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May 2021

Master's thesis

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2021

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ACKNOWLEDGEMENTS

ABSTRACT

Despite being different species with different life histories, anadromous Atlantic salmon (*Salmo salar L.*) and brown trout (*Salmo trutta L.*) are often subjected to the same conservation strategies. Implementation of species-specific management will require extensive knowledge about the marine migration of the two species, and how they differ from each other. In order to investigate early marine migration pathways and progression rates through a fjord system, 38 Atlantic salmon post-spawners and 34 brown trout veterans migrating to sea in spring were tagged with acoustic transmitters in a northern Norwegian river. The tagged fish were registered by listening stations, strategically placed in lines throughout the study area. Correlations between individual biological characteristics (body length, condition factor and estuary exit date) and progression rate were investigated in the inner- and outer fjord systems.

The fjord system had two exits towards the open ocean, where one exit was far more popular than the other for both species. Despite choosing mainly the same migration route, there was a large variation in the temporal habitat use between the two species. From the estuary exit, the Atlantic salmon had a fast, continuous progression, spending on average 37 hours in reaching the fjord system exit. The brown trout on the other hand, had larger intraspecific differences in progression rate, where some individuals migrated through the fjord in just a couple of days, some spent several weeks, and some never reached the fjord system exits at all (29%). The brown trout leaving the fjord system spent on average 546 hours from the estuary to the fjord system exit. Both species were mainly found to start their marine migration from the estuary at falling tide. For Atlantic salmon, no correlation was detected between body length and progression rate in in any of the fjord sections. Estuary exit date and condition factor was found to be correlated with progression rate of Atlantic salmon in the outer fjord system, where a later estuary exit date and a lower condition factor indicated a higher progression rate. For brown trout, body length was positively correlated with progression rate in the outer fjord system, condition factor positively correlated with progression rate in the inner fjord system, and estuary exit date was positively correlated with progression rate for the total distance.

This study found that the early marine migration of Atlantic salmon post-spawners and brown trout veteran migrants from the river Beiarelva overlapped in space, but not to a large degree in time. The higher time usage of brown trout within the fjord system likely resulted in a higher exposure to negative anthropogenic impacts in coastal areas compared to Atlantic salmon. The differences in how individual biological characteristics were correlated with progression rate, illustrates how population dynamics in Atlantic salmon and brown trout could change in similar ways, while still influence temporal habitat use differently. The findings in this study underline the importance of conceiving more focused conservation strategies, better aimed at protecting each individual species and not treating them as a single unit.

SAMMENDRAG

Til tross for å være forskjellige arter med forskjellige livshistorier, er anadrom Atlanterhavslaks (*Salmo salar L.*) og brunørret (*Salmo trutta L.*) som regel underlagt den samme forvaltningsstrategien. Implementering av artsspesifikk forvaltning krever omfattende kunnskap om den marine migrasjonen til de to artene, og om hvordan de skiller seg fra hverandre. For å undersøke marin migrasjonsadferd og progresjonsrate ble 38 utmigrerende laksestøinger og 34 utmigrerende ørretveteraner merket med akustiske merker i en nordnorsk elv. Den merkede fisken ble registrert på lyttestasjoner, strategisk plassert i linjer ut over studieområdet. Korrelasjoner mellom individuelle biologiske karakteristikker (kroppslengde, kondisjonsfaktor og utgangsdato fra estuariet) og progresjonsrate ble undersøkt i det indre- og det ytre fjordsystemet.

Fjordsystemet hadde to ruter ut mot åpent hav, der den ene ruten var langt mer populær enn den andre hos begge arter. Til tross for å velge samme migrasjonsrute, var det stor variasjon i hvor lang tid hver art brukte i ulike deler av fjordsystemet. Fra estuariet hadde Atlanterhavslaksen en rask, kontinuerlig progresjon, og brukte gjennomsnittlig 37 timer på å nå utgangen av fjordsystemet. Brunørreten derimot, hadde langt større intraspesifikke forskjeller i progresjonsrate, der noen individer migrerte gjennom fjordsystemet på et par dager, noen brukte flere uker, mens andre forlot aldri fjordsystemet i det hele tatt (29 %). De individene som forlot fjordsystemet, brukte i gjennomsnitt 546 timer fra estuariet til utgangen. Ingen korrelasjon ble funnet mellom kroppslengde og progresjonsrate hos Atlanterhavslaks i hverken indre- eller ytre fjord. Utgangsdato fra estuariet og kondisjonsfaktor derimot, var korrelert med progresjonsrate hos Atlanterhavslaks i det ytre fjordsystemet, hvor en senere utgangsdato fra estuariet og en lavere kondisjonsfaktor betydde en høyere progresjonsrate. For brunørret var kroppslengde positivt korrelert med progresjonsrate i det ytre fjordsystemet, kondisjonsfaktor var positivt korrelert med progresjonsrate i det indre fjordsystemet, og utgangsdato fra estuariet var positivt korrelert med progresjonsrate for fjordsystemets totale distanse.

Denne studien fant en stor overlapp i arealbruk hos laksestøinger og ørretveteraner fra Beiarelva i tidlig marin migrasjonsfase, men at tiden de brukte inne i fjordsystemet var svært forskjellig. Den høyere tidsbruken hos brunørret inne i fjordsystemet vil sannsynligvis gi en høyere eksponering for negative menneskeskapte påvirkninger i kystnære strøk. Forskjellene i hvordan individuelle biologiske karakteristikker var korrelert med progresjonsrate, illustrerer hvordan populasjonsdynamikk hos Atlanterhavslaks og brunørret kan gjennomgå liknende endringer, mens den temporale habitatbruken samtidig endrer seg i svært forskjellig retning. Funnene i denne studien understreker viktigheten av å vedta fokuserte forvaltningsstrategier myntet på hver enkelt art, og å ikke behandle dem som én enhet.

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INTRODUCTION

Wild Atlantic salmon (*Salmo salar L.*) and brown trout (*Salmo trutta L.*) have a profound social, cultural and economic importance in numerous communities along the entire Northern-European coastline (Pennell & Prouzet, 2009; Liu *et al.*, 2019). Some of the fascination with the salmonid species springs from their ability to migrate from freshwater to saltwater (anadromy), making them accessible to both people living inland and along the coast. Atlantic salmon and brown trout spawn in freshwater, and anadromous populations around the North Atlantic basin regularly coexist in the same rivers and streams (Klemetsen *et al.*, 2003). Anadromy in salmonids developed in response to better feeding opportunities in saltwater compared to in their native freshwater habitats (Gross *et al.*, 1988). Anadromy is advantageous for a fish when the benefits of higher food availability exceed the increased energy use and/or risk of mortality (Klemetsen *et al.*, 2003). River migration in Atlantic salmon and brown trout has been extensively studied. What governs the behaviour when the fish arrive in saltwater, however, remains largely unknown. More knowledge about marine migration pathways, and what underlying mechanisms that are driving migratory behaviour, is therefore needed (Drenner *et al.*, 2012; Birnie-Gauvin *et al.*, 2019).

Although closely related phylogenetically, Atlantic salmon and brown trout are different species with different life histories. Compared to Atlantic salmon, brown trout is more flexible with regards to migration strategies and has a weaker tendency towards anadromy. The decision of whether to migrate or remain stationary is partly governed by genetics and partly by the individual's phenotypic plasticity (Jonsson & Jonsson, 1993; Ferguson *et al.*, 2019). Brown trout have an extraordinary ability to adapt to different environments, allowing them to inhabit a far greater range of habitats than Atlantic salmon (Baglinière, 1999; Klemetsen *et al.*, 2003). Most anadromous Atlantic salmon migrate to the open ocean, while the brown trout mostly stay in coastal areas during the full course of their marine migration (Klemetsen *et al.*, 2003). Atlantic salmon is highly adapted to a life at sea. A high growth rate, well-developed osmoregulatory ability, and a morphology adapted to swimming large distances, helps salmon to take advantage of prey species in open ocean areas (Klemetsen *et al.*, 2003; Aas *et al.*, 2010).

Atlantic salmon post-spawners and brown trout veteran migrants (i.e., brown trout which have previously completed one or more sea-migrations) are far less studied than their smolt and post-smolt conspecifics, despite the importance of these individuals in maintaining a healthy population through high reproductive contribution and genetic variation. A larger body size, especially in females, gives a higher reproductive yield by enabling production of larger, more numerous gametes (Ducharme, 1969; Jensen *et al.*, 2012). Better growth conditions at sea makes it more beneficial for females to migrate, due to production of eggs having a higher investment cost compared to production of sperm (Thorstad *et al.*, 2016; Jensen *et al.*, 2019). The proportion of anadromous individuals is not only dependent on sex, but might also depend on growth rate. Fish with higher growth rates will generally have a higher probability of migrating to sea and migrate at a younger age and smaller body size, compared to slow growing individuals (Økland *et al.*, 1993; Forseth *et al.*, 1999; Theriault & Dodson, 2003; Hendry *et al.*, 2004).

The early marine migration is a critical phase with a high mortality in the life of an Atlantic salmon post-smolt (Thorstad *et al.*, 2012). For a post-spawner however, this phase has been shown to have low mortality rates, and is not considered critical, despite the poor nutritional condition of salmon migrating in spring (Hubley *et al.*, 2008; Hedger *et al.*, 2009; Halttunen, 2011). The difference in mortality between post-smolts and post-spawners indicates an importance of body size in the early phase of Atlantic salmon marine migration.

Some brown trout migrants have been shown to regularly take advantage of outer fjord areas. The individuals reaching and utilizing these areas tend to have a longer body and a lower condition factor compared to those staying closer to the river mouth (Eldøy *et al.*, 2015; Bordeleau *et al.*, 2018; Eldøy *et al.*, 2021). Pelagic fish with high energy-content are often found in the outer parts of fjord systems and have been shown to be a considerable part of the diet of large anadromous brown trout (Rikardsen & Amundsen, 2005; Rikardsen *et al.*, 2006).

In areas with large differences in sea level with changing tide, strong tidal currents can arise. Atlantic salmon smolts have been shown to use tidal transport to assist seaward migration (Lacroix & McCurdy, 1996; Moore *et al.*, 1998; Bendall *et al.*, 2005). Moreover, the timing of movement from the river mouth of both Atlantic salmon post-spawners and brown trout veteran migrants have been observed to be influenced by the tidal cycle (Bendall *et al.*, 2005; Hubley *et al.*, 2008; Hedger *et al.*, 2009; Aarestrup *et al.*, 2015).

A previous study concluded that differences in age, body size and timing of smolt migration between Atlantic salmon and brown trout have been shaped by different habitat preferences in the sea (Jensen *et al.*, 2012). This suggests that these individual biological characteristics play a crucial role in how the fish survive and thrive in their respective marine habitats. Much work remains, however, in understanding what drives migration in the adult life stage, and the individual differences leading to success or failure (Horodysky *et al.*, 2015; Birnie-Gauvin *et al.*, 2019). Lennox *et al.* (2019) suggested the following question as one of the 100 most pressing regarding the future of global fish migration science, conservation, and policy: "*What are the main physical, behavioral, and ecological drivers of swimming performance*". By investigating the effect of biological characteristics on progression rates we can help answer this question and hence contribute towards bridging the knowledge gap existing between behavior and the individual physiology of each fish.

Variability among Atlantic salmon and brown trout when it comes to marine migration behavior should be reflected through the protective measures in place. Despite their different life histories, Atlantic salmon and brown trout are often treated as a single unit and subjected to the same legislation and conservation strategies (Lakse- og innlandsfiskloven, 1992). Implementation of species-specific management limited by season and geographic boundaries will require extensive knowledge about the two species, and how they differ from each other. A comparison of swimming route and progression rate of reproductively important individuals of Atlantic salmon and brown trout from the same river, during the same year, has to my knowledge not been done before.

In this thesis, I investigated the early marine migration behaviour of Atlantic salmon post-spawners and brown trout veteran migrants migrating from the same river in spring, and to what extent the behaviour was correlated with individual biological characteristics. Using acoustic telemetry, spatial and temporal data was collected throughout 2019 in a fjord system in Northern Norway. The main aim of the thesis was to investigate and compare the swimming routes and progression rates of the two species in the inner and outer parts of the fjord system. Body length, condition factor and the estuary exit date were used to explain possible intraspecific and interspecific differences in progression rate, as well as differences in how far each brown trout migrated from the river. In addition, the potential influence of tidal cycles on the timing of marine migration from the estuary was investigated.

Study area

The study was conducted from April to December 2019 in the fjord Beiarfjorden (figure 1, receiver line T2-T4), and the connecting fjord system consisting of the fjord arm Nordfjorden (receiver line T4-T9), the fjord arm Holmsundsfjorden (receiver line T4-T6), and the fjord arm Morsdalsfjorden (receiver line T6-T7). The study area covers 57 km of waterway from the mouth of the river Beiarelva to the two fjord system exits, in addition to 7 km of the lower river stretch.

Beiarelva

Beiarelva has a high influx of glacial water, resulting in low water temperature throughout the year. This creates a large temperature difference relative to the sea in summer. The annual discharge of the river is $1.5 \ 10^9$ m^3/yr (Skarbøvik *et al.*, 2017). Due to storage of water in reservoirs for hydropower production, the water temperature is frequently higher than natural levels in the period June-November. In 1994, the river was treated with rotenone due to an infestation of the ectoparasite *Gyrodactulus salaris*, which had caused high mortality in the Atlantic salmon population. Officially recovered after rotenone treatment in 2001, the river now supports populations of anadromous Atlantic salmon and brown trout. The anadromous population of Arctic charr (*Salvelinus alpinus L.*) never managed to fully recolonize the river after the rotenone treatment, and is today considered close to extinction (Davidsen *et al.*, 2019). The most prominent harmful factors on the populations of anadromous Atlantic salmon and brown trout spawning in Beiarelva, are most likely hydropower regulation and the ectoparasite *Lepeophtheirus salmonis K.* (salmon lice) (Vitenskapelig råd for lakseforvaltning, 2018; 2019).

Beiarfjorden

Beiarfjorden makes up an 18 km stretch from the mouth of Beiarelva (figure 1, line T2) to Kjellingstraumen bridge (line T4). Beiarfjorden has since 2007 been a national salmon fjord. The national salmon fjord program is a series of protective measures put in place to limit interventions and activities that may harm important populations of Atlantic salmon in Norway (Anon, 2006-2007). As a result of these measures, no fish farming facilities are situated within Beiarfjorden. Beiarfjorden is a deep, narrow fjord surrounded by steep cliffs on both sides. The steep cliffs allow fall-winds to pick up high speeds before reaching the water surface. The upper water-layer is therefore highly influenced by unpredictable wind-patterns. The maximum depth of the fjord is 165 m, and most of its area is deeper than 100 m. The only two large shallow areas in the fjord are in the estuary and at the fjord exit close to Kjellingstraumen bridge. The narrow structure of Beiarfjorden causes tidal cycles to have a large influence on currents. With large seasonal differences in influx of freshwater the salinity varies greatly throughout the year. Large parts of Beiarfjorden remain ice-covered throughout the winter, often resulting in large ice movements towards the fjord exit during the spring thaw.

Nordfjorden and the northern exit of the fjord system

Nordfjorden is the approximately 13 km stretch from Kjellingstraumen bridge (figure 1, line T4) and to the northernmost line of receivers at the north exit of the fjord system (line T9). It is the deepest part of the fjord system, with a maximum depth of 398 m and most of the area deeper than 200 m. It is also on average the widest part of the fjord system with a width range of 1.1-2.6 km. The steep cliffs on the eastern side of Sandhornøya cause fall-winds to have high speeds also in Nordfjorden. Two fish farming facilities are located in Nordfjorden, where only one operated during the 2019 season.

Holmsundsfjorden, Morsdalsfjorden and the south-western exit of the fjord system

Holmsundsfjorden is the approximately 11 km stretch from the Kjellingstraumen bridge (figure 1, line T4) and to the southernmost line of receivers at Sandvikneset (line T6). The northern part of Holmsundsfjorden is narrow and shallow, with little water movement, which causes this part of the fjord system to be ice-covered during the winter months. The maximum depth in Holmsundsfjorden is 50 m, with most of its area shallower than 30 m, making it the shallowest part of the fjord system. Like Beiarfjorden, Holmsundsfjorden is part of the area protected by the national salmon fjord program, and therefore has no fish-farming facilities.

Morsdalsfjorden is the approximately 14 km stretch from the Sandvikneset (figure 1, line T6) and to the line of receivers at the south-western exit of the fjord system (line T7). With a maximum depth of 148 m, Morsdalsfjorden is considerably deeper than the connected Holmsundsfjorden. It is also outside the national salmon fjord area and has two fish farming facilities and a ferry-line from Sund to Sandhornøya. The ferry-line and vessels used in surrounding aquaculture facilities results in the fjord-arm having more ship-traffic compared to other parts of the study site. Morsdalsfjorden contains the south-western exit of the fjord system, which is an exposed area subject to weather systems coming in from the Norwegian sea.
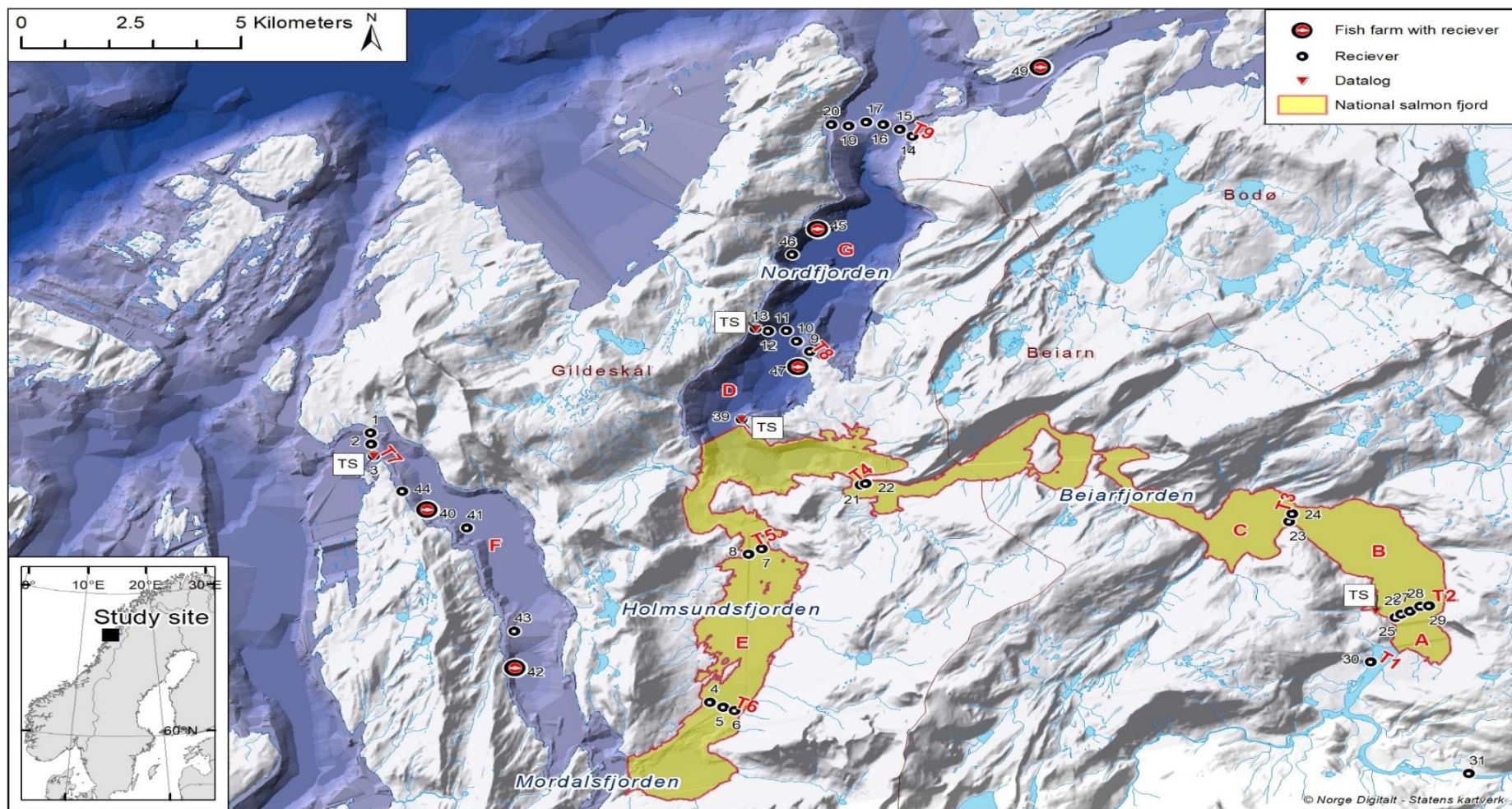
Figure 1. Map over the study site in Nordland, Norway. Black dots represent the position of acoustic receivers. Red dots show the location of fish farms. The receivers labelled "TS" are equipped with a data storage tag recording temperature and salinity. Receiver are labelled with "T" and a number. Sections between receiver lines are labelled with a letter from A to G. The area marked as yellow is protected under the National salmon fjord regulations. Beiarfjorden includes the area between line T2 and T4 (sections B and C). Nordfjorden includes the area between line T4 and T9 (sections D and G). Holmsundsfjorden is the area between line T4 and T6 (sections D and E). Morsdalsfjorden is the area between line T6 and T7 (section F). Red triangles show data storage tags (datalog) recording water temperature and salinity.

Environmental variables

Salinity and water temperature at three different locations during 2019

Water temperature and salinity were monitored at three different locations in the fjord system by data loggers (DST Milli-CT, Star-Oddi Ltd., Reykjavík, Iceland) in the period between 15.04.2019 and 31.12.2019. The three locations were: at line T2 in the inner part of Beiarfjorden (Tverrvika), at receiver 39 close to the exit of Beiarfjorden (Handelsstedet), and at line T7 at the south-western exit of the fjord system (Sund). The data logger (DST) at Sund was attached to the mooring system of a receiver, close to the sea surface (1 m depth). Data loggers in Tverrvika and at Handelsstedet were attached to piers, and the measuring depth therefore varied during the tidal cycle (1-4 m depth). The DST-data were downloaded using the SeaStar software version 8.55 provided by Star-Oddi systems (Reykjavík, Iceland).

There was a difference in mean salinity between Tverrvika (mean = 23‰, SD = 5‰), Handelsstedet (mean = 12‰, SD = 10‰) and Sund (mean = 24‰, SD = 6‰) throughout the 2019 season (ANOVA, $p < 0.001$). Due to a measurement error at Handelsstedet, the salinity measurements between 17.05.2019 and 01.10.2019 were not included. Sund and Tverrvika had similar average salinity but had different patterns throughout the year of 2019 (figure 2). The average salinity in Tverrvika was lower compared to Sund, with larger variations. There was also a difference in water temperature between the three locations throughout 2019 (ANOVA, $p < 0.001$). The water temperature in Tverrvika had the largest variations from May (mean = 6.5 °C) to June (mean = 8.5 °C), and the lowest mean temperature throughout the year (mean = 9 °C, SD = 2 °C). At Handelsstedet, the mean water temperature in 2019 (mean = 9 °C, SD = 2 °C) was similar to that in Tverrvika, but higher in the period from August to November. In both Tverrvika and at Handelsstedet, the water temperature never exceeded 12.5 °C. The mean water temperature at Sund (mean = 10 °C, SD = 3 °C) was higher compared to the other two locations throughout the whole year.
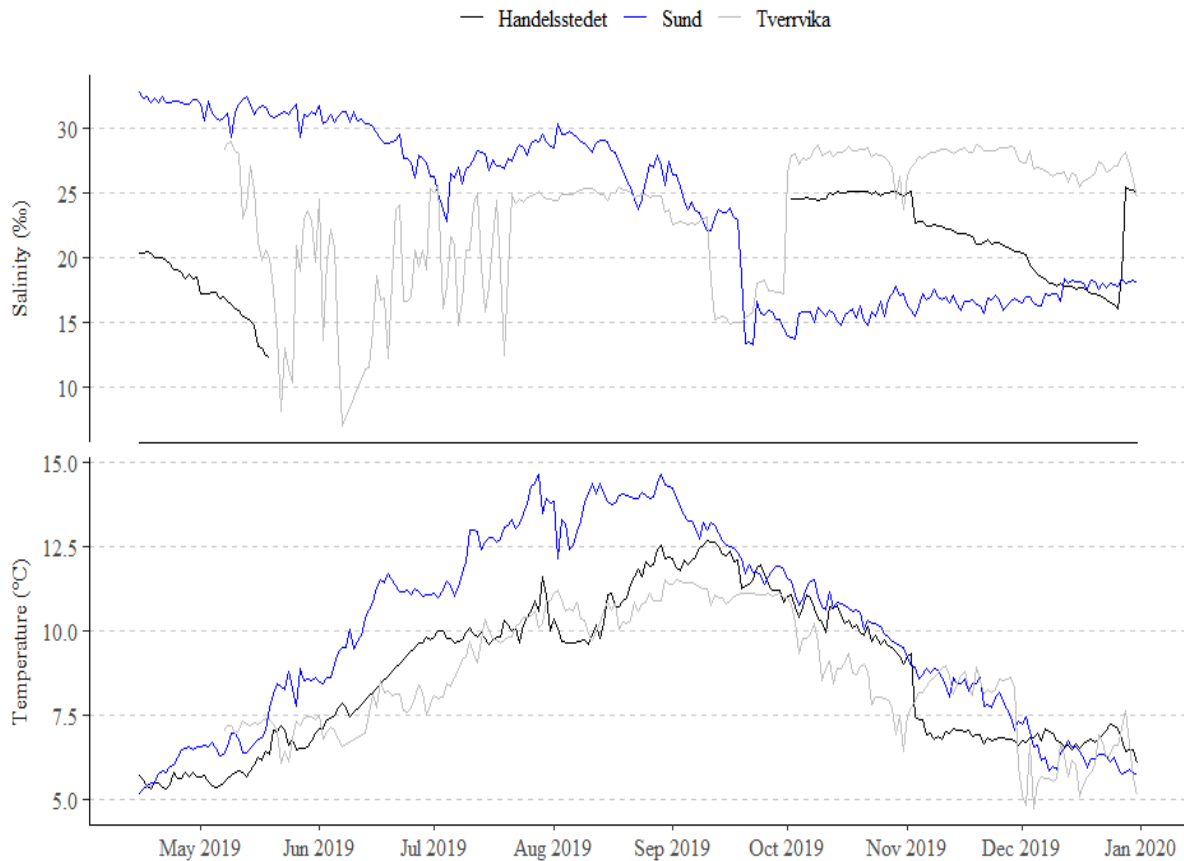
Figure 2. Mean daily water temperature and salinity in the inner part of Beiarfjorden (Tverrvika, line T2), in the Beiarfjorden exit area (Handelsstedet, receiver 39) and at the outer south-western part of the fjord-system (Sund, line T7). The figure shows records from the period between 15.04.2019 and 31.12.2019. Salinity measurements at Handelsstedet between 17.05.2019 and 01.10.2019 were excluded due to a measurement error.

Conductivity and temperature at different depths

Conductivity and temperature at different depths (CTD) were measured at seven different receiver locations at three different dates during 2019. Maximum measurement depth varied between 20 m and 5 m due to different depths, current and weather conditions at the sampling locations (figure 3). The sampling instrument used was STD/CTD model SD204 produced by SAIV A/S (Bergen, Norway). Conductivity was transformed to salinity values using the sampling instrument's onboard software. Salinity increased with increasing depth on all locations, and on average stabilized below 5 m depth at salinities between 32‰ and 34‰. Recordings at locations close to inner lines/receivers (T2, T3, T4) showed increasing temperature with increasing depth, while recordings at outer lines (T5, T7, T8, T9) showed decreasing temperature with increasing depth. Measurements at locations near outer lines were done during summer while inner line measurements were done during spring and autumn. Both salinity and temperature indicate a strong influence on the Beiarfjorden surface waters (< 5 m depth) by influx of cold freshwater from Beiarelva in spring (figure 3).
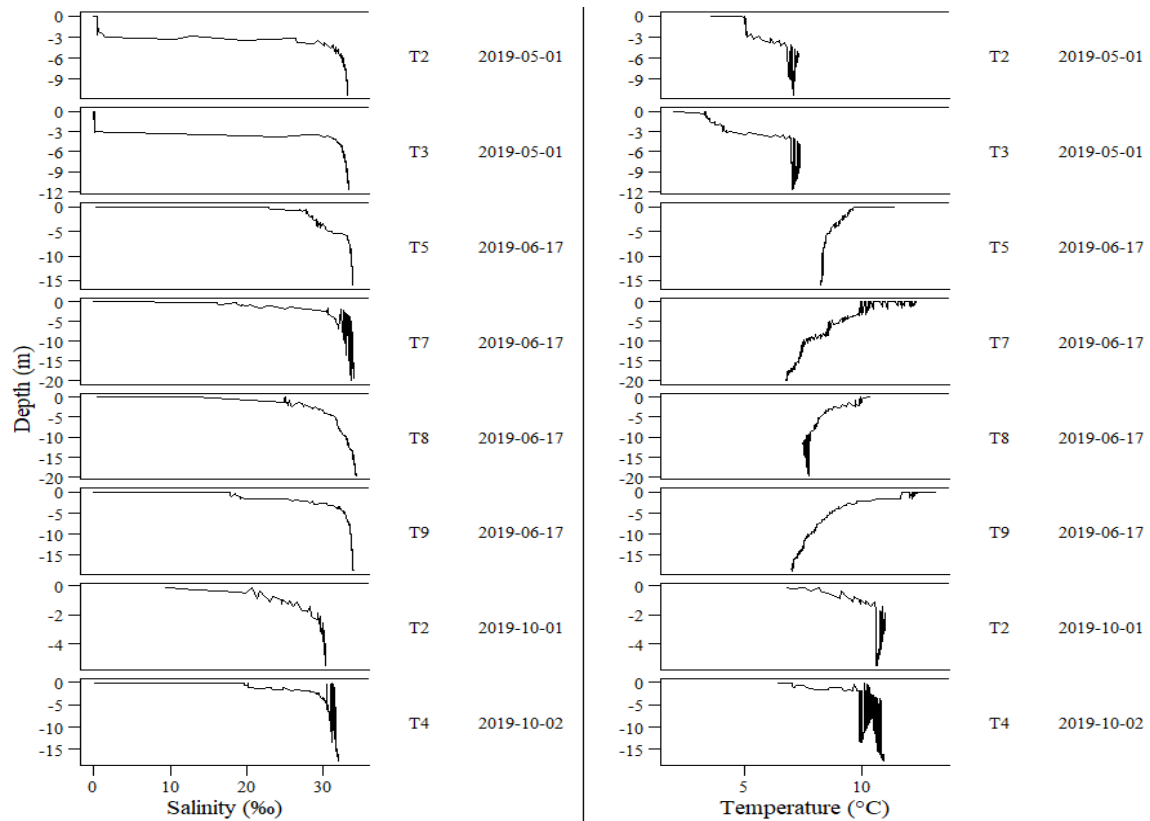
Figure 3. *Salinity and water temperature as a function of depth at seven locations in the fjord system, and their respective sampling dates. Locations where measurements were taken can be seen in the map (figure 1).*

Differences in water level with changing tide

Tidal data were imported from karverket.no and used under a creative common license (CC BY 4.0). Water level was recorded every 10 mins at the permanent water level gauge in Bodø. The water-level had been adjusted based on weather patterns in the area by Kartverket's own algorithms. The adjusted water level varied with 320 cm between maximum high tide and maximum low tide during 2019. The water level data were organized into the four categories high tide, low tide, rising tide and falling tide. High tide/low tide was defined as the time during a tidal cycle with the highest/lowest water level ± 1.5 hours. With two tidal cycles every 24 hours, each of the four categories were divided in-to 6-hour intervals (3 hours per tidal cycle).

Collecting data using acoustic telemetry

Receiver array

Tagged fish were recorded by 40 acoustic receivers deployed in Beiarelva and the connecting fjord system. Of the 40 receivers, 28 were deployed in line transects (receiver lines T1-T9) with 200 m between each receiver in the estuary and 400 m between each receiver in the rest of the fjord system. Ten receivers were positioned outside the receiver lines to serve as backup in case some tagged fish passed the lines undetected. The remaining two receivers were placed in the river. These two receivers were removed during winter due to the large amount of drift-ice in the river after the spring thaw, and then redeployed the following spring. Detection range of the receivers varied based on hydrographical- and weather conditions. Equipment loss made the number of operational receivers variable throughout the study. A minimum of 90% of receivers were operational at any given time during the study period. An overview of receiver loss and deployment of replacement receivers is given in appendix 1.

The acoustic receivers were made by Vemco Inc. (Halifax, Canada). The two models used were the 69 kHz VR2W standard receiver (23/40), and the 69 kHz VR2AR (17/40). Of the 40 receivers, ten were mounted on a rope approximately 5 m below the sea surface. The rope was attached to an anchor on the seafloor and a floater on the sea surface. These ten receivers were deployed close to the shoreline to reduce the chance of entanglement in boat propellers and fishing lines. The two receivers in the river were mounted on a concrete block placed in the middle of the river, with a chain running from the block to the shoreline. The remaining 28 receivers were equipped with an acoustic release system. These receivers were used in deep water, or areas with frequent ship traffic and/or ice movement (e.g., estuary area). Receivers with an acoustic release system can prevent equipment loss, as they do not require a surface attachment or to be retrieved by divers. When receiving a release signal from a transponder, the acoustic release link detaches from the receiver, and the receiver surfaces with the help of an attached float. The acoustic release link and the attached anchor are left on the seafloor. In depths above 112 m, VR2AR receivers with an integrated acoustic release system were used. At depths below 112 m, VR2W receivers were equipped with one of two different acoustic release systems (Subsonic-AR60 release systems, Sub Sea Systems inc., Diamond springs, USA or Vemco Ascent Acoustic Release, Vemco inc., Halifax, Canada). With a rope attached to the release system at the sea floor, the receivers were positioned in the water column 30 m below the sea surface. The main reason all receivers were not equipped with an acoustic release system was a limitation of available equipment. All acoustic data were uploaded to the Ocean Tracking Network (OTN) data warehouse. The OTN data warehouse is a global collection of tracking data from aquatic animals (https://members.oceantrack.org/projects).

Receiver performance

Tagged fish were only recorded when they were within range of a receiver. Hence, the detectability of tagged fish on receivers in receiver lines T2, T3, T4, T5 and T6 (figure 1) was investigated using pinger-tag systems in the VR2AR receivers. The pinger-tag transmits a unique signal, similar to that of a fish tag. If detected on the closest receiver(s) on the same line, the receivers can be assumed to have overlapping detection ranges. The receivers on lines equipped with pinger-tag systems were found to have overlapping detection ranges during 2019. Detectability on receiver lines T1, T7, T8 and T9 was checked by comparing fish registrations on these lines to registrations on lines closer to the river mouth. No fish registered on lines T7, T8 and T9 had passed any of the previous lines without being registered when progressing through the fjord system, showing good receiver performance. The only receiver line with poor receiver performance was line T1, where four fish (6%) swam past undetected. The receivers 39, 40, 41, 42, 43, 44, 45 and 46 were located between lines (figure 1), providing a backup in case of fish swimming past a receiver line without being registered.

Capture, sampling and tagging of fish

In the spring of 2019, 38 Atlantic salmon and 34 brown were caught, sampled, and tagged with internal acoustic transmitters. Capture took place in the lower parts of Beiarelva from 04.04.2019 to 06.05.2019. The fish were caught using rod and reel with lures/flies. The tackle was selected to target post-spawners and veteran migrants, which were distinguished from smolts in the field based on body size. Confirmation of sex and species were done in the lab through molecular analysis of DNA from adipose fin samples.

The fish were anesthetized using Benzoac Vet with a dilution of 15-20 ml per 100 L water (ACD Pharmaceuticals AS, Batch Nr. 18K07) for 3-5 min. Acoustic transmitters from Thelma Biotel (Trondheim, Norway) with a nominal delay of 30-90 sec were surgically implanted into the abdominal cavity of the fish in accordance with the procedure described in Halttunen *et al.* (2010). A 1.5-2 cm long incision was made into the abdominal cavity, anterior to the pelvic girdle. After insertion of the tag, the incision was closed using two separate non-biodegradable sutures (RESORBA Wundversorgung GmbH & Co; 3,0 Resolon). Two different sizes of cylindrically shaped tags from Thelma Biotel were used (ID-MP9L, 69 kHz, length: 29.4 mm, diameter: 9 mm weigh air: 5.2 g and ID-MP13, 69 kHz, length: 33.3 mm, diameter: 12.7 mm, weight air: 11.5 g). Ten ID-MP9L tags were used to tag the smallest fish (body length, 340-430 m, tag burden range: 0.8-2.2%), and ID-MP13 tags were used to tag the remaining 62 fish (body length, 415-1120 mm, tag burden range: 0.1-2.9%). Estimated battery life for the ID-MP9L- and ID-MP13 tags were 13.4 months and 25.9 months, respectively.

Shortly after tagging, non-lethal adipose fin and scale samples were collected. A total of 2 mm^2 of adipose fin was sampled from each fish using sterile iris scissors and stored in RNA*later* solution. Scales (15-20) were sampled from an area around the lateral line close to the caudal fin, using haemostatic forceps. The scales were stored in scale envelopes marked with fish identification (ID-number, species, sex, length, and mass) and capture information (date, location, and method of capture). Prior to recovery, the fish were measured and weighed. Total body length was measured from the tip of the snout to the tip of the caudal fin. After sampling,

the fish were placed in recovery tanks for approximately 10 mins. After recovery, the fish were released at the capture site. All capture, sampling and tagging were done in accordance with the regulations set by the Norwegian Food and Safety Authority (permit 19/23443).

Scale sample analysis to determine life stage

Prior to analysis, 5-10 of the most readable scales from each individual fish were selected using a light-microscope. An imprint of the scale structure was made by pressing the scales onto 1 mm polycarbonate Lexan plates. Using a computer-stereoscope equipped with a camera (Leica M165C, camera: Leica MC170 HD, software: LAS V4.5, Leica systems, Sankt Gallen, Switzerland) the imprint was analysed to determine the age and previously performed sea migrations of each individual fish. Age determination was not possible for one Atlantic salmon due to the scales not being readable. All fish with readable scales were found to previously having completed one or more migrations (i.e., Atlantic salmon post-spawners and brown trout veteran migrants).

Genetic sex- and species determination

Morphological identification of fish species and sex is vulnerable to human error. Both sex and species of the fish in this thesis were therefore determined genetically. The process began by extracting genomic DNA from adipose fin samples using DNeasy Blood & Tissue Kits (Qiagen). For determining species, the Salmo_Mito-951 locus with forward Salmo_Mito-951F (ACCCCTAAACCAGGAAGTCT) and reverse Salmo_Mito-951R (TGCTTTAGTTAAGCTACGCCAACT) primers were used (Karlsson *et al.*, 2013). For sex determination, the Salmo-SdY locus with Salmo-sdY-F (GGGCCTATGAATTTCTGATG) and Salmo-sdY-R (ACAGATTTGCGACATGAACA) were used (Quemere *et al.*, 2014). The 5' end of forward primers were fluorescently labeled with "Hex" for Salmo-Mito-951 and "FAM ATTO565" for Salmo-SdY loci. To amplify the DNA-fragments, a multiplex PCR was conducted in a 5 µl reaction, including 2.5 µl 2x Multiplex PCR Master Mix, 1 µl of primer mix (0.2 µM for each primer), and 1 µl of the extracted genomic DNA. The PCR thermal program (conducted on a MiniAmp thermal cycler, Applied Biosystems, Foster City, USA) was set to 5 min at 95 ℃ initial denaturation, 10 cycles as touchdown PCR for 30 sec at 95 ℃, 1 min at 62 ℃ to -52 ℃ (decreasing temperature 1 ℃ each cycle), and 1 min at 72 ℃. The procedure was followed by 25 cycles at 95 ℃ for 30 sec, 52 ℃ for 1 min and 72 ℃ for 1 min, with a final extension of 10 mins at 72 ℃. After ensuring the amplification of loci on Agarose gel, 1 µl of diluted PCR products (1:15 dilution) was mixed with 8.85 µl of Formamide and 0.15 µl of LIZ 600 size standard (Applied Biosystems). The fragment analysis was conducted with 3130xl Genetic Analyzer (Applied Biosystems). Size of alleles at each locus was determined with the Gene Mapper V4 program (Applied biosystems). All DNA-analysis were conducted at the Department of Biology, NTNU, Trondheim.

Table 1. *Species, sex, number of tagged fish, body length, body mass and Fulton's condition factor of all fish tagged in the spring of 2019. The range is given in parenthesis underneath the mean value.*

Species	Sex	Number of tagged fish (n)	Mean body length (mm)	Mean age (years)	Mean body mass (g)	Mean condition factor (k)
Atlantic salmon	Female	30	877 (610-1120)	8.0 (6-10)	4259 (1280-9000)	0.60 (0.45-0.68)
	Male	8	708 (580-1020)	6.6 (5-10)	2528 (1100-6800)	0.60 (0.54-0.67)
	Both sexes	38	756 (580-1120)	7.7 (5-10)	3885 (1100-9000)	0.60 (0.45-0.68)
Brown trout	Female	9	513 (390-670)	8.9 (7-12)	1163 (450-2680)	0.73 (0.60-0.93)
	Male	25	521 (340-730)	8.2 (6-14)	1328 (240-3320)	0.81 (0.47-0.98)
	Both sexes	34	516 (340-730)	8.4 (6-14)	1261 (240-3320)	0.79 (0.47-0.98)

Data analysis

Telemetry data were downloaded from the receivers using the VUE software version 2.6.1 provided by AMIRIX systems. Data filtration and statistical analysis were done using R version 3.6.1 and R-studio version 1.2.1335 (R core team, 2019). The significance level chosen for statistical analysis (models not included) was $p < 0.05$.

Filtration of tracking data

When using acoustic telemetry data, there is a high probability of having false detections included in the dataset. Identification of acoustic signals is vulnerable to signal collisions. When two acoustic signals collide, a third signal that corresponds with a detectable code can be generated, thus creating a false detection. The likelihood of false detections increases with the number of fish staying within the detection range at the same time (Pincock, 2012). Some areas, like estuaries, will therefore likely have a higher proportion of false detections. False detections can also be created when noise in the environment is registered by the receivers. It is unrealistic to completely remove all false detections from a dataset, but it can be adequately accounted for through analyses (Simpfendorfer *et al.*, 2015).

The total number of registrations in 2019 were 671079. The total number excludes a known set of pingertag ID's (A69-1601-) that were removed prior to filtration. It was decided that a 30-minute filter would considerably reduce the probability of including false registrations while not excluding too many true registrations. The 30-minute filter requires two registrations within an interval of 30 minutes on the same receiver for a registration to be labelled as true. The filter removed 0.4% of registrations. After removal of duplicates and false fish ID's, the remaining proportion of registrations was 99.5%. All registration dates and times used in calculation of progression rate were checked by manually comparing post-filtration registrations to raw data in the VUE software.

Investigating the effect of tidal cycles on marine migration timing

Date and time (D:M:Y h:m:s) for water-level measurements were matched with the first registration on the lines T2 (estuary exit), T4 (Beiarfjorden exit), and T9 (Nordfjorden exit), for each individual fish of both species. These lines were chosen because they covered the route where most of the Atlantic salmon and brown trout progressed through the fjord system. The number of minutes from high tide for each registration was calculated, and then converted to degrees (where hightide is $0°$ and $360°$). The data were plotted in a circular fashion and tested using a Rayleigh's test of uniformity. The test was performed using the "r.test" function in the CircStats package (Jammalamadaka & Sen Gupta, 2001). A Rayleigh's test of uniformity analyses circular data with the alternative hypothesis being that a unimodal distribution exists in the circular data. In this thesis, a unimodal distribution would mean a significant clustering of registrations in one section of the tidal cycle. In the plots, an arrow was used to indicate the mean direction of clustering in the case of a significant result.

Testing differences between groups

All comparisons of biological characteristics in two independent, normally distributed groups were done using Welch two sample t-tests ("t.test" function in base R-studio), assuming unequal variance between groups. Assumption of normality was checked prior to testing using the Shapiro-Wilk's method with the "shapiro.test" function in base R-studio. Differences between non-normally distributed groups where one group had a low sample size (short-distance brown trout migrants, $n = 7$), were tested using a non-parametric Wilcoxon Rank Sum test with the "wilcox.test" function in base R-studio. When testing differences between non-normally distributed paired samples (intraspecific differences in progression rate), a paired two-sample Wilcoxon Rank Sum test was used. Comparisons of temperature and salinity at different sampling locations were done using one-way analysis of variance tests (ANOVA) with the "aov" function in base R-studio. The samples were found to have normal distribution due to the large sample size, in accordance with the central limit theorem.

Calculating progression rate and investigating continuity of progression

Migration progression rate is not the same as migration speed due to progression rate assuming the fish migrating the shortest possible swimming distance between two points, which is most likely not the case (Thorstad *et al.*, 2012). In the present study, distances in the fjord system were measured as the shortest possible swimming distances between receiver lines, using the measuring tool in https://kart.gulesider.no/yellow. Progression rate was calculated as the distance between two lines over the time difference between the first registration on the first line and the first registration on the last line. The progression rate of each fish was calculated in both km/h and in body lengths/sec (bl/sec). Bl/sec was calculated in order to compare with other papers, but not included in the models. Modelling progression rate in km/h instead of bl/sec was chosen due to bl/sec including body length in the calculation. If chosen, body length would be represented in both the response and explanatory variable when running the model.

Progression rate was calculated for Beiarfjorden, Nordfjorden and for the total distance of these two combined. As the progression rate had to be calculated between two set points, a single route had to be chosen when calculating progression rate outside of Beiarfjorden. The route through Nordfjorden was chosen due to it being the preferred route for both species. To investigate how continuous the progression of each species was between different lines in Beiarfjorden and Nordfjorden, the dates corresponding to when 25%, 50%, 75% and 100% of the fish of each species had been detected on lines T2, T4 and T9 were inspected. An even interval between lines would indicate a continuous progression (e.g., if the amount of time between when 50% and 75% of the fish were registered on line T2 was equal to the time on T4, it would indicate a continuous progression between the lines).

Calculating condition factor and checking linear dependence between biological characteristics

Fulton's condition factor (K) (hereafter condition factor) was used as an estimate for the physical condition of a fish. The condition factor was calculated using the formula (Ricker, 1975):

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

All individual biological characteristics were tested for linear dependence (Pearson correlation) using the "cor" function in base R-studio. Condition factor was not correlated with any of the other biological characteristics (body length, estuary exit date) for neither of the species (Pearson correlation, $p > 0.05$).

Modelling influence of body length, condition factor and estuary exit date on progression rate

The influence of body length, condition factor and estuary exit date (explanatory variables) on the progression rate (response variable) was investigated using parametric regression models. Generalized linear models (GLM) were chosen to avoid problems with extreme values in non-normally distributed data. A gaussian distribution was assumed in the GLMs as all explanatory variables were continuous. The GLM combines the explanatory variables to best explain the response and then determines how much each of them contributes to the model. Due to the low sample sizes in the dataset (Atlantic salmon: $n = 37$, brown trout: $n = 21$), the number of explanatory variables and fixed effects was kept low to increase model accuracy. Different models were made for the influence of biological characteristics on the progression rate in Beiarfjorden, in Nordfjorden and for the total distance. All three models were run independently for each species. The fjord sections Beiarfjorden and Nordfjorden were chosen due to these two areas having a high proportion of tagged fish detected, and being geographically different from each other. The reason for not including the estuary area (figure 1, section A) was, in addition to inadequate receiver performance, that several fish of both species were caught and tagged close to receiver 30. If including progression rate from line T1 to T2, observed differences in progression rate could be difficult to separate from tagging effects.

All response- and explanatory model variables were standardised using the "scale" function in base R-studio. The standardization was done prior to modelling in order to compare their different effects on the progression rate (Atchley, 1978). Due to the calculation of condition factor depending on body length, the condition factor had to be adjusted prior to modelling. Condition factor was adjusted using the regression coefficient for the linear relationship between log(body mass) and log(body length) (relative condition factor). The regression coefficient was calculated individually for each species (Atlantic salmon = 3.155, brown trout = 3.194). The relative condition factor is a ratio between measured body mass and the expected body mass, as calculated using the logarithmic regression relationship between the two (Lecren, 1951). The relative condition factor renders condition factor independent of body length, and the two variables can therefore be used in the same model. Estuary exit date (the date when each fish was first detected by one of the receivers in line T2) was converted to Julian date before modelling to get a comparable numeric value. Due to the low sample size of Atlantic salmon males and brown trout females (brown trout females recorded in Nordfjorden, $n = 6$), sex was not included as a model parameter. The sample size was too low to get reliable results from testing differences in biological characteristics between the sexes, even with a non-parametric test. Without accurate results from testing differences in biological characteristics, the potential effects of sex would be impossible to differentiate from other effects.

Multicollinearity between explanatory variables was checked in all models to establish sufficiently low dependencies. A high multicollinearity weakens the precision of parameter coefficients by inflating standard errors and consequently reduces statistical power (McClendon, 2002). The multicollinearity was checked (variance inflation factors (VIF) as a measure) using the "check_colinearity" function in the "performance" R-studio package (Lüdecke *et al.*, 2021). When modelling the effect of body length, adjusted condition factor and estuary exit date on progression rate in the same model, multicollinearity was found to be low for all parameters in all models including Atlantic salmon (VIF ≤ 1.44), and for all parameters in models including brown trout (VIF ≤ 1.29). The multicollinearity was sufficiently low in all explanatory variables to include all in a single model.

Model selection was based on the second order Akaike's information criteria (AICc) using the "dredge" function in the MuMIn R-studio package (Barton, 2020). AICc differs from the more commonly used AIC by correcting for low sample sizes in models where the number of observations is lower than 40 times the number of explanatory variables (Hurvich & Tsai, 1989). AICc testing ranks different models based on how well they explain variation in the data and the number of explanatory variables included in the model, and thus provides an evidence ratio. Δ AICc is the difference in AICc score between the best fitted model (lowest AICc value) and the model it is being compared to. When the function returned several models with Δ AICc < 2, the models were deemed to be of equal fit and conditional model averaging was applied to all alternative models (Δ AICc < 4) in accordance with the recommendations in Burnham and Anderson (2002). Conditional model averaging calculates the average of a parameter coefficient only from the models where that parameter coefficient is included. This means that the result will depend on the number of models where the parameter is included.

When using an information-theoretic approach such as AICc model selection, the p-values cannot explain significance of each explanatory variable (Anderson *et al.*, 2001). P-values are probabilities of the test statistic, and not evidence (Royall, 1997). Therefore, a strength of evidence approach was adapted (i.e., the model output does not determine if the influence of a biological characteristic is "rejected or not", but instead provides evidence of the predictive value). Using a combination of the standard errors from conditional model averaging (model probability) and the number of models where each biological characteristic was included (model likelihood), empirical support for the influence of each model parameter on progression rate was assessed (Burnham *et al.*, 2011). The sign of each coefficient showed the effect-direction, where a positive value suggested a positive relationship with progression rate. The coefficients from either the best fitted model or conditional model averaging were used in graphic representations, where the parameter coefficient (model intercept as zero-value) and standard error from each of the independent variables were shown.

Categorizing tagged brown trout as long distance- or short distance migrants

All the tagged brown trout were categorized as either long-distance or short-distance migrants based on the distance travelled from the estuary (line T2) during the 2019 season. Long-distance migrants were defined as individuals registered on lines T6, T7, T8 or T9 (figure 1). Short-distance migrants were defined as individuals not registered on any of the lines T6, T7, T8 or T9. The relatively long distance chosen as range for short distance migrants (16.7 km from the river mouth) was chosen to get a high enough sample size in order to compare biological characteristics between groups.

RESULTS

Swimming route through the fjord system

Atlantic salmon

Of the 38 tagged Atlantic salmon, 37 exited the estuary area and were registered on lines T2, T3, and T4 (figure 4). The one remaining fish was never registered on any receivers. After passing line T4 and exiting Beiarfjorden, 33 (87%) of the salmon migrated directly northwards and were registered on line T8, while four (11%) migrated southwards and were registered on line T5. All of the four salmon that initially chose the southern route, migrated back north towards line T8 after first having been registered on line T5 or T6. Hence, all the tagged Atlantic salmon finally chose the northern route through Nordfjorden when migrating through the fjord system.

Brown trout

Of 34 tagged brown trout, 33 exited the estuary area and were registered on lines T2 and T3 (figure 4). The one remaining fish was never registered on any receivers. At line T4, 27 of the trout were registered, showing that six of the fish never left Beiarfjorden during the 2019 season (table 2). Of the fish migrating to either of the fjord system exits (24/34, 71%), only four initially migrated southwards through Holmsundsfjorden and Morsdalsfjorden. The remaining 21 trout migrated northwards through Nordfjorden. Overall, the majority of tagged brown trout exited Beiarfjorden (27/34, 79%) and chose the northern route (21/34, 62%) when migrating through the fjord system.

Of the 33 brown trout registered, 26 were defined as long-distance migrants (registered outside of line T4) and seven as short-distance migrants (not registered outside of line T4). When comparing body length, long-distance migrants were found to have longer bodies than short distance migrants (Wilcoxon rank sum test, $p < 0.05$). There was no difference in condition factor or estuary exit date between the two groups (Wilcoxon rank sum test, $p > 0.05$).

Table 2. *Number (n) and proportion (%) of tagged Atlantic salmon and brown trout registered on the different receiver lines during the study period. Beiarfjorden = T1, T2, T3, T4, Nordfjorden = T8, T9, Holmsundsfjorden = T5, T6, Morsdalsfjorden = T7.*

		T1	T2	T3	T4	T5	T6	T7	T8	T9
Atlantic salmon	Number of fish registered	$n = 33$	$n = 37$	$n = 37$	$n = 37$	$n = 4$	$n = 1$	$n = 0$	$n = 37$	$n = 37$
	Percentage of all tagged fish registered	87%	97%	97%	97%	11%	3%	0%	97%	97%
Brown trout	Number of fish registered	$n = 33$	$n = 33$	$n = 33$	$n = 27$	$n = 8$	$n = 7$	$n = 6$	$n = 24$	$n = 23$
	Percentage of all tagged fish registered	97%	97%	97%	79%	24%	21%	18%	71%	68%
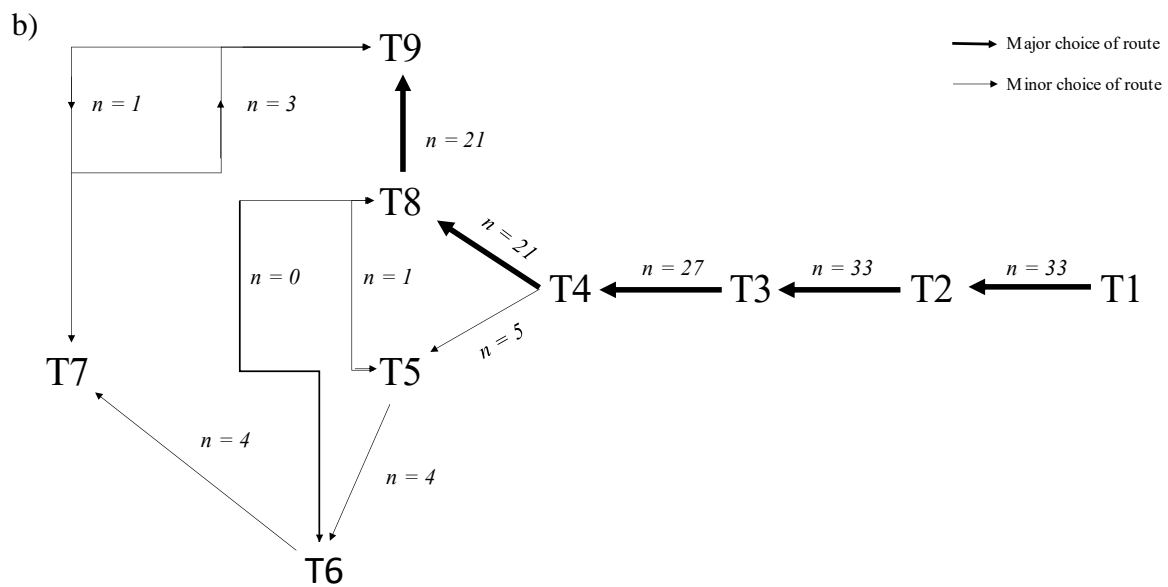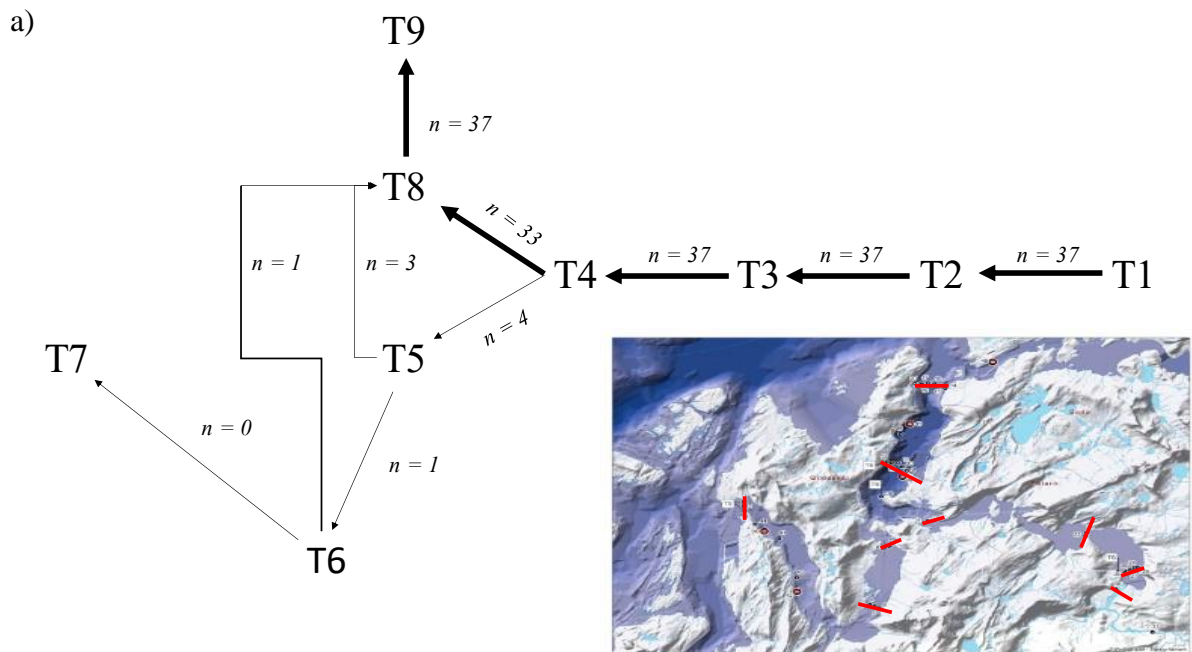
Figure 4. *Swimming direction of Atlantic salmon (a) and brown trout (b) registered in 2019. The figures show a schematic layout of the fjord system. Large arrows show the routes most fish took to the outermost lines (T7 or T9). (n) is the number of fish. Red lines on the map shown between a) and b) correspond to the receiver lines T1-T9. For the brown trout, several fish turned around and was registered on new lines after being registered on T7 or T9 resulting in the proportions seen in table 2, but these registrations are not included in this figure. Route between T6 and T8 is where the fish turned around and moved back north passing line T5.*

Continuity of migration from the estuary exit and through the fjord system

Atlantic salmon

For the 37 Atlantic salmon registered, there were 51 days between the first (09.05.2019) and the last (29.06.2019) estuary exit dates (figure 5). Estuary exit date was not correlated with any of the other biological characteristics (body length, condition factor) (Pearson correlation, $p > 0.05$). There were 52 days between the first estuary exit date and the date when the last Atlantic salmon had been registered on line T9. The time between dates where 25%, 50%, 70% and 100% of the fish had been registered were similar on all lines, indicating a continuous, directional migration through the fjord system by most individuals both in Beiarfjorden and in Nordfjorden (figure 6).

Brown trout

Of the 33 brown trout registered, there were 35 days between the first (02.05.2019) and the last (06.06.2019) estuary exit dates (figure 5). Estuary exit date was not correlated with any of the other biological characteristics (body length, condition factor) (Pearson correlation, $p > 0.05$). There were 92 days between the first estuary exit date and the date when the last brown trout had been registered on line T9. The shorter amount of time between registrations on T4 and T9 compared to between T2 and T4, shows a more continuous progression of in Nordfjorden compared to Beiarfjorden (figure 6). Uneven intervals between T2 and T4 show that some individuals of brown trout spent long periods of time within Beiarfjorden while others had a fast, continuous progression out of the fjord system. The migration of brown trout inside of Beiarfjorden (line T2-T4) was less continuous compared to the migration of Atlantic salmon. The migration of brown trout in Nordfjorden (T4-T9), however, appeared to be continuous, similar to that of Atlantic salmon.
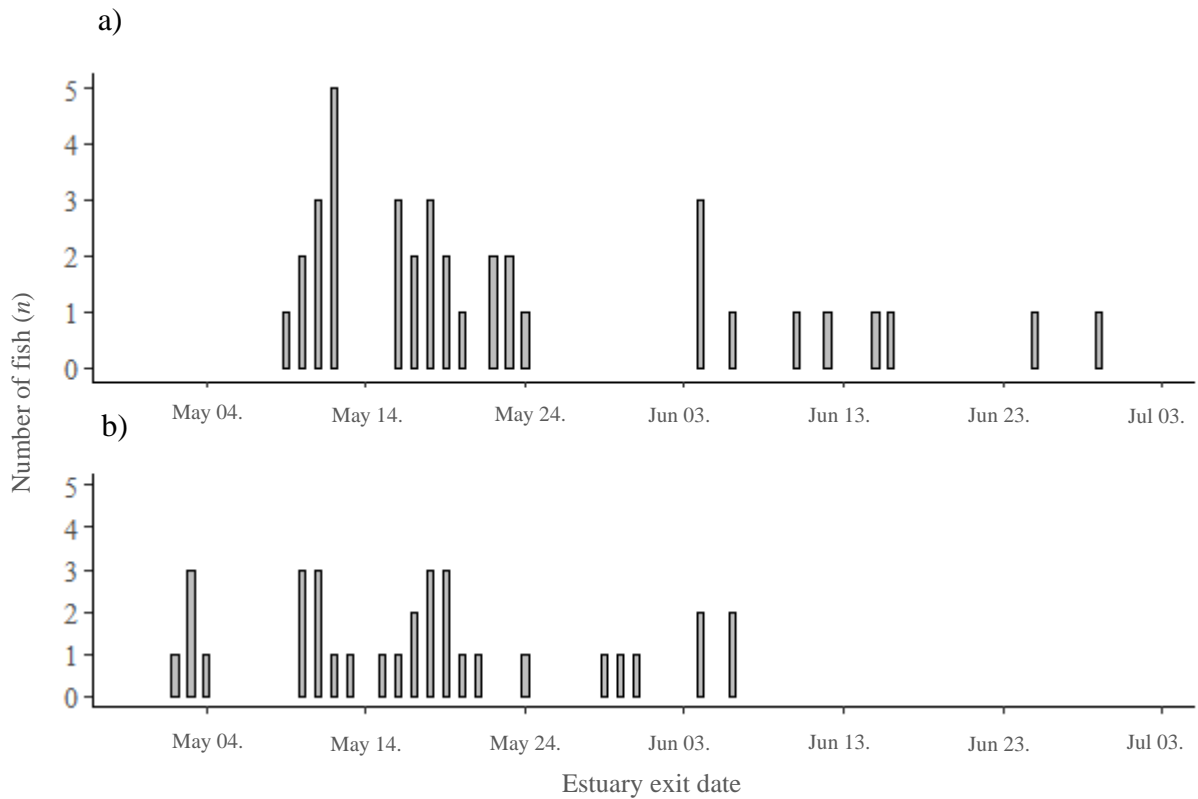
Figure 5. *Estuary exit dates of Atlantic salmon (a) and brown trout (b) tagged and recorded in 2019. Bars show the number of fish (n) leaving the estuary on the date in question.*
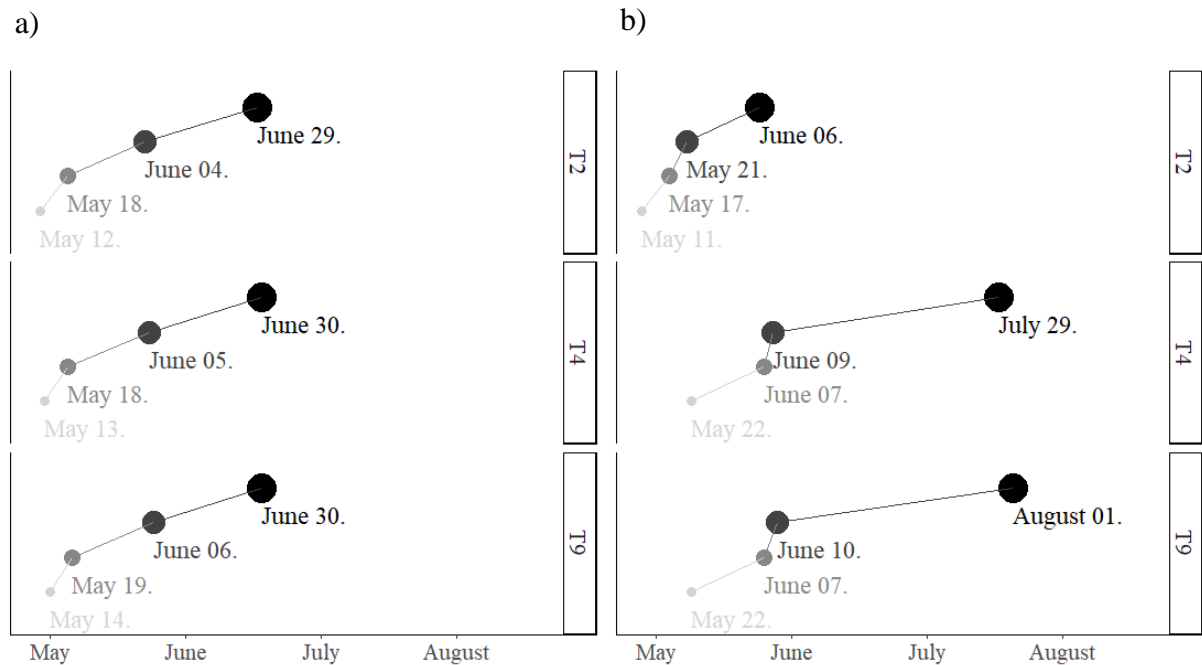
Figure 6. *Continuity of progression during the early marine migration of all tagged Atlantic salmon (a) and brown trout (b). Dates shows when 25% (smallest, lightest grey dot), 50%, 75% and 100% (largest, black dot) of all tagged fish had been registered on the line in question.*

The effect of tidal cycles on the timing of marine migration and progression

Atlantic salmon

For Atlantic salmon, there was a significant clustering of registrations at the estuary exit (T2) during falling tide (figure 7, Rayleigh's test of uniformity, $p < 0.001$). A clustering was also observed in the transition between hightide and falling tide at the exit of Beiarfjorden (T4, $p > 0.01$), and during lowtide at the exit of Nordfjorden (T9, $p < 0.001$). When comparing the time spent between registrations on lines T2, T4 and T9 to recurring tidal cycles, the observed clustering patterns were predictable. I.e., the clusterings of Atlantic salmon registrations at the exit of Beiarfjorden and Nordfjorden appear to be a result of continuous progression after leaving the estuary area, and not necessarily the tidal cycle.

Brown trout

At the estuary exit (T2), brown trout had two significant clusterings of registrations, where one was at late high tide, and one at falling tide, giving a mean direction of clustering during early falling tide (figure 7, Rayleigh's test of uniformity, $p < 0.01$). No clusterings of registrations were observed at the exit of Beiarfjorden (T4) or Nordfjorden (T9), showing a random distribution of registrations throughout the tidal cycle on these lines ($p > 0.05$).
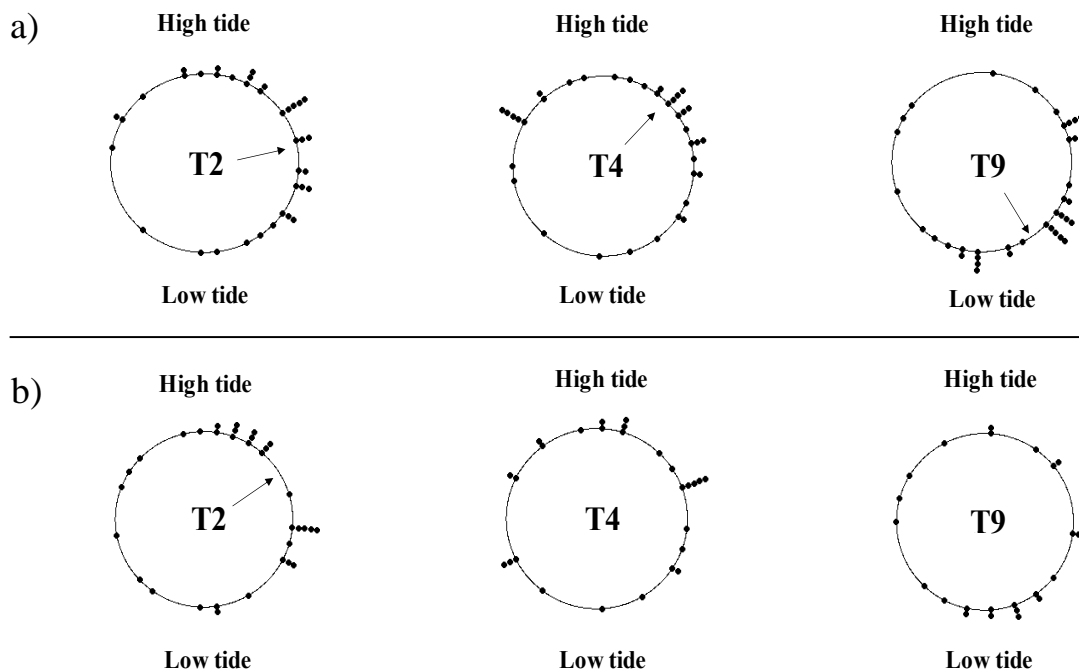
Figure 7. *Timing of estuary exit (line T2), Beiarfjorden exit (line T4) and Nordfjorden exit (line T9) of tagged Atlantic salmon (a) and brown trout (b) in relation to the tidal cycle. The arrows indicate the mean direction of a significant clustering of registrations.*

Progression rate

Atlantic salmon had a higher average progression rate than brown trout for the total distance (figure 8, Wilcoxon rank sum test, $p < 0.001$), in Beiarfjorden ($p < 0.001$) and in Nordfjorden ($p < 0.001$). There was a significantly higher progression rate (km/h) in Nordfjorden compared to Beiarfjorden for both Atlantic salmon (paired sample t-test, $n = 37$, $p < 0.001$) and brown trout (paired sample t-test, $n = 21$, $p < 0.01$).
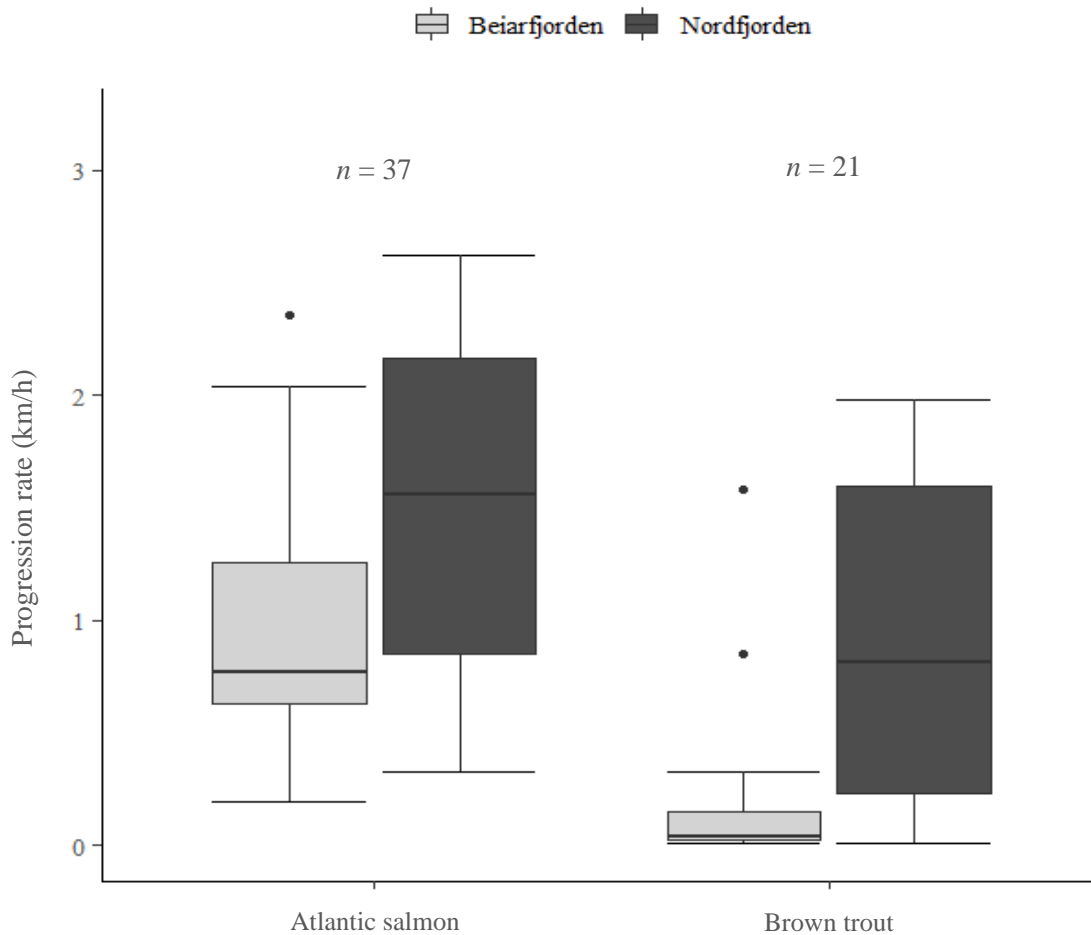
Figure 8. *Progression rate (km/h) in Beiarfjorden and Nordfjorden for Atlantic salmon and brown trout tagged in 2019. Only individuals registered in both areas were compared in this figure (Atlantic salmon, n = 37, brown trout n = 21). The boxplots show median values and interquartile range, while vertical lines represent 95th percentile. Dots outside the boxplots represent outliers.*

Atlantic salmon

On average, the 37 Atlantic salmon post-spawners spent a total of 37 hours in progressing the total distance from line T2 to T9 ($n = 37$, distance = 29.9 km, range = 13-92 hours). The salmon spent on average 24 hours on progressing through Beiarfjorden ($n = 37$, distance = 16.7 km, range = 7-84 hours) and 13 hours through Nordfjorden ($n = 37$, distance = 13.2 km, range = 5-40 hours). The average progression rate was 1.0 km/h (range = 0.3-2.3 km/h) for the total distance, 0.95 km/h (range = 0.2-2.4 km/h) in Beiarfjorden, and 1.5 km/h (range = 0.3-2.6 km/h) in Nordfjorden. The average progression rate in bl/sec was 0.4 bl/sec (range = 0.09-0.7 bl/sec) for the total distance, 0.3 bl/sec (range = 0.06-0.7 bl/sec) in Beiarfjorden, and 0.5 bl/sec (range = 0.09-1.0 bl/sec) in Nordfjorden.

Effect of biological characteristics on progression rate for the total distance

There were five equally well fitted models (Δ AICc < 2) for the progression rate for the total distance (line T2-T9) where the null-model was included. Body length was included in two models, condition factor in one model and estuary exit date in two models. Conditional model averaging showed that all the biological characteristics had standard errors exceeding the coefficient (figure 9). No evidence was therefore found for the influence of any biological characteristics on Atlantic salmon progression rate for the total distance.

Effect of biological characteristics on progression rate in Beiarfjorden

There were two equally well fitted models (Δ AICc < 2) for the progression rate in Beiarfjorden (line T2-T4) where the null-model was included. Body length was included in one of the models, condition factor in none of the models and estuary exit date in none of the models. Conditional model averaging showed that all the biological characteristics had standard errors exceeding the coefficient (figure 9). No evidence was therefore found for the influence of any biological characteristics on Atlantic salmon progression rate in Beiarfjorden.

Effect of biological characteristics on progression rate in Nordfjorden

There were six equally well fitted models (Δ AICc < 2) for the progression rate in Nordfjorden (line T4-T9) where the null-model was included. Body length was included in two models, condition factor in two models and estuary exit date in three models. Conditional model averaging showed that body length had standard errors exceeding the coefficient (figure 9). The standard error for condition factor and estuary exit date did not exceed the parameter coefficient. Due to condition factor only being included in two of the six models, the effect appeared to be small. Estuary exit date was found to have the strongest effect on progression rate, followed by condition factor. The positive coefficient suggests that a later estuary exit date and a lower condition factor resulted in a higher progression rate for Atlantic salmon in Nordfjorden.

Brown trout

On average, the 21 brown trout veterans migrating to the outer parts of the fjord system spent a total of 546 hours in progressing the total distance from line T2 to T9 (n = 21, distance = 29.9 km, range = 59-1883 hours). The trout spent on average 417 hours on progression through Beiarfjorden (n = 27, distance = 16.7 km, range = 11-1260 hours) and 127 hours through Nordfjorden (n = 21, distance = 13.2 km, range = 7-1076 hours). The average progression rate was 0.15 km/h (range = 0.02-0.5 km/h) for the total distance, 0.2 km/h (range = 0.01-1.6 km/h) in Beiarfjorden, and 0.8 km/h (range = 0.01-2.0 km/h) in Nordfjorden. The average progression rate in bl/sec was 0.06 bl/sec (range = 0.01-0.2 bl/sec) for the total distance, 0.07 bl/sec (range = 0.007-0.7 bl/sec) in Beiarfjorden, and 0.4 bl/sec (range = 0.009-0.9 bl/sec) in Nordfjorden.

Effect of biological characteristics on progression rate for the total distance
There were two equally well fitted models (Δ AICc < 2) for the progression rate for the total distance (line T2-T9). Body length was included in both models, condition factor in none of the models and estuary exit date in one of the models. Conditional model averaging showed that neither body length nor estuary exit date had standard errors exceeding the coefficient. Body length had the strongest influence on progression rate, followed by estuary exit date (figure 9). The positive coefficients suggests that a longer body length and a later estuary exit date resulted in a higher progression rate for brown trout for the total distance.

Effect of biological characteristics on progression rate in Beiarfjorden
There were two equally well fitted models (Δ AICc < 2) for the progression rate in Beiarfjorden (line T2-T4). Body length was included in none of the models, condition factor in three models and estuary exit date in two models. Conditional model averaging showed that both body length and estuary exit date had standard errors exceeding the coefficient. For condition factor, the standard errors did not exceed the coefficients (figure 9). The positive coefficient suggests that a higher condition factor resulted in a higher progression rate for brown trout in Beiarfjorden.

Effect of biological characteristics on progression rate in Nordfjorden
There was one single model only including body length (AICc = 59.5) that was the best fit for predicting progression rate in Nordfjorden (line T4-T9). The standard errors for body length did not exceed the coefficient (figure 9). Body length was therefore found to have a strong influence on progression rate. The positive coefficient suggests that a longer body length resulted in a higher progression rate for brown trout in Nordfjorden.

a)

b)
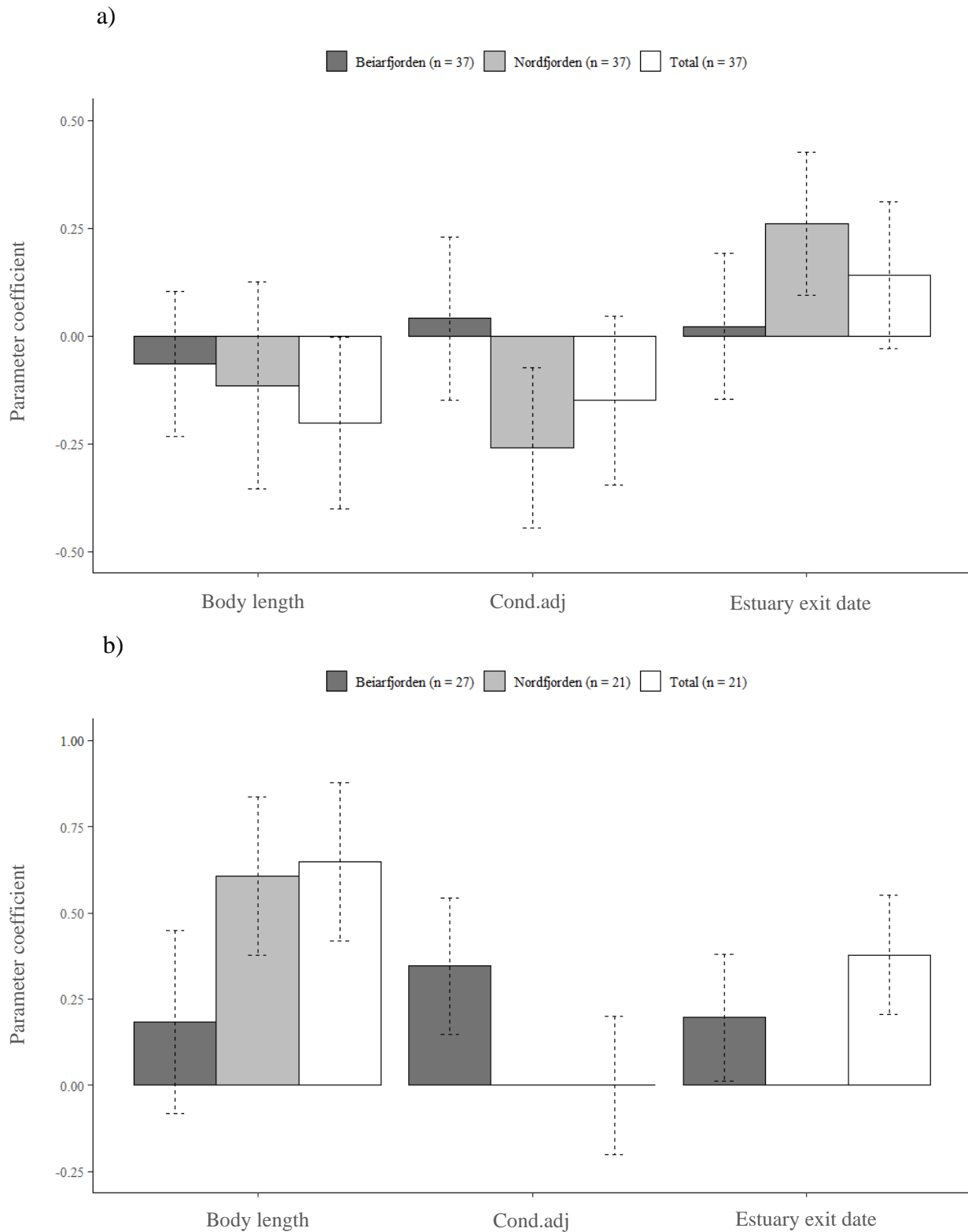
Figure 9. Estimated influence of body length, relative condition factor (cond.adj) and estuary exit date on the progression rate of Atlantic salmon (a) and brown trout (b) in Beiarfjorden, in Nordfjorden and for the total distance. Dark grey bars show Beiarfjorden (T2-T4), light grey bar show Nordfjorden (T4-T9), and white bar show the total distance (T2-T9). A positive coefficient means that the parameter in question has a positive relationship with progression rate. Dotted lines show the standard error of each coefficient. Parameters with a zero-value was not found to be included in any models or in conditional model averaging for the fjord section in question.

DISCUSSION

This study investigated the early marine migration behaviour of Atlantic salmon post-spawners and brown trout veteran migrants as they migrated from the same river in spring. Despite choosing mainly the same migration route, brown trout spent on average far more time within the fjord system compared to Atlantic salmon. Both species were found to start their marine migration from the estuary exit mainly at falling tide. From the estuary exit, the salmon had a fast, continuous progression through the fjord system as they headed towards the open ocean. Brown trout on the other hand, had larger intraspecific differences in progression rate, where some individuals migrated through the fjord in just a couple of days, some spent several weeks, and some never reached the fjord system exits at all. For Atlantic salmon, no correlation was detected between body length and progression rate. Estuary exit date and condition factor was found to be correlated with the progression rate of Atlantic salmon in just the outer fjord system. For brown trout, body length was correlated with the progression rate in the outer fjord system, condition factor in the inner fjord system, and estuary exit date for the total distance.

The fjord system had two exits towards the open ocean, where one exit was far more popular than the other. All the tagged Atlantic salmon exited the fjord system and took the northern route through Nordfjorden. Most brown trout that exited Beiarfjorden chose, like Atlantic salmon, mainly the northern route. Adult Atlantic salmon are thought to navigate back to their home river based on learning cues of area-characteristics imprinted during outward migration as smolts (Hansen *et al.*, 1993). During outward migration, Atlantic salmon smolts have been observed to actively use preferred migration routes, not necessarily aligning with the most direct routes to their ultimate destination (Newton *et al.*, 2021). If the northern route has area characteristics making it preferable to a migrating salmon smolt, the fish might later have used this same route as a post-spawner. An exclusive route preference in a fjord with two exits has been observed for both brown trout smolts and veteran migrants in a Danish fjord system (Kristensen *et al.*, 2018a; 2019). They suggested an inherited preference due to a historical lack of a secondary exit. The fjord system in the present study has historically always had two exits, suggesting that other factors influence the choice of route. A possible explanation for the preference of the northern route of the brown trout veterans might instead be unfavourable conditions in the south. Healy *et al.* (2017) observed route-specific survival in rainbow trout smolts, where fish that chose some specific routes had higher survival and migration rates than others. The southern fjord section in the present study could have ingoing surface currents, high densities of predators and parasites, and/or low densities of prey species, making the northern areas around Nordfjorden preferable. Route preference might also shift from one year to another, as was observed by Aldven *et al.* (2015), suggesting that preference could change with changing conditions.

The migration of Atlantic salmon post-spawners and brown trout veteran migrants overlapped in space, but not to a large degree in time. The reason for a large overlap in space was the preference of both species towards a single fjord system exit, along with the high proportion of brown trout migrating long distances from the river. The proportion of brown trout long-distance migrants was higher in this study compared to previous studies (Eldøy *et al.*, 2015; Bordeleau *et al.*, 2018; Atencio *et al.*, 2021). The optimal temperature for growth in brown trout

is reported to be between 12 °C and 17 °C (Elliott & Hurley, 2000; Larsson, 2005). The temperature-measurements in the inner- and middle fjord system revealed temperatures staying below 12.5 °C during the full course of 2019, and rarely exceeding 11 °C in the inner part of Beiarfjorden. The long-migrating trout could therefore have been moving towards higher water temperatures favourable for growth (Jensen *et al.*, 2014). The brown trout spent on average more than 20 times the number of hours in progressing the total distance from the estuary to the fjord system exit compared to Atlantic salmon. Despite the two species having overlapping estuary exit dates, the time they spent together in the fjord was short. To my knowledge, this is the first study investigating overlap in time and space between Atlantic salmon post-spawners and brown trout veteran migrants. The result of overlapping migrations in space but not in time suggests a limited competition between the two species in the adult life stage during early marine migration from Beiarelva.

Most Atlantic salmon and brown trout left the estuary at falling tide. A preference for migrating from the estuary area at falling tide aligns with the findings of previous studies for both Atlantic salmon post-spawners (Hubley *et al.*, 2008; Hedger *et al.*, 2009) and brown trout veteran migrants (Bendall *et al.*, 2005; Aarestrup *et al.*, 2015). Leaving the estuary at falling tide would enable the fish to use outflowing tidal currents to assist migration. A fast progression upon leaving the river would help the fish to quickly escape the estuary, an area often characterized by salmonid predators such as harbour seals (*Phoca vitulina*) (Carter *et al.*, 2001; Middlemas *et al.*, 2006; Wright *et al.*, 2007). Previous studies have explained intraspecific variation in progression rate with different exploitation of tidal currents (Hansen *et al.*, 1993; Halttunen *et al.*, 2009). However, if this were the case in this study, it would be reasonable to expect the effect to be most profound in Beiarfjorden, closer to the river mouth. Instead, the progression rate of both species was higher in Nordfjorden than in Beiarfjorden. Moreover, progression rate measures the pace of a fish relative to the ground. Without measuring the effects of water transport, it is difficult to say to what extent tidal cycles contributed to differences in progression rate. I therefore suggest future studies consider the effects of water transport in the upper water layer when investigating the influence of tidal cycles on progression rate. One could, for instance, use current meters at different locations in the study area to measure how water velocity changes with different geography, wind patterns, and proximity to the river.

The Atlantic salmon spent on average 37 hours progressing through the fjord system. The average progression rate observed in the present study aligned with the findings of Hedger *et al.* (2009) from Gaspe Bay, was lower than in Halttunen *et al.* (2009) in the Alta fjord, and higher than the progression rates observed by Hubley *et al.* (2008) in Moshers Bay. These comparisons show varying progression rates between different populations of Atlantic salmon post-spawners. A possible explanation for these differences might be the geography and environment of the study sites. Higher salinities have been associated with accelerated migration in Atlantic salmon smolts (Hedger *et al.*, 2008; Martin *et al.*, 2009; Thorstad *et al.*, 2012). The higher salinities in the Alta fjord compared to the other studies, including the present study, might explain the higher progression rates. Moreover, different geography and depth between the systems will likely result in differences in surface currents and consequently movement speed in the upper water layer.

A later estuary exit date and a lower condition factor indicated in a higher progression rate of Atlantic salmon in the outer fjord system. Hedger *et al.* (2009) similarly concluded that migration speed in Atlantic salmon post-spawners was dependent on the departure time from the estuary area. A positive relationship between a later departure time from the estuary and progression rate could be explained by an extended stay in the estuary area, a phenomenon found among several other Atlantic salmon populations (Cunjak *et al.*, 1998; Hubley *et al.*, 2008; Lacroix, 2013; Bordeleau *et al.*, 2019). An extended period spent foraging in the estuary area might allow the salmon to improve their physical condition and consequently undertake rapid migration upon sea entry. Moreover, low-conditioned Atlantic salmon could have been feeding within Beiarfjorden after leaving the estuary. Extensive feeding of Atlantic salmon post-smolts immediately after sea entry has been observed in Northern Norwegian populations (Rikardsen *et al.*, 2004). With a difference in feeding opportunities between fjord sections, the low-conditioned fish might have been delayed in Beiarfjorden because of foraging activity, while using Nordfjorden more as a transport stage. A delay in in Beiarfjorden due to foraging activity could explain the lower average progression rate of Atlantic salmon observed in Beiarfjorden compared to Nordfjorden.

Body length did not seem to influence Atlantic salmon progression rate in either of the fjord sections. Longer fish have a higher swimming capacity than shorter fish, using less energy at swimming the same distance in the same amount of time (Schmidt-Nielsen, 1972; Booth *et al.*, 1997). With an active migration of the post-spawning Atlantic salmon through the fjord system, and short- and long individuals having the same progression rate, the shorter fish would have to spend more energy to travel at the same pace. In this respect, it is important to consider that progression is not fully comparable to migration speed, as the fish is unlikely to swim the shortest possible distance between receiver lines (Thorstad *et al.*, 2012). Like in the present study, Hedger *et al.* (2009) found progression rate to be independent of body length in Atlantic salmon post-spawners. There could be unfavourable conditions within the fjord system such as predators and/or parasites that give an incentive to smaller fish to quickly head towards the open ocean, but this remains speculative.

The brown trout had a lower average progression rate compared to Atlantic salmon, but some individuals were much faster than others. The average progression rate of brown trout veteran migrants in the present study was slightly higher than the progression rates observed by Aldven *et al.* (2015) in Himleån, but far higher than the ones found by Aarestrup *et al.* (2015) in the Randers fjord. The higher progression rates in the present study compared to the other studies can be largely attributed to the fast migration of long-distance migrants in Nordfjorden, where some individuals had progression rates comparable to those of Atlantic salmon. A fast, continuous progression with increased proximity to the sea has also been observed in brown trout veterans in two Danish rivers (Kristensen *et al.*, 2019). Danish brown trout veterans have previously been proposed to adapt foraging patterns similar to Atlantic salmon in order to optimize growth (Kristensen *et al.*, 2018b). A similar migration pattern would mean a fast, continuous progression to an area outside the fjord system. The fast, long-distance migrating brown trout in the present study could, like the Danish trout, be using the outer fjord system more as a transport stage towards areas with higher water temperatures and preferable feeding grounds.

The long-distance brown trout migrants were found to be larger than short-distance migrants. The phenomena of brown trout having longer migration distances with increasing body size has been observed in other fjord systems (Jensen *et al.*, 2014; Jonsson & Jonsson, 2014; Eldøy *et al.*, 2021). Brown trout is a gape-limited predator, where larger fish often become mainly piscivorous (Klemetsen *et al.*, 2003; Davidsen *et al.*, 2017). Larger, pelagic fish are most often found in the outer parts of fjord systems and have been shown to be a considerable part of the diet of large anadromous brown trout (Knutsen *et al.*, 2001; Rikardsen & Amundsen, 2005; Rikardsen *et al.*, 2006). The outer-fjord system might therefore have been more attractive to larger fish. The low sample size of short-distance migrants ($n = 7$) might, however, have inflated the effect-size estimation when comparing biological characteristics between groups.

Even though the smallest individuals stayed in the inner fjord, larger long-distance migrants had higher progression rates than smaller ones. The positive correlation between body length and progression rate was only detected in Nordfjorden and for the total distance, suggesting that body length mostly affected long-distance migrants. Body length has been observed to be positively correlated with both stamina and burst speed in brown trout (Ojanguren & Brana, 2003). Better stamina in fish with longer bodies could potentially result in faster progression. Furthermore, survival in seawater of brown trout is size-dependent due to a larger fish having lower risk of being eaten by predators (Wagner *et al.*, 1969; Finstad & Ugedal, 1998; Ugedal *et al.*, 1998; Klemetsen *et al.*, 2003; Jonsson & Jonsson, 2006). A lower predation risk might enable large brown trout to engage in less predator avoidance behaviour compared to smaller individuals, and consequently progress faster to preferred areas.

Condition factor was positively correlated the progression rate of brown trout in the inner fjord system, but had no influence on migration distance. The 27 individuals that reached the exit of Beiarfjorden consisted mostly of long-distance migrants (26/27). Winter-depleted brown trout can have a period of compensatory growth when starting to feed upon entering the sea (Johnsson & Bohlin, 2005). The best-conditioned trout among long-distance migrants in the present study may not have needed to recondition right away, and instead progressed faster to the outer fjord system compared to low-conditioned individuals. Previous studies have found that brown trout with poor body condition ventured further from the river compared to their better conditioned congeners (Eldøy *et al.*, 2015; Bordeleau *et al.*, 2018; Eldøy *et al.*, 2021). This correlation was not found among the fish in this study. Eldøy *et al.* (2021) observed that brown trout with lower condition factor tended to have riskier migration behaviour in terms of migrating further and spending more time at sea. They hypothesized that low-conditioned individuals would have more to gain from migrating longer distances. The results from the present study suggests that the risk-reward ratio of brown trout from Beiarelva looks different from that of Eldøy *et al.* (2021). Risk factors such as a high density of predators and/or parasites in the outer fjord-system, might have made the risk of migrating outside of Beiarfjorden for low-conditioned individuals high.

In a northern Norwegian fjord, the environmental conditions are likely to change considerably during May and June. During these two months, the estuary exit dates in the present study varied with 51 days for Atlantic salmon and 35 days for brown trout. The mean water temperature in the estuary during the first week of May was 2 °C higher compared to the last week of June. In

several poikilothermic fish species, white muscles have been found to be recruited at lower swimming speeds in lower water temperatures, resulting in reduced maximum sustainable swimming speeds (Rome *et al.*, 1990; Taylor *et al.*, 1996; Hvas *et al.*, 2017). The positive correlation between estuary exit date and progression rate in both species might therefore have been a result of higher temperatures at later dates causing higher swimming speeds, and consequently higher progression rates. It is also possible that changes in water temperature over time brought changes in prey-composition at different locations, and therefore differences in time spent feeding between different fjord sections (e.g., Jensen *et al.*, 2014).

The example of water temperature being a possible cause of the detected correlation between estuary exit date and condition factor illustrates an important point. A correlation found in a model is not necessarily the same as a direct effect. Using parametric regression models with low sample sizes to explain a biological phenomenon is a simplification of reality, and must be treated as such. Hence, correlations between migration behaviour and biological characteristics should be investigated and discussed alongside environmental variables. The present study discussed correlations between migration behaviour and biological characteristics alongside water temperature, salinity and tidal currents. Previous studies have found correlations between migration behaviour and photoperiod in Atlantic salmon and brown trout smolts (Hedger *et al.*, 2008; Aldven *et al.*, 2015; Vollset *et al.*, 2017). Photoperiod was not included in this study due to there being midnight-sun during June, July, and August. Without measuring the actual light intensity, it was difficult to categorize fish registrations in relation to the photoperiod. I therefore suggest measuring light intensity in future studies investigating marine migration behaviour of Atlantic salmon post-spawners and brown trout veterans.

Norwegian legislation regarding management of anadrome salmonids addresses Atlantic salmon and brown trout as a single unit, and does not reflecting their different population dynamics and life histories (Lakse- og innlandsfiskloven, 1992; Birnie-Gauvin *et al.*, 2019). Norway holds approximately 25% of the world's healthy Atlantic salmon populations, giving the Norwegian government a particular responsibility in protecting the species (Anon, 2006-2007; Hindar *et al.*, 2011). Consequently, the salmon tends to be prioritized in management over other anadrome salmonid species. For instance, one of the major efforts to combat negative anthropogenic impacts on Norwegian salmonid populations, the national salmon fjord program, is designed specifically for Atlantic salmon (Anon, 2006-2007). This study found that Atlantic salmon post-spawners from Beiarelva spent on average 37 hours in the fjord system. Consequently, conservation efforts in the coastal area would need to be effective in protecting each individual for a few days. The brown trout veterans, however, used on average several weeks in reaching the fjord system exit, and some never left the fjord system at all. Spending more time within the fjord system likely gives the brown trout population a higher exposure to negative anthropogenic impacts in coastal areas compared to Atlantic salmon. Specific examples include recreational fishing and exposure to pathogens from open-cage aquaculture, where the latter have been shown to pose a higher risk for anadromous brown trout than for Atlantic salmon (Grefsrud *et al.*, 2018). The brown trout in this study, however, spent far more time in progressing through the inner fjord compared to the outer fjord. No fish-farming facilities are located within the inner fjord, potentially limiting the negative impacts from aquaculture on brown trout veterans from Beiarelva.

Individual biological characteristics affected early migration behaviour in terms of progression rate differently in Atlantic salmon post-spawners and brown trout veteran migrants. Horodysky *et al.* (2015) stated that a species-specific understanding of the link between behavior and physiological abilities in fish could help improve stock assessments and describe essential habitats. This thesis has taken an important step in that direction by describing migration behavior in two salmonid species and identifying underlying mechanisms worthy of further investigation. When we delve into the drivers behind migration behavior, we begin to realize how changes in the biology of each species may result in very different outcomes. In management terms, negative anthropogenic impacts might change the population dynamics of Atlantic salmon post-spawners and brown trout veterans from Beiarelva in similar ways, while still influence temporal habitat use differently. To exemplify, a change in body size composition of the two salmonid populations in Beiarelva, due to size selective fishing, could potentially alter the marine area use of the brown trout population entirely, while not affecting the Atlantic salmon at all.

In conclusion, the present study found that the early marine migration of Atlantic salmon post-spawners and brown trout veterans from the river Beiarelva overlapped in space, but not to a large degree in time. Brown trout had larger intraspecific differences in progression rate and spent more time in the fjord system compared to Atlantic salmon. The short temporal overlap during early marine migration from Beiarelva, suggested a limited competition between the two species in this migration phase. Using more time within the fjord system likely gives the brown trout a higher exposure to negative anthropogenic impacts in coastal areas compared to Atlantic salmon. Body length, condition factor and estuary exit date was found to influence progression rate differently in Atlantic salmon post-spawners and brown trout veteran migrants. The differences in how individual biological characteristics were correlated with progression rate, illustrates how population dynamics in Atlantic salmon post-spawners and brown trout veterans could change in similar ways, while still influence temporal habitat use differently. The findings in this study underline the importance of conceiving more focused conservation strategies, better aimed at protecting each individual species and not treating them as a single unit.

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APPENDIX 1

Table A1. *Biological characteristics of Atlantic salmon tagged in the spring of 2019. Sex and species were DNA-confirmed using adipose fin samples.*

Transmitter ID	Condition factor (k)	Sex	Body length (mm)	Age (yrs.)	Body mass (g)
A69-1303-5763	0.67	F	820	8	3700
A69-1303-5767	0.61	M	600	5	1320
A69-1303-5768	0.60	F	800	9	3050
A69-1303-5769	0.55	F	880	8	3760
A69-1303-5770	0.64	F	1120	9	9000
A69-1303-5771	0.63	F	990	9	6140
A69-1303-5772	0.61	F	890	8	4280
A69-1303-5773	0.53	F	670	6	1600
A69-1303-5776	0.68	F	800	7	3500
A69-1303-5778	0.68	F	1020	10	7200
A69-1303-5780	0.45	F	820	8	2500
A69-1303-5781	0.56	M	580	5	1100
A69-1303-5807	0.61	M	650	6	1720
A69-1303-5809	0.60	M	640	6	1580
A69-1303-5811	0.54	M	640	6	1420
A69-1303-5815	0.54	F	920	8	4200
A69-1303-5816	0.67	M	887	9	4700
A69-1303-5817	0.60	F	890	10	4260
A69-1303-5818	0.63	F	830	9	3600
A69-1303-5819	0.55	F	850	8	3380
A69-1303-5820	0.62	F	840	6	3690
A69-1303-5821	0.67	F	900	8	4900
A69-1303-5822	0.60	F	830	7	3400
A69-1303-5823	0.55	F	960	9	4840
A69-1303-5824	0.60	F	800	8	3080
A69-1303-5825	0.66	F	890	8	4640
A69-1303-5826	0.63	F	995	NA	6220
A69-1303-5827	0.55	F	820	7	3020
A69-1303-5828	0.56	F	610	7	1280
A69-1303-5829	0.61	F	880	8	4160
A69-1303-5830	0.56	F	1010	8	5760
A69-1303-5831	0.60	F	850	8	3680
A69-1303-5832	0.61	F	830	7	3500
A69-1303-5833	0.63	F	960	8	5580
A69-1303-5834	0.58	M	650	6	1580
A69-1303-5836	0.63	F	960	8	5600
A69-1303-5837	0.64	M	1020	10	6800

Table A2. Biological characteristics of brown trout tagged in the spring of 2019. Sex and species were DNA-confirmed using adipose fin samples.

Transmitter ID	Condition factor (k)	Sex	Body length (mm)	Age (yrs.)	Body mass (g)	Distance group
A69-1303-5748	0.76	F	430	7	600	short
A69-1303-5749	0.68	F	420	9	500	short
A69-1303-5750	0.80	M	390	6	450	short
A69-1303-5751	0.76	F	390	8	450	long
A69-1303-5756	0.61	M	340	7	240	long
A69-1303-5757	0.73	M	380	7	400	long
A69-1303-5758	0.70	F	420	8	520	long
A69-1303-5759	0.84	M	350	8	360	short
A69-1303-5760	0.97	M	340	7	680	short
A69-1303-5761	0.80	M	410	6	550	long
A69-1303-5764	0.96	M	630	9	2400	long
A69-1303-5765	0.75	M	520	9	1060	long
A69-1303-5774	0.80	M	500	6	1000	long
A69-1303-5777	0.47	M	440	8	400	long
A69-1303-5782	0.75	M	650	9	2060	long
A69-1303-5784	0.74	M	560	7	1300	short
A69-1303-5785	0.83	M	510	7	1100	long
A69-1303-5795	0.85	M	730	9	3320	long
A69-1303-5796	0.60	F	670	10	1800	long
A69-1303-5797	0.79	M	590	7	1620	long
A69-1303-5798	0.87	M	530	8	1300	long
A69-1303-5799	0.71	F	540	8	1120	long
A69-1303-5800	0.98	M	680	14	3080	long
A69-1303-5801	0.82	M	550	10	1360	long
A69-1303-5802	0.91	M	500	9	1140	short
A69-1303-5804	0.83	M	640	8	2180	long
A69-1303-5805	0.93	F	660	10	2680	long
A69-1303-5806	0.77	M	660	12	2220	long
A69-1303-5808	0.82	F	650	12	2240	long
A69-1303-5810	0.83	M	540	7	1300	long
A69-1303-5812	0.66	F	440	8	560	long
A69-1303-5814	0.91	M	540	8	1440	long
A69-1303-5835	0.81	M	530	8	1200	long

Table A3. Deployed receivers in the Beiarn fjord system and in the Beiarn river. Receivers marked in grey was lost. If replaced, the replacement receivers are listed underneath the lost receiver with new deployment date and same position. VR2AR receivers were equipped with an integrated acoustic release system. VR2W* receivers were equipped with an external acoustic release system

Station no.	Deployment date	Deployment lat.	Deployment long.	Bottom depth (m)	Rope length (m)	Instrument depth (m)	Model	Serial no.
1	26.03.2019	67.08899	14.04654	40	35	5	VR2W	119128
2	26.03.2019	67.08606	14.04690	50	5	45	VR2AR	548213
3	26.03.2019	67.08291	14.04828	35	30	5	VR2W	119137
4	26.03.2019	67.01849	14.22641	20	5	15	VR2AR	548214
5	26.03.2019	67.01730	14.23351	48	5	43	VR2AR	548215
6	26.03.2019	67.01641	14.23922	22	5	17	VR2AR	548211
7	26.03.2019	67.05934	14.25210	35	5	30	VR2AR	548216
8	26.03.2019	67.05782	14.24532	30	5	25	VR2AR	548218
9	27.03.2019	67.11172	14.27573	27	22	5	VR2W	119119
9	25.02.2020	67.11172	14.27573	35	5	30	VR2AR	547127
10	27.03.2019	67.11449	14.26887	211	181	30	VR2W*	119090
11	27.03.2019	67.11723	14.26330	350	320	30	VR2W*	119139
12	27.03.2019	67.11704	14.25364	225	195	30	VR2W*	119133
13	27.03.2019	67.11768	14.24712	65	60	5	VR2W	119140
13	25.02.2020	67.11768	14.24712	30	5	25	VR2AR	547128
14	27.03.2019	67.16911	14.32802	19	14	5	VR2W	119129
15	06.05.2019	67.17093	14.32141	117	87	30	VR2W*	119130
16	06.05.2019	67.17216	14.31275	117	87	30	VR2W*	119132
17	06.05.2019	67.17275	14.30366	120	90	30	VR2W*	119125
19	27.03.2019	67.17174	14.29448	112	107	5	VR2W	119123
20	27.03.2019	67.17210	14.28522	50	45	5	VR2W	119149
21	27.03.2019	67.07649	14.30353	28	5	23	VR2AR	548212
22	27.03.2019	67.07690	14.30611	26	5	21	VR2AR	548217
23	01.05.2019	67.06757	14.52788	55	5	50	VR2AR	547923
24	01.05.2019	67.06969	14.52972	105	5	5	VR2AR	547922
25	01.05.2019	67.04239	14.58405	25	5	20	VR2AR	547126
26	01.05.2019	67.04322	14.58713	27	5	23	VR2AR	547122
27	01.05.2019	67.04403	14.59172	21	5	30	VR2AR	547125
28	01.05.2019	67.04528	14.59680	25	5	20	VR2AR	547123
29	01.05.2019	67.04552	14.60157	22	5	17	VR2AR	547124
30	01.05.2019	67.03050	14.57294	3	1	2	VR2W	119078
31	01.05.2019	67.00123	14.62489	3	1	2	VR2W	119136
39	28.03.2019	67.09359	14.24049	10	5	5	VR2W	119077
40	26.03.2019	67.06882	14.07683	108	103	5	VR2W	119124
41	26.03.2019	67.06403	14.09761	96	91	5	VR2W	119121
42	26.03.2019	67.02715	14.12420	111	5	5	VR2W	119135
43	26.03.2019	67.03683	14.12342	70	65	5	VR2W	119151
44	26.03.2019	67.07355	14.06351	10	5	5	VR2W	119079
45	27.03.2019	67.14435	14.27891	196	5	5	VR2W	119081
46	27.03.2019	67.13739	14.26586	196	191	5	VR2W	119134
47	27.03.2019	67.10777	14.26984	355	5	5	VR2W	119114
49	27.03.2019	67.18774	14.39462	79	5	5	VR2W	119127