a combination of different invertebrates and smaller fish species. All of the sea trout tracked in this study had a body length larger than 29 cm, indicating that fish could be an important prey (Rikardsen et al., 2007). Though, other studies have recorded sea trout with a body length of ≥ 40 cm primarily preying on fish (Haluch & Skora, 1997). Davidsen et al. (2017) found in a study on sea trout feeding ecology that all size groups included in the study (213- 730 mm) were feeding on marine fish, though, larger sea trout had an increased dependence upon marine fish as prey. This could suggest that sea trout with a larger body length, were more frequently preying on fish, which could demand a higher acceleration to capture, thus, resulting in a higher activity level. As discussed above, smaller sea trout may have to increase activity level to avoid dominant sea trout and/or predators while larger sea trout may have a high activity level due to increased predation on fish. The combination of this may explain why body length was not correlated to activity level. As the body length for the tagged sea trout ranged from 290 mm to 615 mm, the variation in body length was so large that potential correlations between body length and activity levels should have been detected, if they existed.

Influence of habitat and season on the swimming depth

Season and habitat had an impact on the depth use of the sea trout. Spring and summer were the seasons when the sea trout had a deeper depth use in general within the estuary. The river channel was the habitat with the deepest mean swimming depth, followed by sheltered intertidal mudflats, then exposed intertidal mudflats.

There was a significant difference in depth use between most seasons within the three estuarine habitats when it came to the mean daily depth use of the fish. Spring was the season that had the overall deepest depth use within the three estuarine habitats, with summer being the season that was clearly the deepest in the river channel. In general, within the estuary, the sea trout stayed closer to the surface in winter and autumn. Previous studies found that trout move to the deeper layers when the surface temperatures reached 17 °C (Kristensen et al., 2018), possibly because that growth optimum for sea trout is at approximately 16 °C for the trout (Elliott & Elliott, 2010; Elliott, 1994), where the preferred water temperature is between 12-16 °C (Larsson, 2005). This could explain why the sea trout in the river channel stayed more frequently in the deeper layers during summer. Watz and Piccolo (2011) found that the sea trout tended to rest on the substrate when the temperatures were below 8 °C, which could be an explanation as to why the sea trout frequently used the deeper layers in spring in the present thesis. Spring is one of the seasons with the lowest experienced temperatures, with March being one of the months with the coldest temperatures, due to the ice melting in the river of Stjørdal making the surface water temperatures colder in the estuary during spring. The depth use could also be affected by feeding, where the fish swam to the marine layer close to the bottom to feed on marine prey. That could explain why the sea tout were more frequently close to the bottom during summer in the river channel since this habitat has a thicker marine layer, and the consumption rate is highest at this time of the year. The feeding behavior could also explain why spring and summer in general had the deepest swimming depth. The osmoregulation is poor in cold water (Larsen et al., 2008), suggesting that the sea trout avoids environments that have a combination of low temperature and high salinities. This supports the findings in the present thesis, where the fish stayed closer to the surface during the colder months (winter), and avoided the marine layer, since osmoregulation is energy demanding, and the fish has lower energy at colder temperatures. This could suggest that sea trout choose colder brackish water than warmer marine water during seasons with cold water temperatures. The water temperature had a steady decline during autumn, where colder water temperature could be an explanation as of why the sea trout stayed closer to the surface. However, autumn is the start of the spawning season, where the consumption rate is low and energy is needed for a high fecundity, which could explain why the sea trout avoided the deeper marine layer.

There was a significant difference in depth use between the river channel and the other two habitats. The river channel was the deepest habitat (5-6 m), while exposed- and sheltered intertidal mudflats were shallow (2-3), depending on the tidal water and time of year. Although there was a difference in depth between the three estuarine habitats, does not necessarily mean that the swimming depth would be different. Eldøy et al. (2017) found that sea trout had different swimming depths within different habitats, although that study had the whole estuary defined as one of the habitats. The different abiotic characteristics between the three habitats mentioned earlier could be a factor that affects the swimming depth, where it is linked to the marine layer and the prey availability this layer potentially provides for the sea trout.

In conclusion, the present thesis shows for the first time that sea trout activity and depth use differ within season and within different habitats inside the same estuary. Further, the findings support previous studies showing that estuaries are important habitats for the sea trout. The estuary of river Stjørdalselva were used by the sea trout during all seasons of the year and contains several habitats with different unique characteristics, indicating that the estuary as a whole can provide the necessary needs for the sea trout. The sheltered intertidal mudflats was more frequently used during winter, suggesting that this habitat is an important over-wintering area where the sea trout could conserve energy. The other two habitats, exposed intertidal mudflats and river channel, were more frequently used during spring and summer, and had the highest mean activity level this time of the year, suggesting that these habitats were important foraging areas for the sea trout. The swimming depth varied with season and habitats, where summer and spring had a deeper depth use in general within the overall estuary. Further, depth use was deeper in the river channel compared to the exposed- and sheltered intertidal mudflats. These results could indicate that abiotic factors such as salinity and temperature affect where in the water column the sea trout swims. This also could suggest that feeding behavior affects the swimming depth within the estuary. Both findings related to activity level and swimming depth indicates how the estuary were used in time and space by the sea trout. The construction of the new highway (E-6) next to the estuary of river Stjørdalselva, which plans to fill up part of the exposed intertidal mudflats, will result in a loss of potential feeding areas, which could lead to a higher competition of the available food sources that are left in the remaining part of the estuary. The present study provides new, and supports existing, knowledge on the habitat use of the sea trout in the estuary of river Stjørdalselva, that could be important for the management of the sea trout population and decision makers that are involved in the road development here or future projects elsewhere. The findings will be crucial when plans are made for mitigated or compensatory measures for the sea trout. Although this study has investigated a specific estuary, and different sea trout populations in other estuaries may have different behaviors, this study could provide important knowledge on the ecology of the sea trout, that could be helpful in future development projects affecting estuarine habitats and the sea trout that lives there.

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6. APPENDIX

The residence time for the sea trout within the study area

The residence time (percentage) within the different zones differed for the sea trout during different seasons (Figure A1). The fjord was mostly used during the summer, whereas the upstream river was used late summer/ autumn and winter linked to the spawning season. The three estuarine habitats were used throughout the year, where the sheltered intertidal mudflats showed the highest residence time at winter (2021/2022).

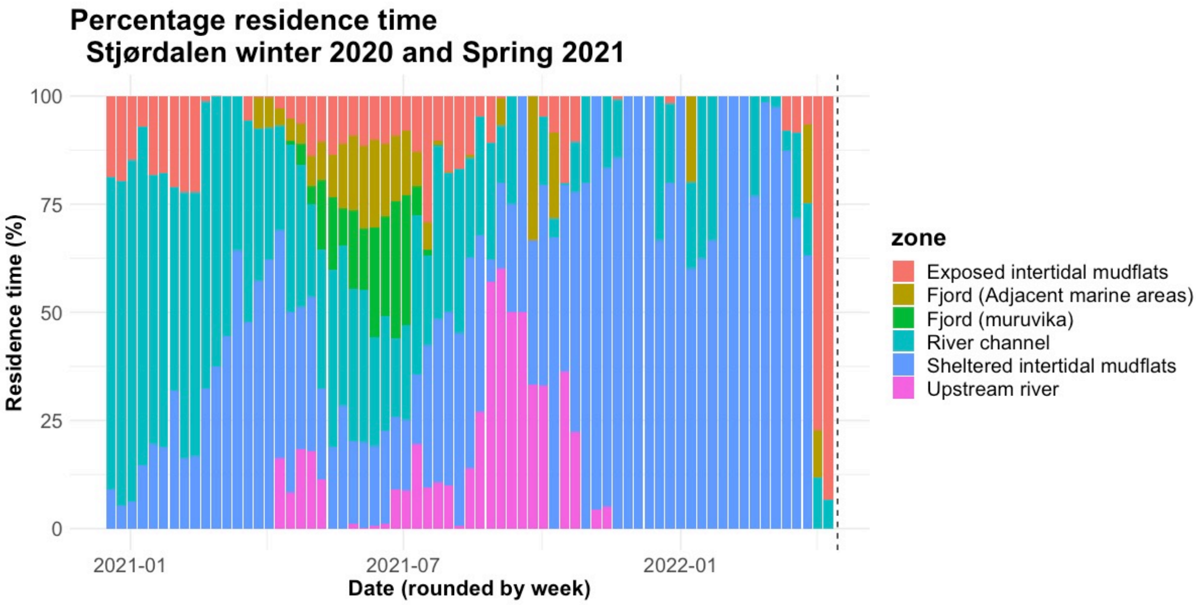

Figure A1: *Percent residence time for the tagged sea trout in; the exposed intertidal mudflats (red), the river channel (turquoise), sheltered intertidal mudflats (blue), fjord (adjacent marine area (beige)), fjord (muruvika (green), upstream river (pink), during the study period.*

The overall detections of each individual sea trout within the study area

Figure A2: *The overall period for detection of individual tagged sea trout in the study area. The different colors represent the different zones.*

The mean temperature, activity level and swimming depth for each month

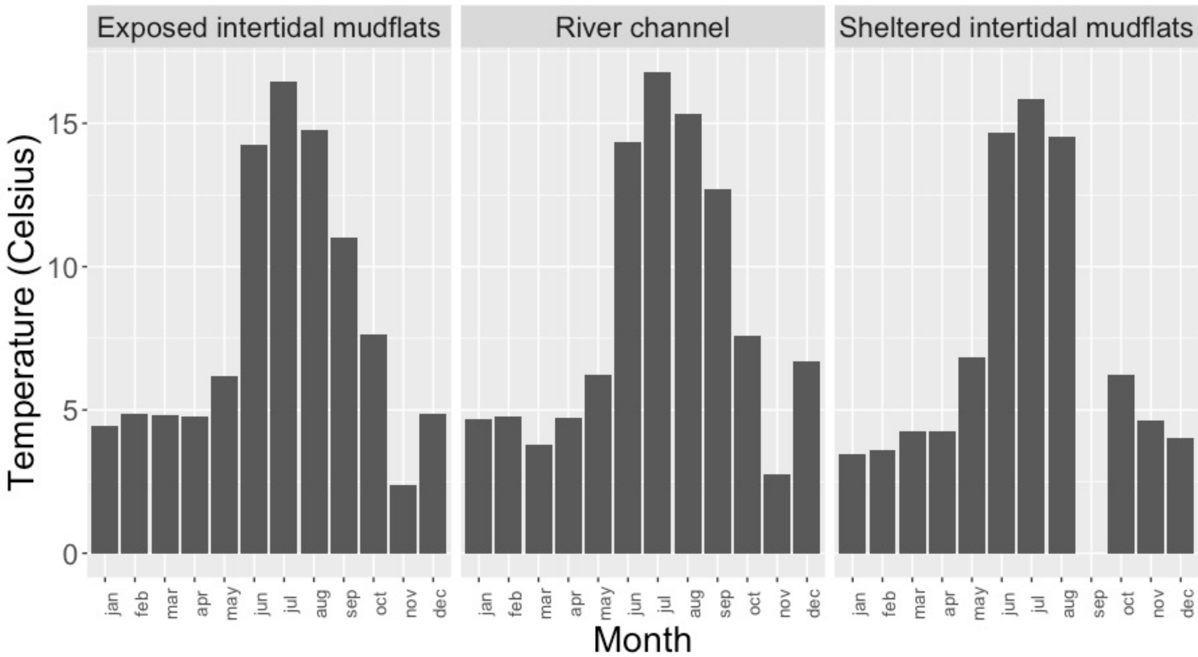

Figure A3: *The mean experienced temperature within the three estuarine habitats for each month (January- December).*

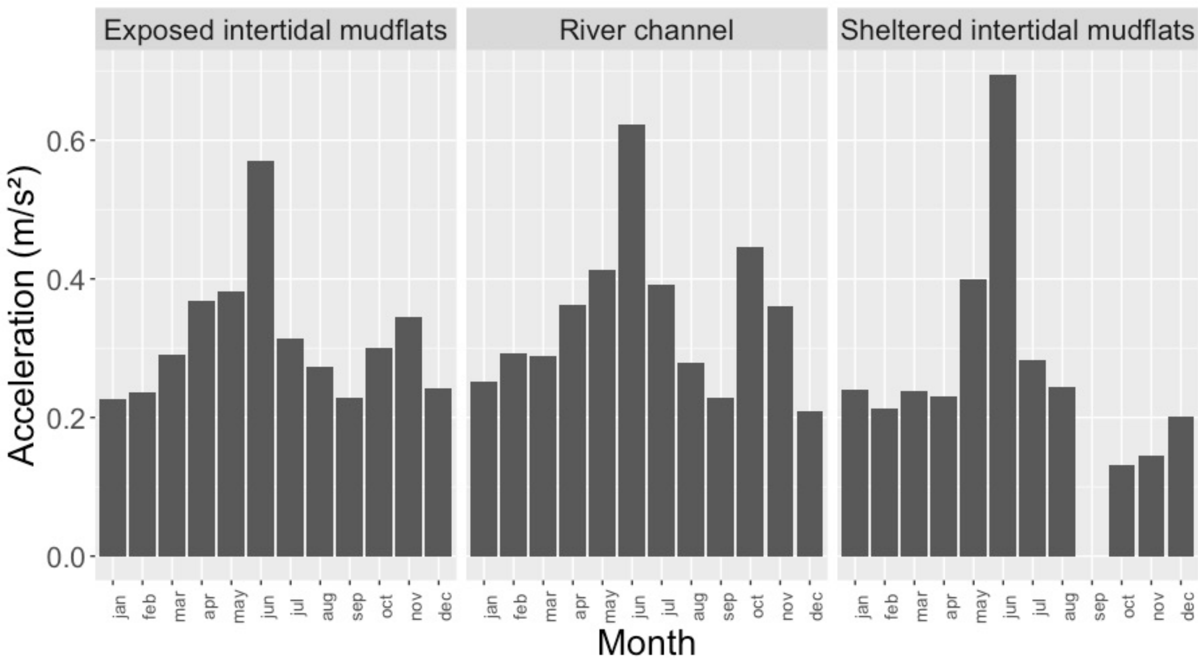

Figure A4: *The mean activity level within the three estuarine habitats for each month (January- December).*

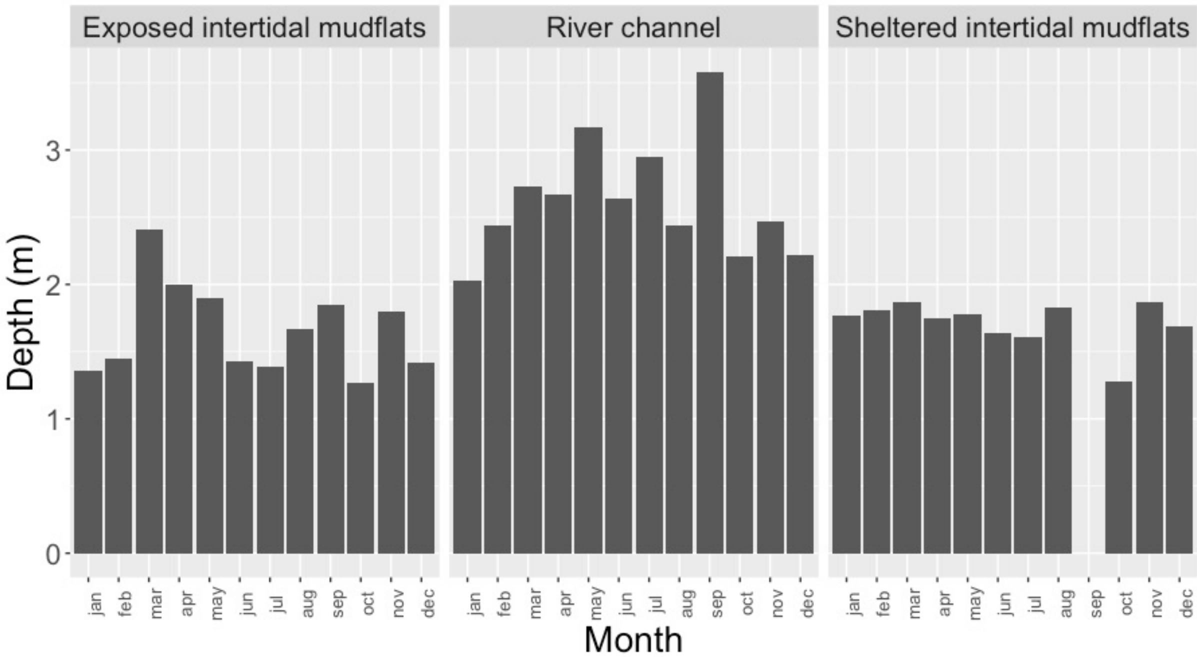

Figure A5: *The mean depth use within the three estuarine habitats for each month (January- December).*

General linear model- Activity level

Table A: *Conditional model averaging summary statistics for mixed effect models with Δ AICc<2 for the effect of season (S), Habitat (H), total body length (L) and sex (s) on individual mean activity level. Significant values (P ≤ 0.05) are highlighted by the asterisk mark (*).*

	Estimate	Std.error	Z-value	p
(Intercept)	0.3370	0.0823	4.092	4.28e-05 ***
Season (spring)	0.0383	0.0305	1.253	0.2103
Season (summer)	0.0723	0.0326	2.220	0.0264 *
Season (winter)	-0.0158	0.0340	0.467	0.6405
Total body length	-0.0003	0.0002	1.604	0.1086
Habitat (River channel)	0.0365	0.0209	1.744	0.0812
Habitat (Sheltered)	-0.0812	0.0223	3.634	0.0003 ***
Sex (male)	0.0354	0.0288	1.230	0.2186

General linear model- Depth use

Table B: *Conditional model averaging summary statistics for mixed effect models with Δ AICc<2 for the effect of season (S), total body length (L), habitat (H), and sex (s) on individual mean activity level. Significant values (P ≤ 0.05) are highlighted by the asterisk mark (*).*

	Estimate	Std.error	Z-value	p
(Intercept)	1.5796	0.3158	5.002	6e-07 ***
Season (spring)	0.4034	0.1712	2.356	0.0185 *
Season (summer)	0.2311	0.1846	1.251	0.2108
Season (winter)	0.0186	0.1889	0.099	0.9214
Total body length	-0.0009	0.0071	1.379	0.1679
River channel	1.1078	0.1212	9.144	<2e-16 ***
Sheltered	0.0844	0.1272	0.662	0.5077
Sex (male)	0.1583	0.1182	1.339	0.1805

The effect of total body length on the activity level

Table C: *The P-value from a one-way ANOVA test with acceleration as output and total body length as variable within different seasons and habitats. Number of fish (n) represented in each habitat at different seasons. Significant values (P ≤ 0.05) are highlighted by the asterisk mark (*).*

Season	**Habitat**	**n**	**P-value**
Winter	Exposed	5	0.35
Winter	River channel	10	0.92
Winter	Sheltered	10	0.43
Spring	Exposed	14	0.44
Spring	River channel	23	0.92
Spring	Sheltered	20	0.05*
Summer	Exposed	11	0.57
Summer	River channel	13	0.32
Summer	Sheltered	7	0.92
Autumn	Exposed	4	0.19
Autumn	River channel	4	0.25
Autumn	Sheltered	5	0.17

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