

Nanna Norderud

# River migration of sea trout *Salmo trutta* in River Beiarelva, Northern Norway

Master's thesis in Natural Science with Teacher Education  
Supervisor: Jan Grimsrud Davidsen  
Co-supervisor: Sindre Håvarstein Eldøy  
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Norwegian University of Science and Technology  
Faculty of Natural Sciences  
Department of Biology



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*Nanna Norderud*

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# Abstract

Sea trout (*Salmo trutta*) return to the river for spawning and often also for overwintering, and unsuccessful river migration can threaten the population viability. The present thesis investigated the river migration of 44 veteran sea trout in River Beiarelva in Northern Norway. The sea trout were tracked for one year (August 2020 - August 2021), with main focus on the autumn migration in 2020. Acoustic telemetry was used to assess individual migration patterns between the tidal influenced stretch and the upstream freshwater stretch of the river. Individual's total body length, body condition factor and sex were linked to behavioural metrics to evaluate if these characteristics could explain the observed behaviour.

Upstream migrants entered the freshwater stretch above the tidal zone between 19 August and 28 September, consistent with the peak of upstream migrants in other northern sea trout populations. From August to December, the sea trout spent on average significant less time in the upstream freshwater zone of the river (mean = 41 days) than in the tidal influenced zone (mean = 55 days). The majority of the tagged sea trout (75%) entered the upstream freshwater stretch, probably for spawning. Larger sea trout, sea trout in better body condition and males, in particular, were more likely to enter freshwater than smaller individuals, individuals in poorer body condition and females. This could likely be explained by a higher proportion of immature individuals among the smaller sea trout, sea trout in poorer body condition and, particularly, among females.

The downstream migration from the upstream freshwater stretch to the tidal influenced waters occurred mainly between 2 October and 21 November ( $n = 22$ ), although six sea trout descended over winter (December – April). The relatively shorter freshwater residence suggest that the tidal zone is a favourable habitat to reside in between August and December, likely due to unfavourable conditions in the upstream freshwater stretch and/or better growth opportunities in the tidal influenced stretch. Sea trout were detected on all receivers deployed in the anadromous stretch of the river, except the receiver deployed farthest upstream in the tributary Tollåga. Total body length, body condition factor and sex had limited effects on timing of upstream migration, migratory distance in the river, timing of downstream migration and freshwater residence time, suggesting that other intrinsic or environmental factors, not included in this thesis, could be important for the autumn river migrations of sea trout. This thesis highlights the importance of tidal influenced parts of rivers for sea trout populations, and implies that the species may be especially susceptible to habitat alternations and fishing pressure in the lower parts of rivers.





## Sammendrag

Sjørørret (*Salmo trutta*) vandrer tilbake til elva for gyting og ofte også for overvintring, og forholdene under denne kritiske delen av sjørørretens livsløp er avgjørende for bestandens levedyktighet. Denne oppgaven undersøkte vandringene til 44 sjørørretveteraner i Beiarelva i Nord-Norge. Sjørørreten ble fulgt i ett år (august 2020 – august 2021), med hovedfokus på vandringsatferden i elva høsten 2020. Akustisk telemetri ble brukt for å undersøke individuelle vandringsmønstre mellom den tidevannspåvirkede strekningen og elvestrekningen oppstrøms tidevannssonen. Individenes kroppslengde, kondisjonsfaktor og kjønn ble knyttet til deres atferd for å vurdere om disse karakteristikkene kunne forklare den observerte atferden.

Sjørørreten gikk opp i elvestrekningen over tidevannssonen mellom 19. august og 28. september, i samsvar med tidsperioden for oppvandring i tidligere studier på andre nordlige sjørørretbestander. Fra august til desember tilbrakte sjørørreten i gjennomsnitt signifikant kortere tid i elva oppstrøms tidevannssonen (gjennomsnitt = 41 dager) enn i tidevannssonen (gjennomsnitt = 55 dager). Majoriteten av de merkede sjørørretene (75%) gikk opp i ferskvannsstrekningen, trolig for å gyte. Større sjørørret, sjørørret i bedre kondisjon og spesielt hannfisk hadde større sannsynlighet for å gå opp i ferskvann enn mindre individer, individer i dårligere kondisjon og hunnfisk. Dette kan sannsynligvis forklares med en høyere andel umodne individer blant de mindre sjørørretene, sjørørretene i dårligere kondisjon og spesielt blant hunnfisk.

Nedvandringen fra elvestrekningen oppstrøms tidevannssonen til tidevannssonen foregikk hovedsakelig mellom 2. oktober og 21. november ( $n = 22$ ), men seks individer vandret ned over vinteren (desember – april). Den relativt korte oppholdstiden i ferskvann tyder på at tidevannssonen er et gunstig habitat å oppholde seg i mellom august og desember, sannsynligvis på grunn av ugunstige forhold i elvestrekningen oppstrøms tidevannssonen og/eller bedre vekstmuligheter i tidevannssonen. Sjørørret ble registrert på alle lyttestasjoner i anadrom strekning av elva, bortsett fra lyttestasjonen plassert lengst opp i sideelva Tollåga. Kroppslengde, kondisjonsfaktor og kjønn hadde begrensede effekter på tidspunktet for oppvandring, vandringsdistanse i elva, tidspunktet for nedvandring og oppholdstid i elva oppstrøms tidevannssonen, noe som tyder på at andre iboende eller miljømessige faktorer, som ikke var inkludert i denne oppgaven, kan være viktige for sjørørretens elvevandring om høsten. Denne oppgaven fremhever betydningen av elvers tidevannspåvirkede områder for sjørørretbestander og foreslår at arten kan være spesielt sårbar for habitatendringer og fisketrykk i de nedre delene av elva.



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# 1 Introduction

The brown trout (*Salmo trutta*) is a remarkable species in terms of having a worldwide distribution and highly diverse life-history strategies (Klemetsen *et al.*, 2003). The species is greatly valued for social and economic reasons, particularly as a resource for recreational angling (Butler *et al.*, 2009; Liu *et al.*, 2019). Brown trout can be either freshwater resident or anadromous, the latter form commonly termed sea trout. Being anadromous, sea trout spawn in freshwater and migrate to estuarine and coastal waters for feeding and growth. Anadromy is a life-history strategy governed by trade-offs between better growth opportunities and increased mortality risks at sea (Thorstad *et al.*, 2016). Consequently, there is a fine-tuned balance between timing and duration of marine migrations versus freshwater residence, where the most beneficial strategy varies within and among populations. What governs the migration from freshwater to marine areas have been extensively studied (Thorstad *et al.*, 2016; Jensen *et al.*, 2019; Eldøy *et al.*, 2021), whereas the determinants of the return to freshwater is more poorly understood. Sea trout return to freshwater for spawning and/or overwintering (Klemetsen *et al.*, 2003). During the river migration sea trout face several challenges, such as passing of obstacles and waterfalls, altered water temperatures and increased predation risk during periods of low water levels (Jonsson & Jonsson, 2009). If upstream migration is not successfully undertaken, it may influence the population recruitment and viability. Hence, the upstream migration marks a critical phase in sea trout life history.

The returning sea trout are defined as veteran migrants and consist of both immature and mature individuals (Thorstad *et al.*, 2016). Veteran sea trout typically return to freshwater during summer and autumn, and often to their river of origin (Klemetsen *et al.*, 2003). However, sea trout from smaller rivers may spend winter months in neighbouring larger watercourses providing better conditions for overwintering (Aldvén & Davidsen, 2017). The timing of upstream migration varies considerably within and among populations (Thorstad *et al.*, 2016). In Norwegian sea trout populations, upstream migration has been reported in all months between April and December, but a peak of upstream migrants is usually seen in August and September (Jensen, 1968; Berg & Berg, 1989; Jonsson & Jonsson, 2002).

The timing of upstream migration may depend on local environmental conditions as well as individual status such as size, sex, age, and energy stores. Upstream migration can be initiated by water flow and sometimes water temperature, particularly early in the season and in small streams (Jonsson & Jonsson, 2002; Jonsson & Jonsson, 2009). The general perception is that water flow influences upstream migration through enabling passing of obstacles and waterfalls (Jonsson, 1991), as well as decreasing the visibility to predators (Abrahams & Kattenfeld, 1997). In some rivers, the timing of upstream migration seems to vary with size and sex, where larger sea trout and males ascend earlier than smaller sea trout and females (Jensen, 1968; Berg & Berg, 1989). However, other studies report no trend in timing of upstream migration with size and sex (Jonsson & Jonsson, 2002).

The duration of freshwater residence and timing of downstream migration varies greatly within and among rivers. Some sea trout return to estuarine or marine waters

immediately after spawning season, whereas others remain in freshwater for weeks or months (Berg & Berg, 1989; Jensen & Rikardsen, 2008; Östergren & Rivinoja, 2008). In a Danish river, residence time in freshwater ranged between 2 and 163 days with mean residence time of 70 days (Aarestrup & Jepsen, 1998). In the study there was no significant difference in residence time between females and males, and residence time did not correlate with size. Sea trout in an English river entered estuarine and coastal waters after 4 to 70 days in freshwater following spawning (Bendall *et al.*, 2005). The English study also found no relationship between residence time in freshwater and sex, but larger individuals descended earlier than smaller individuals. Most sea trout in the north Norwegian River Vardnes resided in freshwater during winter, and males spent more time in freshwater and descended the river later than females (Berg & Berg, 1989). On the contrary, sea trout from River Skibotn in Northern Norway descended to estuarine waters shortly after spawning, where they stayed for a long period during winter (Jensen & Rikardsen, 2008). The great variation in timing of downstream migration and duration of freshwater residence is assumed to depend on river conditions as well as differences in growth opportunities and mortality risks in freshwater and marine habitats (Berg & Berg, 1989; Jonsson & Jonsson, 2002; Jensen & Rikardsen, 2008).

During the last decades, sea trout stocks in many countries have declined (ICES, 2013) and the same trend is seen in Norway (Anon, 2019). Several southern and western Norwegian populations are in poor state, whereas north Norwegian populations currently are in better states. However, this could rapidly change with the expansion of warmer water and aquaculture northwards (Vollset *et al.*, 2021). In Norway, the far largest negative impact on sea trout populations is that of salmon lice (*Lepeophtheirus salmonis*), followed by agriculture, hydropower regulations, road crossing, overexploitation and habitat alternations, respectively (Anon, 2019). Sea trout faces several of these threats upon their return to freshwater. The river migration plays a crucial role in the sea trout life-history as sea trout return to freshwater to spawn and/or overwinter. However, the migratory behaviour may vary greatly within and among populations, calling for local management strategies focused on the plasticity in individual migratory behaviour. Knowledge on when and where sea trout reside during river migration allows for focused management strategies aiming at protecting sea trout in the critical phase of this part of their life, as well as conserving important river habitats utilized by sea trout. Implementation of such strategies can sustain a coexistence of healthy sea trout populations and the social and economic interests of recreational angling.

The objective of this study was to describe river migration behaviour of veteran sea trout in River Beiarelva, Northern Norway, with main focus on the autumn migration. Acoustic telemetry and sampling of individual physiological characters (total body length, body mass, sex and number of seasons at sea) were combined to quantify variation in the migration patterns. The migratory behaviours investigated were 1) decision to migrate upstream, 2) timing of upstream migration, 3) migratory distance in the river, 4) timing of downstream migration and 5) residence time in freshwater. Individuals' total body length, body condition factor and sex were linked to the behavioural metrics to evaluate if these characteristics could explain the observed behaviour. Knowledge provided by this study will be useful for development of effective management strategies focusing on the river phase of sea trout veterans.

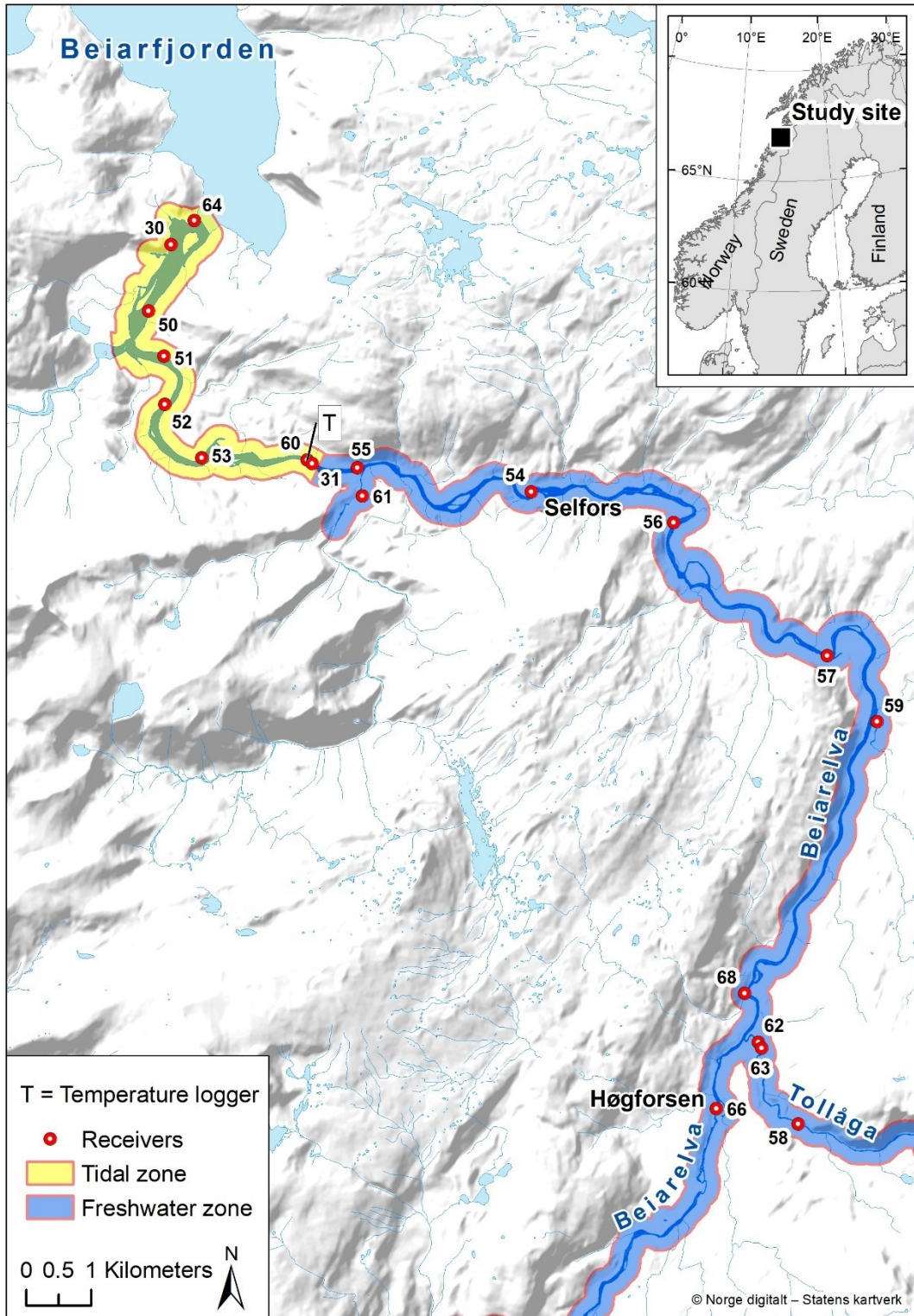
## 2 Materials and methods

### 2.1 Study site

This study was conducted in Beiarelva water course (Figure 1), Nordland County, Norway from August 2020 to August 2021, with main focus on the period from August to December 2020. River Beiarelva drains from glacial areas north of the glacier Svartisen to the innermost part of the fjord Beiarfjorden (Holmqvist, 2004). The total river length measures 63.44 km and the watercourse has a natural catchment area of 1065 km<sup>2</sup> (NVE, 2021). The first seven km of the river is influenced by tide (Hellen *et al.*, 2016). The anadromous stretch consists of the 27 km from the river mouth to Høgforsen waterfall and connects to several tributaries and streams. Several potential spawning grounds are found on the anadromous stretch, including a large one located in Tollåga (Hellen *et al.*, 2016). The total productive area of the anadromous stretch is approximately 1.16 mill m<sup>2</sup> (Hellen *et al.*, 2016). Sea trout were captured in the estuarine areas of Beiarelva. The fish were subsequently tracked by acoustic receivers from the river mouth to Høgforsen approximately 27 km upstream, covering the entire anadromous stretch. In addition, receivers were deployed approximately 2 km upstream the tributary Tollåga (approximately 28 km from river mouth; Figure 1).

Due to the discharge of cold glacial waters from glacier Svartisen, the water temperatures of Beiarelva are low throughout the year (Davidsen *et al.*, 2020). However, owing to regulations for hydropower purposes in the 1960's and in 1993 the water temperatures have increased (Hellen *et al.*, 2016), presumably providing better growth conditions for Atlantic salmon (*Salmo salar*) and brown trout (Davidsen *et al.*, 2020). In particular, the transfer of water in 1993 from the upper parts of Beiarelva to Lake Stor-Glomvatnet in Meløy municipality have contributed to an increase in water temperature during summer (1.1 °C by Selfors and 0.4 °C above Tollåga) as well as a decrease in water flow from spring to autumn as less cold glacial water is fed into the river (Hellen *et al.*, 2016). The mean water flow have been 33 m<sup>3</sup>s<sup>-1</sup> at Selfors after 1993 (Holmqvist, 2004).

Beiarfjorden is a deep, narrow fjord covering a waterway of 18 km from the river mouth of Beiarelva to Kjellingstraumen bridge. Most of the fjord is deeper than 100 meters, but two shallow areas are found in the estuarine areas and in the fjord exit by Kjellingstraumen bridge. By Kjellingstraumen, Beiarfjorden divides into two fjord systems; Holmsundfjorden and Nordfjorden. Since 2007, Beiarelva and Beiarfjorden has been a protected National Salmon Water course and a protected National Salmon Fjord, with the purpose of protecting wild Atlantic salmon populations from harmful interventions and activities (DKMD, 2006). Owing to this, there are no fish farming facilities within Beiarfjorden, but open-net pen salmon aquaculture is established in the fjord complex outside the protected area.



**Figure 1:** Map of the study site showing the anadromous stretch of River Beiarelva. Colour marking indicate the tidal influenced section of the river (yellow) and the upstream freshwater section of the river (blue). Deployed acoustic receivers are indicated by red circles. "T" denotes the position of the deployed temperature logger.

## 2.2 Water temperature

Water temperature was measured by a datalogger (Star Oddi model DST centi-CT, Reykjavik, Iceland) at receiver 60 in the uppermost part of the tidal zone (Figure 1). The data logger measured the water temperature every fourth hour between 11 August and 9 December (Figure 2). In this period the water temperature ranged between 0.2°C and 12.3 °C, with an overall average of 4.9 °C (SD = 3.4°C). The water temperatures decreased from August to December where average temperatures in August, September, October and November and December combined was 9.4 °C (SD = 1.3°C), 7.0 °C (SD = 1.6°C), 3.9 °C (SD= 3.0°C) and 1.6 °C (SD = 1.0°C), respectively.



**Figure 2:** Water temperatures from August to December 2020 in the uppermost part of the tidal influenced stretch of River Beiarelva. Temperatures were measured at receiver 60 (Figure1) every fourth hour.



## 2.3 Data collection with use of acoustic telemetry

### 2.3.1 Capture, sampling and tagging of sea trout

A total of 50 sea trout were captured, sampled and tagged with internal acoustic transmitters between 11 and 24 August 2020. The sample consisted of veteran migrants, defined as individuals with total body length above 37 cm. All fish were caught in the estuary of River Beiarelva using gillnets. To minimize stress, the nets were monitored continuously, at least every 20 minutes. After capture, the fish were kept in holding nets for up to four hours at the tagging location. Prior to tagging, the fish were anesthetized for three to five minutes in a tarpaulin-covered tub using 15-20 ml Benzoaq Vet (ACD Pharmaceuticals AS, Batch Nr. 18K07) diluted with 100 L water. Cylindrical acoustic transmitters (Vemco, model V13T-1x-BLU-1, 69kHz), measuring 13 mm in diameter, were surgically implanted in the body cavity. An incision of 1.5-2 cm was made in the abdominal cavity and a disinfected transmitter was carefully inserted. The incision was closed with two-three separate sutures (RESORBA Wundversorgung GmbH & Co; 3,0 Resolon). The estimated battery life for the V13T-1x-BLU-1 tags were 33.5 months. The surgical implantation was done by approved personnel to ensure animal welfare.

Immediately after surgical implantation, adipose fin, scale tissue and morphometric measurements were sampled. A small adipose fin clip of approximately 2 mm<sup>2</sup> was sampled and stored in RNA solution for DNA sex and species determination. To determine age and migration history, 10-20 scales were sampled from the posterior end of the fish above the lateral line. The fish were weighed, and total body length was measured. Following sampling, the fish were put in a recovery tank for up to 15 minutes and released to a calm site close to the tagging location. The experimental procedures were approved by the Norwegian National Animal Research Authority (permission number 20/108785).

### 2.3.2 Tracking of sea trout

Movement patterns of tagged sea trout were tracked in River Beiarelva from August 2020 to August 2021 by a total of 19 deployed acoustic receivers (Vemco Inc., Halifax, Canada, model VR2W, 69kHz). The receivers were deployed in the anadromous stretch of the river from the river mouth and approximately 28 km upstream (Figure 1). Each receiver was attached to a concrete block, chained to the shoreline, and submerged to the river bottom. The depth of the river receivers varied between 1 and 2 meters. The receivers were regularly examined during the study period to check battery and download data. Due to ice formation on the river the receivers were removed during winter (9 December 2020 – 29 April 2021). As the main scope of the present study was river migration during autumn, the majority of tracking data included in this study was from 11 August to 9 December 2020, but some data from April to August 2021 was examined and, thus, included.

### 2.3.3 Receiver performance

In acoustic telemetry, the detectability of tagged fish varies depending on the location of deployed receivers, and the detection range of receivers at each deployment site. The detection range of the tags varies with transmitter specifications, ambient background noise and hydrological conditions affecting the propagation of sound waves such as water flow, air bubbles in the water, heavy rain and waves. Consequently, the detection range may vary considerably both on spatial and temporal scales.

Receiver performance was evaluated by estimating the proportion of passing fish that was detected on certain receivers. The receiver performance was evaluated for three receivers (31 and 60 combined, and 55; Figure 1) located in the transition between the tidal influenced stretch of the river and the freshwater stretch of the river. These receivers were considered as important for the behavioural metrics covered in this thesis. Receiver performance was calculated for receiver 31 and 60 combined as they were located only 90 meters apart. In total, 33 sea trout were registered moving from the tidal influenced stretch to the freshwater stretch above this, while 28 fish were registered moving from the freshwater stretch to the tidal influenced stretch. In general, the receiver performance was poorer during downstream than upstream migration for all three receivers, as well as poorer on receiver 55 than on receiver 31 or 60 during both upstream and downstream migration. All fish detected on the receivers further up in the freshwater stretch were detected on receiver 31 or 60 during upstream migration, indicating a 100% detection success. During downstream migration, the detection success on the same two receivers was 57% as only 16 out of 28 fish were detected. The receiver performance on receiver 55 during upstream migration was 91% (30 out of 33 individuals detected), while it was 36% (10 out of 28 individuals) during downstream migration.

The performance differences between receiver 55, 31 and 60 can be explained by differences in river conditions surrounding the receivers and/or differences in swimming behaviour during upstream and downstream migration. Receiver 55 were deployed in a backwater, whereas receivers 31 and 60 were deployed in runs. In addition, receiver 55 was at some point covered in sediments which may have reduced the detection range of the receiver, and consequently the receiver performance. The poorer receiver performance on all three receivers during downstream migration compared to upstream migration is likely caused by increased swimming speed during downstream migration when the fish swim with water currents rather than against.

### 2.3.4 Determination of sex, species and age

Sex and species were genetically determined by analysing the adipose fin clip at the NTNU University Museum DNA lab following methods described in Eldøy *et al.* (2021). Individual age and previous number of marine migrations were determined by analysing fish scales at the NTNU University Museum Microscopy lab. Four – eight of the most readable scales were imprinted on 1 mm Lexan plates using a pressing iron. The imprints were analysed with a camera equipped computer-stereoscope (Leica M165C, camera: Leica MC170 HD, software: Leica Application Suite X, Leica systems, Sankt Gallen, Switzerland). Back calculation of age and number of previous marine migrations were done in accordance with the method described by Dahl (1910) and Lea (1910).

## 2.4 Data analysis

Download of telemetry data from receivers were conducted using the VUE software version 2.7.0 provided by AMIRIX Systems Inc. All statistical analyses were performed in R studio version 1.4.1717 (RStudio Team, 2021) and R version 4.1.1 (R Core Team, 2020).

### 2.4.1 Filtration of tracking data

If several tagged fish are within the detection range of a receiver at the same time, there is a probability that two acoustic signals collide and a third, false signal is recorded (Pincock, 2012). The probability of false detections increases with the number of fish staying in the same area at the same time. This makes frequently used areas more vulnerable to false detections. Filtration of data can remove false detections, although it is unrealistic to eliminate all false detections while retaining a sufficient amount of true detections (Pincock, 2012).

After removal of duplicates and false fish ID's the tracking data consisted of 1150274 detections from the 19 receivers recorded between 11 August 2020 and 12 August 2021. To remove false detections a 30-minute filter were applied to the tracking data, but only for receivers located within the tidal influenced water of the river (below receiver 31, Figure 1). This filter excluded all subsequent detections on the same receivers with a time interval exceeding 30 minutes. Hence, only subsequent detections on the same receiver recorded within a time interval of 30 minutes were included in the filtered data set. For the remaining receivers located above the tidal zone, all initial detections were included because fewer fish were recorded simultaneously on receivers in this part of the river reducing the likelihood of false detections. The filter removed 0.76% of the detections, giving a filtered data set of 1141523 detections.

### 2.4.2 Characteristics of tagged sea trout

Total body length, number of seasons at sea, Fulton's condition factor and sex were included as characteristics of tagged sea trout to describe the study population and as explanatory variables of individual migratory behaviour in statistical analyses (see section 2.4.4 below). Total body length was included as an indicator of an individual's size, whereas Fulton's condition factor reflected the physical body condition of an individual. Number of seasons at sea was used as an age indicator rather than total age as total age could not be estimated for the majority of tagged sea trout.

#### 2.4.2.1 Calculation of Fulton's condition factor

Fulton's condition factor (K) was calculated with the following formula (Ricker, 1975):

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

#### 2.4.2.2 Linear dependence between characteristics of tagged sea trout

Linear dependence was tested for all individual characteristics (total body length, number of seasons at sea, condition factor and sex) using the 'cor.test' function in the 'base' package of R-studio. The condition factor correlated moderately with body length and number of seasons at sea (Pearson correlation;  $-0.5 < r < -0.3$ ,  $p < 0.05$ ), whereas body length and number of seasons at sea correlated strongly (Pearson correlation;  $0.5 < r < 1.0$ ,  $p < 0.05$ ). Number of seasons at sea were excluded as an explanatory variable in the statistical analyses due to the strong correlation with body length but were included in the data analysis to describe the age distribution of the tagged sea trout.

#### 2.4.3 Definitions of migratory behaviours in the river

##### 2.4.3.1 Dividing the river in two zones

Sea trout were tracked during river migration by receivers covering the anadromous stretch of the river (Figure 1). For data analyses, the anadromous stretch was divided in two zones, 1) a tidal zone and 2) a freshwater zone upstream the tidal zone. The tidal zone consisted of the tidal influenced stretch from river mouth (receiver 64) to receiver 60 and 31, approximately 7 km upstream. The freshwater zone consisted of the remaining anadromous stretch, from receiver 55 to receiver 66 and receiver 58, approximately 27 km and 28 km upstream, respectively. Detections on receivers 64, 30, 50, 51, 52, 53, 31 and 60 were assigned to the tidal zone, and detections on receivers 55, 61, 54, 56, 57, 59, 68, 62, 63, 58 and 66 were assigned to the freshwater zone.

##### 2.4.3.2 Timing of upstream migration

Timing of upstream migration was estimated for 33 individuals migrating upstream between August and December 2020. Upstream migration was defined as moving from the tidal zone to the upstream freshwater zone. The timing of the upstream migration for an individual was defined as the initiation of migration from the tidal zone to the freshwater zone, estimated as the date and time of the first detection on receiver 31 or 60 followed by detection on any upstream receiver (Figure 1). The timing was converted to Julian dates (1 January = Day 1) prior to statistical analyses.

In addition to examining the timing of upstream migration, the decision to migrate upstream (here viewed as freshwater zone entry) was investigated. The decision to migrate upstream was estimated for 44 individuals, where individuals that entered the freshwater zone were defined as upstream migrating individuals ( $n = 33$ ) and individuals that stayed in the tidal zone the entire period between August and December were defined as tidal zone residents ( $n = 11$ ).

Six of the 50 tagged individuals were excluded from investigation of the decision to migrate upstream as they either never entered the river ( $n = 3$ ) or disappeared within approximately 1 month after entering the river and never entered the freshwater zone ( $n = 3$ , Appendix 1).

#### *2.4.3.3 Migratory distance in the river*

Migratory distance in the river was estimated for 41 individuals between August and December 2020. The migratory distance was estimated as the maximum distance (km) an individual was detected upstream from the river mouth (receiver 64, Figure 1).

The six individuals excluded from the investigation of the decision to enter freshwater, was also excluded from estimation of migratory distance in the river due to the same reasons as described above. In addition, three individuals that entered the freshwater zone, but disappeared from receiver recordings within approximately 1 month were excluded due to uncertainty of whether the observed maximum distance reflected their true dispersal potential (Appendix 1).

#### *2.4.3.4 Timing of downstream migration*

Out of 33 sea trout that migrated upstream, 28 were subsequent detected in the tidal zone between August 2020 and August 2021. The remaining five upstream migrants disappeared from receiver recordings in the freshwater zone (Appendix 1). The timing of downstream migration was estimated for 22 out 28 individuals (79%) migrating downstream between August and December 2020. The timing of downstream migration was defined as the timing of entry in the tidal zone, estimated as the date and time of the last detection on receivers 31 or 60 given that the previous detection was on any receiver in the freshwater zone. Some individuals migrated downstream but was not detected on receiver 31 or 60 during downstream migration ( $n = 7$ , 32% of 22 downstream migrants). In this case, timing of downstream migration was estimated as the date and time of the last detection on any receiver in the tidal zone given that the previous detection was on any receiver in the freshwater zone. This approach did not give the exact date and time of the last detection on receiver 31 and 60 for these individuals, but due to the short distances between receivers in the tidal zone it was likely that the recorded timing was close to the real (unrecorded) timing on receiver 31 and 60. The timing of downstream migration was converted to Julian dates (1 January = Day 1) prior to statistical analyses.

Out of the 28 sea trout that was detected in the tidal zone after upstream migration, six (21%) migrated downstream during winter (9 December - 29 April). The timing of downstream migration was not estimated for these individuals as receivers were not deployed in this period due to ice formation on the river. For these sea trout, tracking data from April to August 2021 was used to assess whether downstream migration occurred during winter (9 December - 29 April), or in spring and/or summer (29 April - 12 August).

#### *2.4.3.5 Residence time in freshwater*

Residence time in the freshwater habitat upstream the tidal zone was estimated for 41 individuals between August and December 2020. The residence time was estimated as the total number of days an individual spent in the freshwater zone (receiver 55 to receiver 66 or 58, Figure 1) between August and December. An individual's residence time was calculated by summing up all timespans between subsequent detections on

receivers within the freshwater zone. Detections of transitions to and from the zone were removed prior to calculations to avoid overestimating the residence time.

In addition to residence time in freshwater, the residence time in the tidal zone (receiver 64 to receiver 31) was estimated with the same approach as described above. The residence time in the tidal zone was estimated to give an indication of the time spent in the freshwater stretch relative to the time spent in the tidal influenced water. However, since sea trout were captured and released within and just outside the tidal zone, it was likely that individuals had spent time in the tidal zone prior to tagging. Thus, the tidal zone residence time was an estimate on the time spent in the tidal zone after tagging.

The nine individuals excluded from estimation of migratory distance in the river was also excluded from estimation of residence time for the same reasons as mentioned above (Appendix 1).

#### 2.4.4 Statistical analyses

Total body length, condition factor and sex between groups of tagged sea trout were compared using Welch Two Sample T-test or Wilcoxon Rank Sum Test based on whether data was normally distributed or not. In addition, residence time in the freshwater zone compared to residence time in the tidal zone was assessed by Wilcoxon Rank Sum Test. Normality was checked using the Shapiro-Wilk's method with the 'shapiro.test' function in the 'base' package in R. Differences between independent and normally distributed groups were assessed by Welch Two Sample T-test with the 't-test' function in the 'base' package in R, assuming unequal variance. Comparisons between non-normally distributed groups were assessed by Wilcoxon Rank Sum Test with the 'wilcox.test' function in the 'base' package in R. For all comparison tests, level of significance was set to  $p < 0.05$ .

The effects of body length, condition factor and sex on the migratory behaviour questioned in this study was investigated by fitting generalized linear models (GLMs). Separate GLMs were fitted with timing of upstream migration, migratory distance in the river, timing of downstream migration and residence time in freshwater as continuous response variables with gaussian error structure. The decision to enter freshwater during upstream migration was investigated by GLMs with the decision to enter freshwater as the response variable with binomial error structure (entered or not). Explanatory variables were body length (L), condition factor (CF) and sex (S) in all global models (Response variable = L + CF + S). To avoid collinearity between Fulton's condition factor and body length the adjusted condition factor, calculated with the log(mass)-log(length) regression coefficient for tagged individuals, was included in the models rather than Fulton's condition factor. The coefficient was 2.846 and the adjusted condition factor was calculated with the following formula:

$$K = \frac{\text{wet body mass (g)} \cdot 100}{\text{body length (cm)}^{2.846}}$$

Continuous response variables and continuous explanatory variables were standardised prior to model fitting with the 'scale' function in the 'base' package in R. Standardisation allowed for comparison of variables of different units, by comparing the magnitude of effects. All models were fitted with the 'glm' function in the 'stats' package in R.

Collinearity between explanatory variables was assessed with the 'check\_collinearity' function in the 'performance' package in R. The collinearity was low for all explanatory variables in all models ( $VIF \leq 1.44$ ). An individual with unknown sex was excluded from data sets used in all model fittings due to sex being an explanatory variable.

Model selection was based on the second order Akaike's Information Criteria (AICc). The second order Akaike's Information Criteria (AICc) was used rather than Akaike's Information Criteria (AIC) due to the small sample size ( $n$ ) to estimated parameter ( $K$ ) ratio ( $n/K < 40$  in all models), as advocated by Burnham and Anderson (2003). The AIC is an estimate of the prediction error of a model calculated from the log-likelihood and the number of estimated parameters in the model (Burnham & Anderson, 2003). In AICc model selection, candidate models are ranked based on their AICc value and the best model explaining the variation in data in hand has the lowest AICc. It is common to use the  $\Delta AICc$  to find the best models as AICc values are relative.  $\Delta AICc$  is calculated by subtracting the AICc value of a model from the best fitted model (i.e., the lowest AICc value). When making inferences, all candidate models with  $\Delta AICc < 2$  should be considered as they have substantial support (Burnham & Anderson, 2003). The AICc model selection was conducted with the 'dredge' function in the 'MuMIn' package in R. In cases when several models were supported ( $\Delta AIC < 2$ ), coefficients estimate of explanatory variables were obtained by conditional model averaging on all alternative models ( $\Delta AICc < 4$ ). Model averaging computes weighted estimates based on the Akaike weights (Burnham & Anderson, 2003).

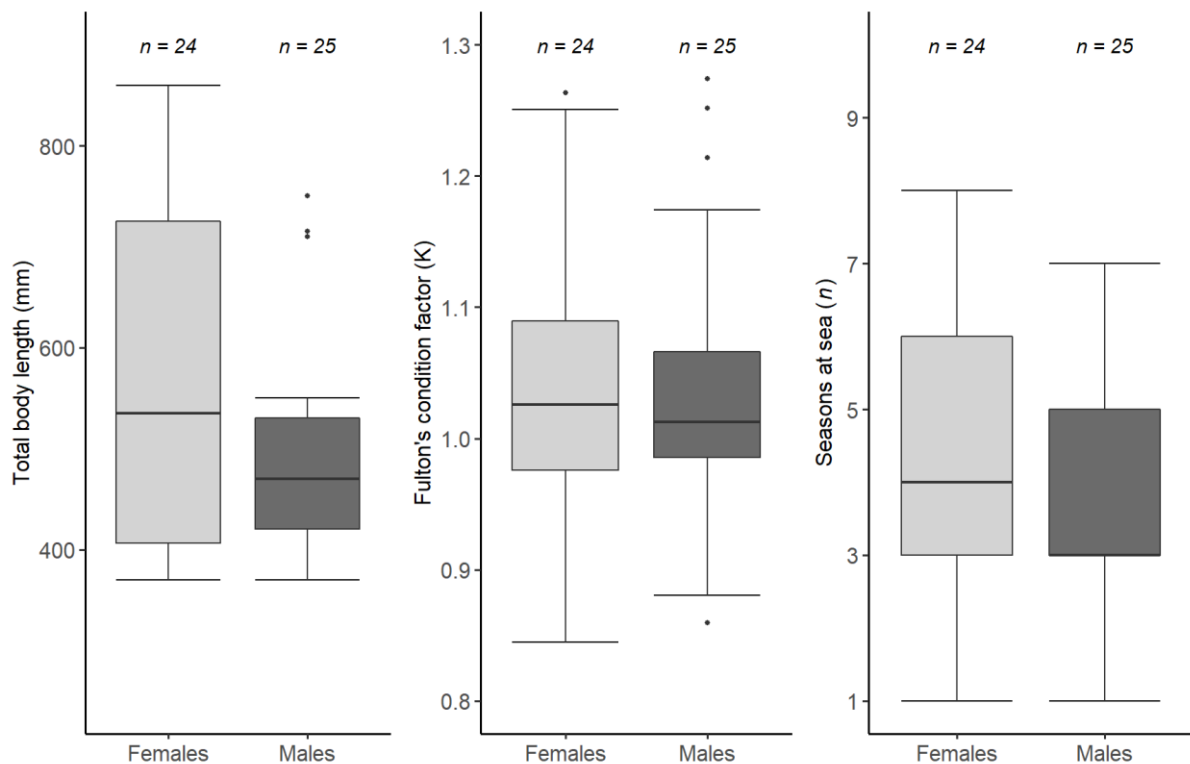
The AICc model selection is an information-theoretic approach to statistical analysis. In an information-theoretic approach test statistics and p-values are inappropriate as hypothesis testing and the information-theoretic approach are different analysis paradigms (Anderson *et al.*, 2001). Instead of reporting whether a parameter is significant or not, as done in hypothesis testing, effect sizes and their precision (in this thesis given as standard errors) are given based on the best selected models for the investigated data (Anderson *et al.*, 2001).

## 3 Results

### 3.1 Characteristics of tagged fish

In total, 50 veteran sea trout were tagged (24 females, 25 males and 1 unknown). At capture, total body length (hereafter body length) ranged between 370 mm and 860 mm (mean = 521 mm, SD = 140 mm), number of seasons at sea ( $n$ ) ranged between 1 and 9 (mean = 4, SD = 2) and Fulton's condition factor ranged between 0.84 and 1.27 (mean = 1.04, SD = 0.11).

There were no significant differences between females and males in body length (Wilcoxon Rank Sum Test;  $n = 49$ ,  $p > 0.05$ ), Fulton's condition factor (Welch Two Sample T-test;  $n = 49$ ,  $p > 0.05$ ) or in number of seasons at sea (Wilcoxon Rank Sum Test;  $n = 49$ ,  $p > 0.05$ , Figure 3).



**Figure 3:** Total body length, Fulton's condition factor and number of seasons at sea for female and male tagged sea trout at the time of capture. The box-and-whisker plots show median values (bold lines), interquartile interval (box, where 50% of the data is found), the 5<sup>th</sup> and 95<sup>th</sup> percentiles (whiskers) and outliers (dots). Sample size ( $n$ ) of female and male sea trout are denoted at the top of each box.



### 3.2 Upstream migration vs. tidal zone residency

Overall, data from 44 sea trout were included in different aspects of the river migration. However, since some individuals showed none or inconsistent tracking data for the different migratory behaviours, not all individuals were included in all analyses (Appendix 1). Among the overall 44 fish, 11 (25%, 9 females, 2 males) were tidal zone residents, whereas 33 (75%, 12 females, 20 males and 1 unknown) migrated into freshwater between August and December. There was no significant difference in body length (Wilcoxon Rank Sum Test;  $n = 44$ ,  $p > 0.05$ ), Fulton's condition factor (Wilcoxon Rank Sum Test;  $n = 44$ ,  $p > 0.05$ ) and number of seasons at sea (T-test;  $n = 44$ ,  $p > 0.05$ ) between upstream migrating individuals and tidal zone residents (Table 1).

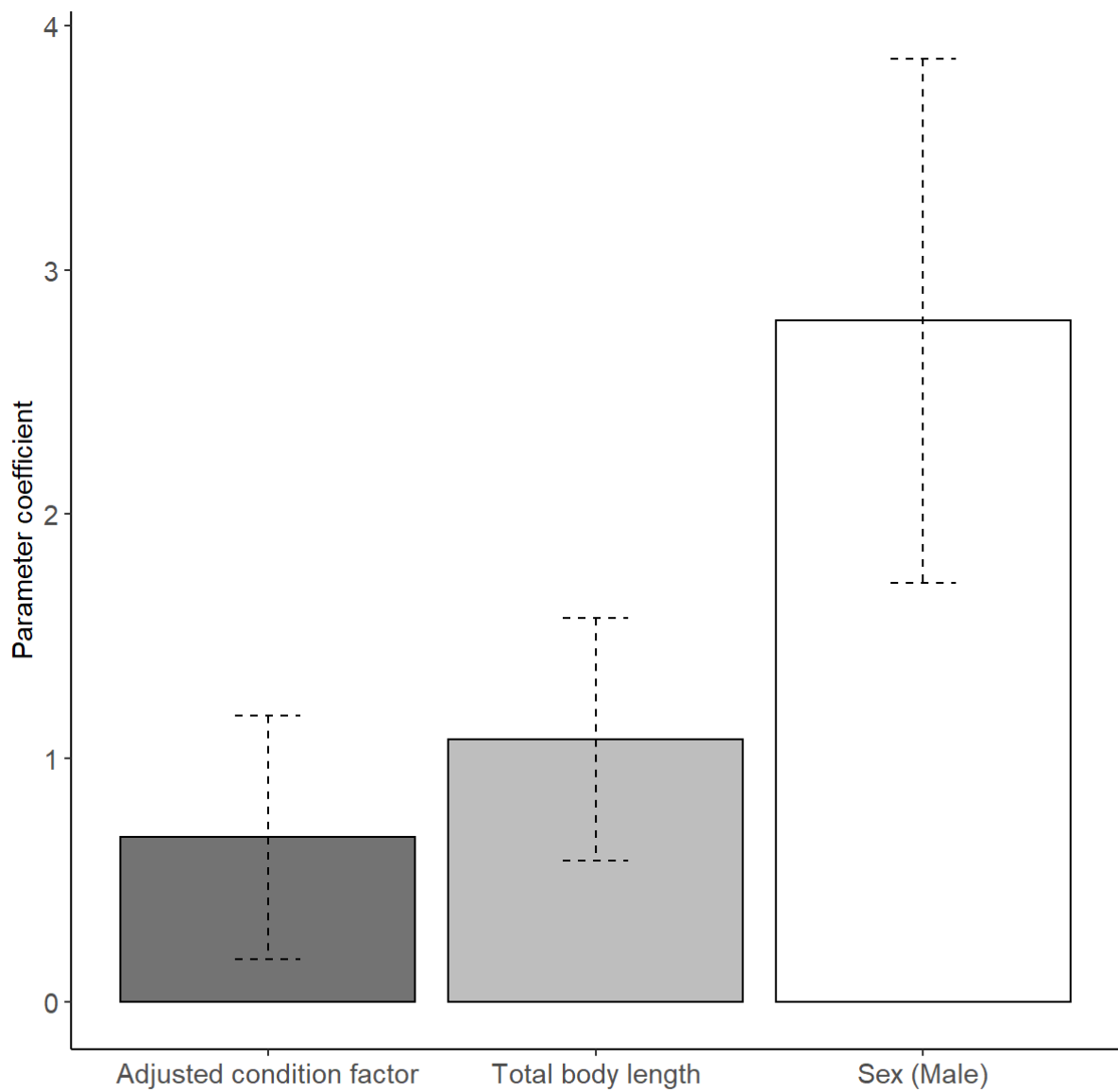
**Table 1:** Number of seasons at sea, total body length and Fulton's condition factor at the time of capture for sea trout that only stayed in the tidal zone ( $n = 11$ ) and upstream migrating individuals ( $n = 33$ ).

	<i>n</i>	Seasons at sea ( <i>n</i> )	Total body length (mm)	Condition factor ( <i>K</i> )
<b>Tidal zone residents</b>	11	4	478 ± 125	1.04 ± 0.15
<b>Upstream migrants</b>	33	5	546 ± 141	1.03 ± 0.09

The effects of body length, condition factor and sex on the decision to migrate upstream (i.e., enter freshwater) was examined for 43 individuals, excluding an individual with unknown sex. Model selection supported two models ( $\Delta AICc < 2$ ), where body length and sex were included in both (Table 2). Conditional model averaging ( $\Delta AICc < 4$ ) suggested that sex, body length, and condition factor influenced the decision to enter freshwater (Figure 4). Sex had the strongest effect on the decision to enter freshwater, followed by body length and condition factor, respectively (Figure 4). Parameter estimates indicated that males were more likely to migrate upstream than females, and that larger individuals of both sexes and individuals in better condition of both sexes were more likely to migrate upstream compared to smaller individuals and individuals in poorer condition (Figure 4).

**Table 2:** Model selection of generalized linear models on the decision to migrate upstream into freshwater of sea trout ( $n = 43$ ), showing the six best models. Models were fitted with binomial error structure. *L* = length, *S* = sex, *CF* = adjusted condition factor and intercept = null model. The models are ranked by decreasing  $\Delta AICc$  value, with the supported models shown in bold ( $\Delta AICc < 2$ ).

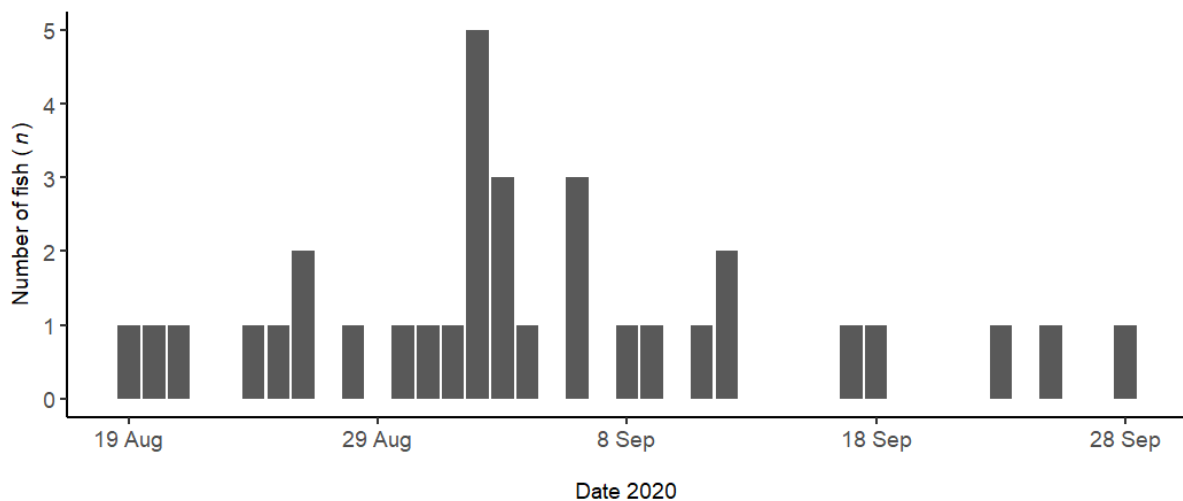
Model tested	AICc	$\Delta AICc$	AICc weights	DF
<b>L + S</b>	<b>43.1</b>	<b>0.00</b>	<b>0.454</b>	<b>3</b>
<b>CF + L + S</b>	<b>43.3</b>	<b>0.28</b>	<b>0.394</b>	<b>4</b>
S	46.4	3.32	0.086	2
CF + S	47.9	4.82	0.041	3
L	50.7	7.59	0.010	2
Intercept	51.0	7.93	0.009	1



**Figure 4:** Estimated effects of adjusted condition factor, total body length and sex on the decision to migrate upstream of sea trout ( $n = 43$ ) based on conditional model averaging ( $\Delta AICc < 4$ ). A positive parameter coefficient indicates a positive relationship between the parameter and the decision to migrate upstream. Error bars (dashed lines) indicate the standard error of each parameter coefficient. Parameter estimates are relative and indicate the magnitude of each effect relative to the other effects.

### 3.3 Timing of upstream migration

Timing of upstream migration was estimated for the 33 sea trout that migrated into the freshwater zone. Timing of upstream migration varied with 40 days from 19 August to 28 September, where most sea trout migrated upstream 2 September ( $n = 5$ , Figure 5). The effects of body length, condition factor and sex on the timing of upstream migration was examined for 32 individuals, excluding an individual with unknown sex. Two models were supported by model selection ( $\Delta AICc < 2$ ), the null model and a model including body length (Table 3). Conditional model averaging ( $\Delta AICc < 4$ ) suggested that larger individuals migrated upstream later than smaller individuals (Table 4). Sex and condition factor had uncertain effects on the timing of upstream migration as the estimated standard errors exceeded the parameter estimates (Table 4).



**Figure 5:** Timing of upstream migration of tagged sea trout ( $n = 33$ ) entering the freshwater stretch upstream the tidal influenced stretch of River Beiarelv.

**Table 3:** Model selection of generalized linear models on the effects on timing of upstream migration of sea trout ( $n = 32$ ), showing the six best models. Models were fitted with gaussian error structure. Intercept = null model, L = total body length, S = sex and CF = adjusted condition factor. The models are ranked by decreasing  $\Delta AICc$  value, with supported models shown in bold ( $\Delta AICc < 2$ ).

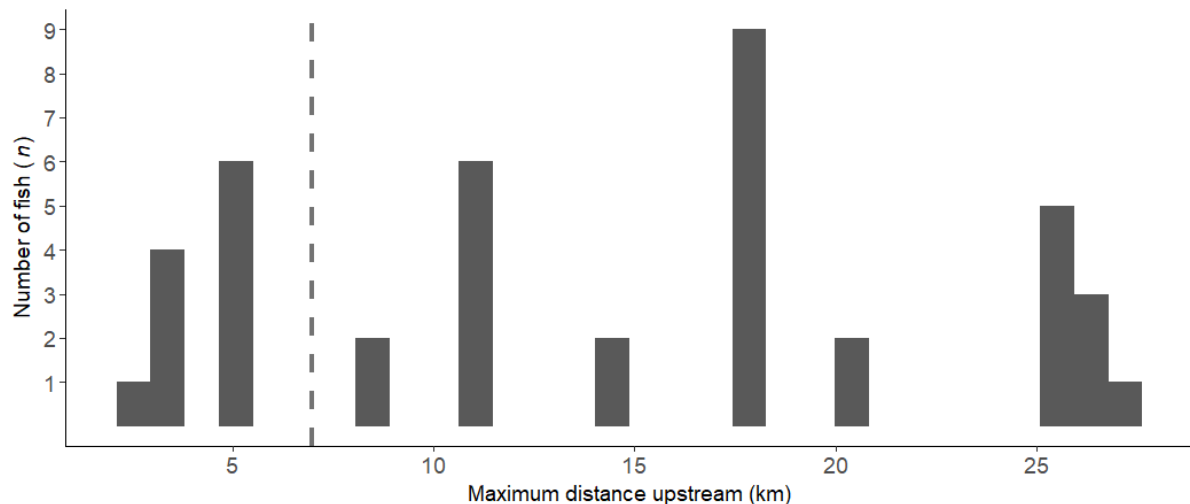
<b>Model tested</b>	<b>AICc</b>	<b><math>\Delta AICc</math></b>	<b>AICc weights</b>	<b>DF</b>
<b>L</b>	<b>93.9</b>	<b>0.00</b>	<b>0.361</b>	<b>3</b>
<b>Intercept</b>	<b>95.2</b>	<b>1.28</b>	<b>0.190</b>	<b>2</b>
S	96.0	2.08	0.128	3
L + S	96.4	2.53	0.102	4
CF + L	96.4	2.56	0.100	4
CF	97.6	3.72	0.056	3

**Table 4:** Parameter estimates and estimated standard errors of the effects on timing of upstream migration of sea trout ( $n = 32$ ). The parameter estimates are based on conditional model averaging ( $\Delta AICc < 4$ ) of generalized linear models with gaussian error structure. Parameter estimates are standardized and indicate the magnitude of each effect relative to the other effects.

<b>Effect</b>	<b>Estimate</b>	<b>Std. Error</b>
Intercept	0.04867	0.23745
Length	0.33263	0.18408
Sex (Male)	-0.31381	0.42953
Adjusted condition factor	-0.02815	0.17959

### 3.4 Migratory distance in the river

Migratory distance in the river was estimated for 41 individuals (20 females, 20 males, 1 unknown) entering the river between August and December. Sea trout were recorded on all receivers except receiver 58 in the tributary Tollåga during upstream migration. The maximum distance moved upstream from river mouth ranged from 3 km to 27 km (mean = 15 km, SD = 8 km, Figure 6), where most sea trout moved a maximum distance of 18 km upstream ( $n = 9$ ).



**Figure 6:** Maximum migratory distance from river mouth and upstream for tagged sea trout ( $n = 41$ ) entering River Beiarelva between August and December. The dashed line indicates the end of the tidal influenced zone of the river.

The effects of body length, condition factor and sex on the migratory distance in the river was examined for 40 individuals, excluding an individual with unknown sex. Model selection identified four alternative models ( $\Delta AICc < 2$ ), including the null model (Table 5). Conditional model averaging ( $\Delta AICc < 4$ ) indicated that sex had the strongest influence on migratory distance, followed by body length, where males and longer individuals of both sexes migrated farther upstream than shorter individuals of both sexes and females (Table 6). The effect of condition factor was limited as the estimated standard errors exceeded the parameter estimate (Table 6).

**Table 5:** Model selection of generalized linear model on the effects on migratory distance in the river of sea trout ( $n = 40$ ), showing the best six models. Models were fitted with gaussian error structure. Intercept = null model, L = total length, S = sex and CF = adjusted condition factor. The models are ranked by decreasing  $\Delta AICc$  value, with the supported models shown in bold ( $\Delta AICc$ ).

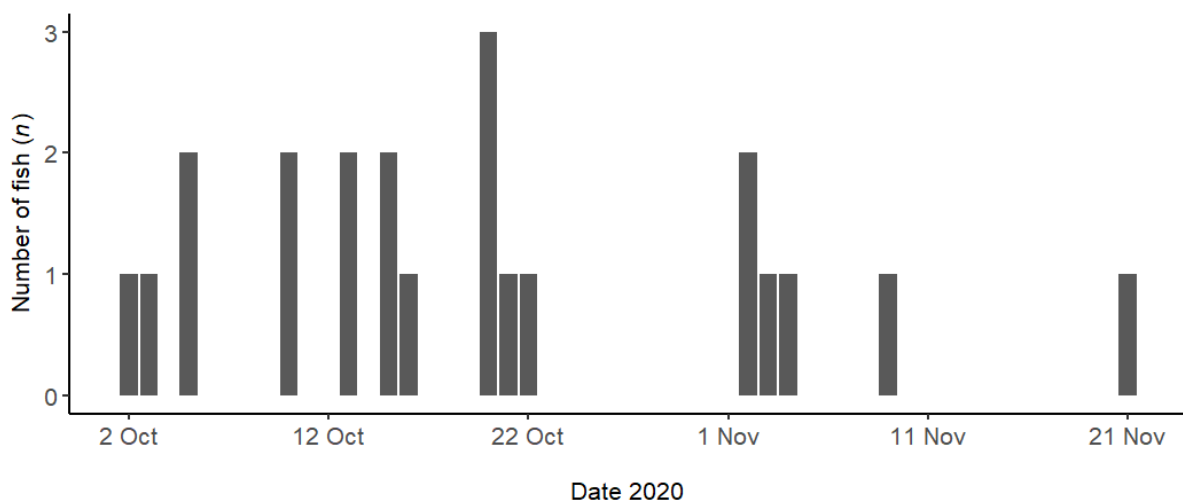
<b>Model tested</b>	<b>AICc</b>	<b><math>\Delta AICc</math></b>	<b>AICc weights</b>	<b>DF</b>
<b>Intercept</b>	<b>116.0</b>	<b>0</b>	<b>0.272</b>	<b>2</b>
<b>L</b>	<b>117.0</b>	<b>0.98</b>	<b>0.167</b>	<b>3</b>
<b>S</b>	<b>117.0</b>	<b>1.03</b>	<b>0.163</b>	<b>3</b>
<b>L + S</b>	<b>117.4</b>	<b>1.38</b>	<b>0.137</b>	<b>4</b>
CF	118.1	2.14	0.093	3
CF + L	119.1	3.10	0.058	4

**Table 6:** Parameter estimates and estimated standard errors of the effects on migratory distance in the river of sea trout ( $n = 40$ ). The parameter estimates are based on conditional model averaging ( $\Delta AICc < 4$ ) of generalized linear models with gaussian error structure. Parameter estimates are standardized and indicate the magnitude of each effect relative to the other effects.

<b>Effect</b>	<b>Estimate</b>	<b>Std. Error</b>
Intercept	-0.11767	0.21152
Length	0.20604	0.16118
Sex (Male)	0.40201	0.31850
Adjusted condition factor	0.09131	0.15968

### 3.5 Timing of downstream migration

Among 33 individuals migrating into the freshwater stretch above the tidal zone, 22 (8 females, 13 males and 1 unknown) were recorded returning to the tidal zone between August and December 2020. The remaining 11 individuals either migrated downstream over winter (December 2020 – April 2021,  $n = 6$ ) or disappeared from receiver recordings during the study period ( $n = 5$ , Appendix 1). Hence, among upstream migrants with subsequent detection in the tidal zone ( $n = 28$ ), 79% displayed downstream migration between August and December. For these individuals timing of downstream migration varied between 2 October and 21 November (range: 50 days, Figure 7), where most individuals migrated downstream 20 October ( $n = 3$ ).



**Figure 7:** Timing of downstream migration of tagged sea trout ( $n = 22$ ) returning to the tidal influenced stretch of River Beiarelva. Six sea trout returned to the tidal zone between December and April, but exact timing of downstream migration could not be estimated for these individuals.

The effects of body length, condition factor and sex on the timing of downstream migration was assessed for 21 individuals, excluding an individual with unknown sex. Three models were supported by model selection ( $\Delta\text{AICc} < 2$ ), including the null model, a model including sex and a model including condition factor (Table 7). Conditional model averaging ( $\Delta\text{AICc} < 4$ ) indicated that sex had the strongest effect on timing of downstream migration, followed by condition factor (Table 8). Males and individuals in better condition of both sexes migrated downstream later than females and individuals in poorer condition of both sexes. Body length had limited effect on the timing of downstream migration as the estimated standard error exceeded the parameter estimate (Table 8).

**Table 7:** Model selection of generalised linear models on the timing of downstream migration of sea trout ( $n = 21$ ), showing the six best models. Models were fitted with gaussian error structure. Intercept = null model, CF = adjusted condition factor, L = total body length and S = sex. The models are ranked by decreasing  $\Delta AICc$  value, with the supported models shown in bold ( $\Delta AICc < 2$ ).

<b>Model tested</b>	<b>AICc</b>	<b><math>\Delta AICc</math></b>	<b>AICc weights</b>	<b>DF</b>
<b>Intercept</b>	<b>64.0</b>	<b>0.00</b>	<b>0.396</b>	<b>2</b>
<b>S</b>	<b>65.7</b>	<b>1.68</b>	<b>0.171</b>	<b>3</b>
<b>CF</b>	<b>65.8</b>	<b>1.81</b>	<b>0.161</b>	<b>3</b>
L	66.7	2.73	0.101	3
CF + S	67.2	3.23	0.079	4
L + S	68.5	4.55	0.041	4

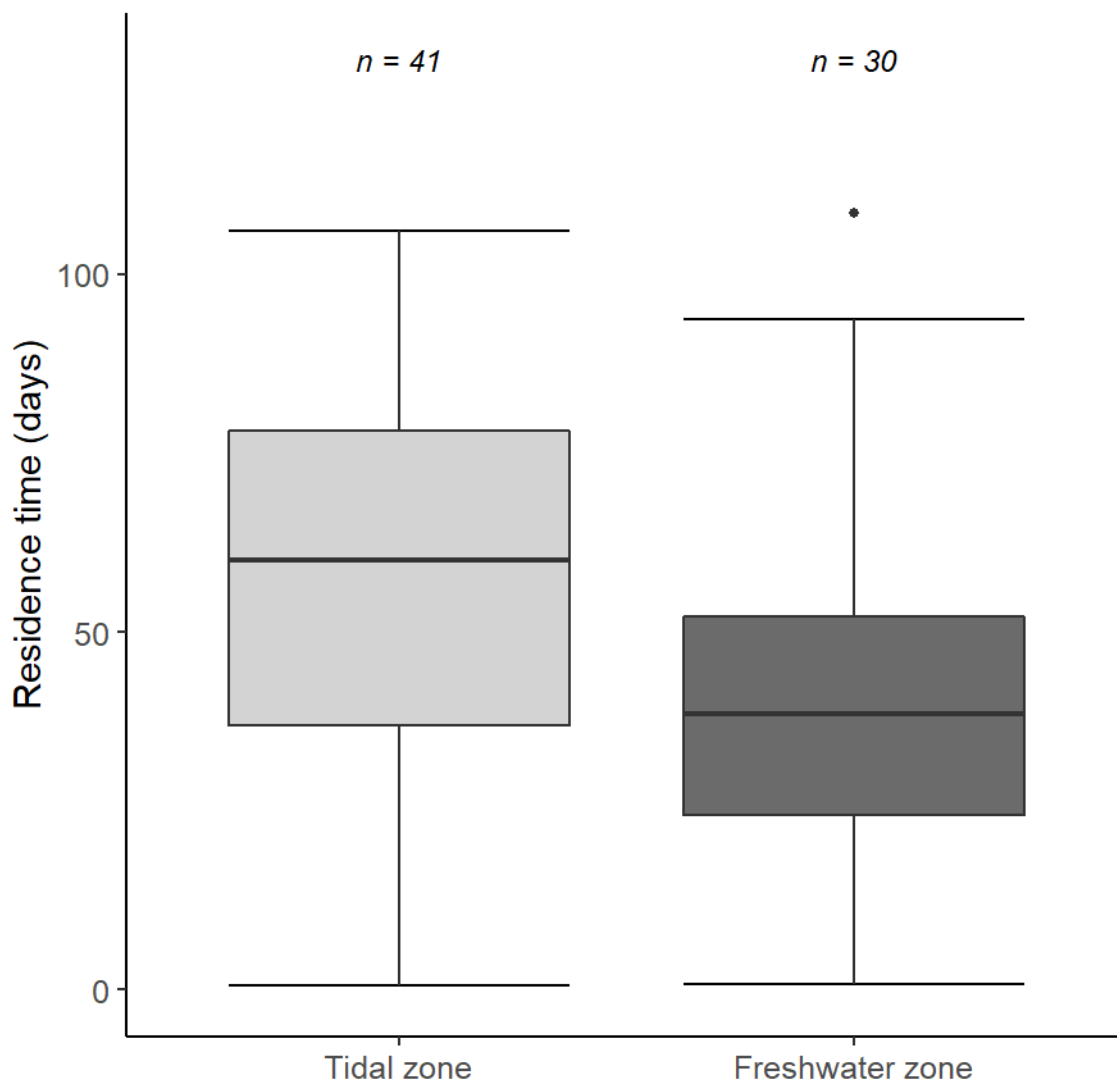
**Table 8:** Parameter estimates and estimated standard errors of the effects on the timing of downstream migration of sea trout ( $n = 21$ ). The parameter estimates are based on conditional model averaging ( $\Delta AICc < 4$ ) of generalized linear models with gaussian error structure. Parameter estimates are standardized and indicate the magnitude of each effect relative to the other effects.

<b>Effect</b>	<b>Estimate</b>	<b>Std. Error</b>
Intercept	-0.05856	0.30071
Sex (Male)	0.48873	0.46184
Adjusted condition factor	0.22599	0.22499
Length	-0.02328	0.23648



### 3.6 Residence time in freshwater

Residence time was estimated for 41 tagged sea trout (20 females, 20 males and 1 unknown) between August and December. In total, 30 individuals (73%, 11 females, 18 males, 1 unknown) stayed in both the tidal zone and the freshwater zone above, whereas 11 individuals (27%, 9 females, 2 males) only stayed in the tidal zone. Overall, the tagged sea trout spent on average 41 days (SD = 28 days, range = 1-109 days) in the freshwater zone and 55 days (SD = 32 days, range = 1-106 days) in the tidal zone (Figure 8). Time spent in the freshwater zone was significantly less than time spent in the tidal zone between August and December (Wilcoxon Rank Sum Test;  $n = 41$ ,  $p < 0.05$ ).



**Figure 8:** Residence time (days) of tagged sea trout in the tidal zone and the freshwater zone between August and December. The box-and-whisker plot show median values (bold lines), interquartile interval (box, where 50% of the data is found), the 5<sup>th</sup> and 95<sup>th</sup> percentiles (whiskers) and outliers (dots). Sample size ( $n$ ) of the total number of sea trout residing in each zone are denoted at the top of each box.

The effects of body length, condition factor and sex on the number of days spent in freshwater was examined for 40 individuals, excluding an individual with unknown sex. Four models were supported by model selection ( $\Delta AICc < 2$ ), including the null model and three models where sex and body length was included as explanatory variables (Table 9). Conditional model averaging ( $\Delta AICc < 4$ ) suggested that males spent more time in freshwater than females during upstream migration (Table 10). Body length and condition factor had limited effects on the number of days spent in freshwater as the estimated standard errors exceeded the parameter estimates (Table 10).

**Table 9:** Model selection of generalized linear models on the number of days spent in freshwater between August and December of sea trout ( $n = 40$ ), showing the six best models. Models were fitted with gaussian error structure. Intercept = null model, CF = adjusted condition factor, L = length and S = sex. The models are ranked by decreasing  $\Delta AICc$  value, with the supported models shown in bold ( $\Delta AICc < 2$ ).

Model tested	AICc	$\Delta AICc$	AICc weights	DF
<b>Intercept</b>	<b>117.7</b>	<b>0.00</b>	<b>0.290</b>	<b>2</b>
<b>S</b>	<b>118.3</b>	<b>0.51</b>	<b>0.224</b>	<b>3</b>
<b>L</b>	<b>119.4</b>	<b>1.67</b>	<b>0.126</b>	<b>3</b>
<b>L + S</b>	<b>119.4</b>	<b>1.68</b>	<b>0.125</b>	<b>4</b>
CF	119.9	2.19	0.097	3
CF + S	120.7	2.94	0.067	4

**Table 10:** Parameter estimates and estimated standard errors of the effects on freshwater residence time of sea trout ( $n = 40$ ). The parameter estimates are based on conditional model averaging ( $\Delta AICc < 4$ ) of generalized linear models with gaussian error structure. Parameter estimates are standardized and indicate the magnitude of each effect relative to the other effects.

Effect	Estimate	Std. Error
<b>Intercept</b>	-0.1076	0.2220
<b>Sex (Male)</b>	0.4426	0.3215
<b>Length</b>	0.1563	0.1651
<b>Adjusted condition factor</b>	-0.0511	0.1623

## 4 Discussion

River migration in autumn plays an important role in the life history of sea trout as sea trout enters freshwater to spawn and/or overwinter (Klemetsen *et al.*, 2003). The present thesis investigated the river migration of 44 veteran sea trout in River Beiarelva in Northern Norway. The sea trout were tracked for one year (August-August), with main focus on the autumn migration (August-December).

### 4.1 Upstream migration vs. tidal zone residency

The majority of the tagged sea trout (75%) entered the freshwater stretch above the tidal zone between August and December. Total body length, condition factor and sex influenced the decision to enter the freshwater zone, where larger individuals, individuals in better condition and males were more likely to enter. Sea trout return to freshwater for spawning and/or overwintering and upstream migrating individuals can, thus, consist of both spawners and immature individuals (Thorstad *et al.*, 2016). Spawners seek fast-running, stone and gravel habitat offering suitable conditions for spawning (Ottaway *et al.*, 1981; Klemetsen *et al.*, 2003), whereas overwintering sea trout seek sheltered, slow-running habitats such as pools or lakes (Huusko *et al.*, 2007). Differences in the motivation to migrate upstream may manifest in different behavioural strategies during upstream migration. The maturity of sea trout was not assessed in the present study. However, considering that the tagged sea trout had on average performed four previous marine migrations and previous knowledge on the age at maturity for northern sea trout populations (L'Abée-Lund *et al.*, 1989; Jonsson & L'Abée-Lund, 1993), it is likely that the majority of the tagged sea trout were spawners.

Sex had the strongest effect on the decision to move upstream from the tidal zone to the upstream freshwater zone, where males were more likely to enter the freshwater zone than females. There was no significant difference in number of previous marine migration between females and males. Males usually reach sexual maturity at a younger age and, often, more variable, and smaller size than females (Jonsson, 1989; L'Abée-Lund *et al.*, 1989; Jonsson & L'Abée-Lund, 1993). Since no fish smaller than 37 cm were tagged in the present study, it is possible that more tagged males than females were sexual mature, which could explain the higher tendency among males to enter freshwater. The sex difference in age and size at maturity is likely related to that male and female reproductive success are unequally dependent on size. For salmonids in general, as female size increases so does egg mass, number of eggs produced and ultimately their reproductive success (Heinimaa & Heinimaa, 2004). Males can exhibit two mating strategies, either as small satellites or large dominants, making male reproductive success less dependent on size, although larger individuals have a competitive advantage during mating (Fleming & Reynolds, 2004). The results of the present study also indicated that the tendency to enter freshwater above the tidal zone increased with body size. In addition, there was a strong positive correlation between body length and number of previous marine migrations. This suggests that upstream migrants entering freshwater were older and perhaps, mature, whereas tidal residents were younger and immature. In River Beiarelva, spawning grounds are typically located in the freshwater zone or tributaries connected to this zone (Hellen *et al.*, 2016), supporting the hypothesis that spawners entered freshwater. Thus, the lower tendency

to enter freshwater among smaller individuals, individuals in poorer condition and females could be attributed to a higher proportion of immature sea trout among these individuals. However, as there is some, but limited, potential spawning habitat in the river and tributaries draining into the river zone defined as tidal influenced, the possibility that also tidal zone residents were mature and spawned cannot be excluded.

Although it is likely that most upstream migrants entered freshwater to spawn, sea trout may enter freshwater to overwinter regardless of maturity (Jonsson, 1985; Berg & Berg, 1989; Jonsson & Jonsson, 2002; Östergren & Rivinoja, 2008). There is a general perception that the freshwater habitat is safer but less productive, whereas the marine habitat has higher mortality rates but better growth opportunities (Thorstad *et al.*, 2016; Jensen *et al.*, 2019). Growth rates are higher at sea than in freshwater (Jonsson, 1985; L'Abée-Lund *et al.*, 1989), but the predation risk increases, particularly for small individuals (Lyse *et al.*, 1998; Dieperink *et al.*, 2001). In addition, the high salinity levels in sea water in combination with low water temperatures during winter may be stressful for sea trout (Larsen *et al.*, 2008). It has been assumed that north Norwegian sea trout populations overwinter in freshwater (Berg & Berg, 1989), whereas southern populations are frequently observed in marine waters during winter (Knutsen *et al.*, 2004; Olsen *et al.*, 2006). However, more recent studies shows that northern populations also may utilize marine and estuarine waters during autumn and winter (Jensen & Rikardsen, 2008; 2012). It has been suggested that salmonids choose overwintering habitat according to the asset-protection principle (Clark, 1994; Halttunen *et al.*, 2013), where individuals with low reproductive assets (i.e., low probability of future reproduction) accept the risky, marine habitat offering better growth opportunities, whereas individuals with high reproductive assets choose the safer freshwater habitat to protect their high valued assets. However, this principle only applies if freshwater conditions are suitable for overwintering. Especially, smaller rivers without access to lakes might exhibit poor winter conditions in terms of low water levels and unstable ice conditions, making sea trout more benign to marine habitats for overwintering (Jonsson & Jonsson, 2002; Knutsen *et al.*, 2004; Olsen *et al.*, 2006). In larger rivers, the lack of lake access and/or better growth opportunities in marine waters have been suggested to be the main drivers for marine winter residency for sea trout (Jensen & Rikardsen, 2012). River Beiarelva is a relatively large river, but it lacks access to a lake. In addition, the tidal zone is mainly deep and slow running, likely offering more stable overwintering conditions than the upstream river stretches. Thus, the higher tendency among smaller sea trout, sea trout in poorer conditions and females, which were more likely to be immature individuals, to reside in the tidal zone between August and December, could be explained by poor overwintering conditions in the upstream freshwater habitats and/or better growth opportunities in the tidal zone. According to the asset-protection principle these individuals should choose the riskier and more productive marine habitat as their reproductive success is more dependent on growth. In addition, compared to freshwater and full-strength sea water, the tidal zone might be a more beneficial habitat for overwintering as it offers higher growth potential than freshwater, better refuges from predators and less stressful salinity levels than marine waters (Thorpe, 1994).

## 4.2 Timing of upstream migration

Upstream migration, defined as entering the freshwater stretch upstream the tidal zone, occurred between 19 August and 28 September, where the highest number of sea trout entered freshwater 2 September. The timing of upstream migration is consistent with the peak of upstream migration observed in several north Norwegian rivers (Sjursen *et al.*, 2020; Sjursen *et al.*, 2021a; Sjursen *et al.*, 2021b). For salmonids, the time of arrival at spawning ground is critical for the reproductive success, as it has to match optimal conditions for embryonic development and offspring survival during hatching (Elliott & Hurley, 1998; Einum & Fleming, 2000). There is a general perception that spawning time is under selection and that the environmental conditions the offspring experience after hatching are the major selective agents. Accordingly, the timing of upstream migration appears to be adapted to local conditions ensuring a match between migratory opportunities and the optimal time for spawning. This local adaptation was shown in a study on Atlantic salmon where individuals from eight Norwegian populations were released in River Imsa prior to upstream migration (Jonsson *et al.*, 2007). Atlantic salmon from northern populations (62–69 N°) moved upstream approximately 1 month earlier than individuals from southern populations (59–60 N°), indicating a genetic effect on the timing of upstream migration. The earlier ascent in northern populations were assumed attributed to the earlier timing of spawning in these populations. In River Beiarelva, sea trout mainly spawn in the end of September and the beginning of October (Davidsen *et al.*, 2020). Hence, an upstream migration occurring in the end of August and September matches the timing of spawning in the river.

The results of the present study indicated a trend of larger sea trout migrating upstream later than smaller ones. This result contradicts those reported for sea trout in several north Norwegian rivers (Sjursen *et al.*, 2020; Sjursen *et al.*, 2021a; Sjursen *et al.*, 2021b). The referred reports indicated a trend of larger sea trout ascending earlier than smaller ones, however some large sea trout also migrated upstream later than the smaller ones. In addition, in these reports, upstream migration extended over a longer period, in some rivers starting in June or July, whereas upstream migration in the present study started in August. In the present study, any potential upstream migration occurring earlier than August was not recorded as sea trout were captured and tagged in this month. Hence, there is a possibility that the largest sea trout already had migrated upstream upon the commence of tracking, explaining the contradictory results between River Beiarelva and other north Norwegian rivers. Considering the moderate sample size, and that the null model was equally good as the model including body length, the trend observed in present study need to be treated with caution. This also suggests that other intrinsic or environmental factors that were not included in the current study may better explain the variation in timing of upstream migration of sea trout in River Beiarelva, than the tested explanatory variables.

Sex was not identified as an important factor for the timing of upstream migration in the present study. Some previous studies have shown a sex-bias in timing of upstream migration where females ascend later than males (Jensen, 1968; Berg & Berg, 1989). This has typically been linked to the higher growth potential in the marine habitat and the reproductive success of females being more dependent on size (Jonsson, 1985; Berg & Berg, 1989). Consequently, fitness gains are higher for females in the marine habitat, favouring prolonged marine migrations and a later descent. The reason for the

contradictory results between the present and previous studies may be attributed to differences in the location of where timing of upstream migration was estimated. In the present study, upstream migration timing was defined as the transition from the tidal zone to the freshwater stretch above this zone, which excluded migration within the first seven km of the river. It is possible that estimation of timing of upstream migration at river mouth, rather than at freshwater entry, would have revealed other trends. However, the timing of upstream migration found in this study are consistent with the peak of return to the estuary found for sea trout returning to River Beiarelva in 2019 and 2020 (Steinkjer, 2021), suggesting that most sea trout migrate upstream in August and September in River Beiarelva. Thus, the limited effect of sex found in the present study indicate that other intrinsic or environmental factors may better explain the variation in timing of upstream migration.

There have been limited numbers of previous studies on the drivers for river migration behaviour for sea trout. However, some studies on sea trout suggest that water flow initiate the upstream migration, particularly early in the migratory period (Berg & Berg, 1989; Jonsson & Jonsson, 2002). Water flow is thought to influence upstream migration for salmonids through enabling upstream movements and passing of obstacles (Jonsson, 1991), while turbidity is assumed to decrease the risk of predation for fish species in general (Abrahams & Kattenfeld, 1997). Large sea trout may be particularly vulnerable to low water flow as they are more dependent on high water flow during upstream movement (Jensen & Aass, 1995). For Atlantic salmon, the influence of water flow on timing of upstream migration is usually seen in smaller rivers (Jonsson *et al.*, 2007) and not in larger ones (Thorstad & Heggberget, 1998). It is likely that this applies to sea trout as well. River Beiarelva is a relatively large river with glacial water input during summer months (Hellen *et al.*, 2016). This suggest that water flow probably played a minor role in delaying the timing of upstream migration of large sea trout in the present study. Yet, as very high water flow can decrease and halt upstream migration for sea trout (Jensen & Aass, 1995; Jonsson & Jonsson, 2002), the influence of water flow on timing of upstream migration in River Beiarelva should be assessed in future research.

Water temperature can also influence the timing of upstream migration by restricting the ability of activity at extreme values (Jonsson & Jonsson, 2009). In the present study upstream migration occurred during August and September where the mean water temperatures measured in the uppermost part of the tidal zone was 9.4 °C (SD = 1.3°C) and 7.0 °C (SD = 1.6°C), respectively. These temperatures are within the incipient lethal temperature range of sea trout (Elliott, 1994), suggesting that temperatures to a little extent restricted the ability of upstream movement and, thus, the timing of upstream migration. However, in future studies both the effect of water temperature and water flow should be included in statistical models to properly understand their influence on timing of upstream migration in River Beiarelva.

### 4.3 Migratory distance in the river

The great variation in migratory distance in the river found in this study indicate that most parts of the anadromous stretch of River Beiarelva is utilized by sea trout. One exception is the uppermost parts of the anadromous stretch as only few tagged individuals were detected here. Sex and body length were found to some degree influence the migratory distance, where larger individuals and males tended to migrate

farther upstream. The tidal zone of River Beiarelva consist to a greater extent of deep pools and slow running water than the upstream freshwater zone, perhaps offering better shelter opportunities. In the freshwater zone the water is merely fast-running and the highest proportion of spawning grounds are located in this part of the river (Hellen *et al.*, 2016). It has been suggested that sea trout can spawn in brackish water (Landergren & Vallin, 1998). Although there are some few potential spawning grounds in the main river in the tidal influenced zone, and in smaller tributaries draining into the tidal zone, it is likely that most mature sea trout enters the freshwater stretch upstream the tidal zone for spawning. Hence, differences in maturity among long and short distance migrants may explain the observed effect of sex and body length on migration distance. A recent study on the stock status of sea trout in River Beiarelva showed that fry (0+), one year olds (1+) and older juvenile sea trout ( $\geq 2+$ ) resided in all parts of the freshwater zone, but the majority of older juvenile sea trout were found in the lower parts of the zone (Davidsen *et al.*, 2020). As it is likely that younger year classes were captured close to the spawning ground, the results from (Davidsen *et al.*, 2020) suggest that spawning occurred in all parts of the freshwater zone upstream the tidal influenced zone. Although the study by Davidsen *et al.* (2020) did not include the tidal zone of the river, the results support the assumption that mature sea trout entered freshwater and migrated farther upstream for spawning.

#### 4.4 Timing of downstream migration and residence time in freshwater

The tagged sea trout spent on average significantly fewer days in the freshwater zone than in the tidal zone between August and December, but there was great variation in the time spent in each of the two zones. Some tagged sea trout (25%) never entered the freshwater zone, and among the freshwater ascending sea trout returning to the tidal zone, 79% descended to the tidal zone in autumn and was frequently recorded in this zone until 9 December. These results suggest that the tidal zone is an important habitat for sea trout between August and December. The tidal zone is a part of the estuary which compared to freshwater and full-strength sea water may provide better conditions during autumn and winter because of the higher growth potential, better refuges from predators and less stressful salinity levels offered by this habitat (Thorpe, 1994). Thus, favourable conditions in the tidal zone compared to freshwater and marine waters could explain the greater residence time in the tidal zone found in the present study.

The majority of freshwater ascending sea trout (79%) returning to the tidal zone, descended the river between 2 October and 21 November. Six sea trout (21%) migrated downstream over winter (December-April), but the exact timing of downstream migration for these six individuals could not be determined as receivers were not deployed in the river during this period. Previous studies indicate that timing of downstream migration varies greatly within and among rivers, where some sea trout descend almost immediately after spawning and others reside in freshwater for weeks or months (Jonsson & Jonsson, 2002; Bendall *et al.*, 2005; Jensen & Rikardsen, 2008; Östergren & Rivinoja, 2008). In River Skibotn, a north Norwegian river where spawning occurs at the same time as in River Beiarelva, almost all sea trout descended to the tidal zone approximately one month later (Jensen & Rikardsen, 2008), than the fish in the present study. However, as six sea trout descended the river during winter in River

Beiarelva, it is likely that the timing of downstream migration extended over a longer period than the observed. It is also possible that these six individuals overwintered in freshwater and descended to the tidal zone in spring. In a recent master's thesis, sea trout from River Beiarelva were found to descend the river in May and June (Steinkjer, 2021). In this study the timing of downstream migration was defined as entry in the innermost part of the fjord, while it in the current was defined as movement from the freshwater zone to the tidal zone of the river. This could explain the difference in timing of the downstream migration between the current and the previous study.

In the present study, sex, body length and condition factor had limited effect on the timing of tidal zone entry after a residence in the upstream freshwater stretch of the river. Sex and condition factors were included in models that were equally good as the null model, but the standard error of their estimates was close to the parameter estimate, suggesting limited effects of these explanatory variables. Nevertheless, the present study also suggested that males spent more time in the freshwater zone upstream the tidal zone than females, but there was no difference in timing of upstream migration between males and females. Although, the effect of sex on the duration of freshwater residence also was weak, these results combined suggest that males to some degree spent more time in freshwater and descended later to the tidal zone than females. The results of the present study are consistent with Berg and Berg (1989) who found that males spent more time in freshwater and descended later than females in River Vardnes, Northern Norway. Female reproductive success is more dependent on size than male reproductive success (Fleming & Reynolds, 2004), possibly favouring prolonged sea residency for females and an earlier descent to the tidal zone. Other studies from Danish and English rivers reported no difference between females and males in freshwater residence time and timing of downstream migration (Aarestrup & Jepsen, 1998; Bendall *et al.*, 2005). However, geographic location and river characteristics have strong effect on the freshwater residency of sea trout (Thorstad *et al.*, 2016), possibly explaining this inconsistency among studies.

A previous study on Atlantic salmon revealed that post-spawned kelts with low body condition left the river earlier during the winter or spring than those with better condition factor (Halttunen *et al.*, 2013). It has also been observed that Atlantic salmon kelts and sea trout veterans with increased plasma cortisol levels returned earlier to sea (Birnie-Gauvin *et al.*, 2019). Plasma cortisol is a stress hormone which is thought to be induced by depleted energy reserves. Individuals with low energy reserves and thus low reproductive asset should, according to the asset-protection principle (Clark, 1994), be more benign to the marine habitat where the growth opportunities are better. In the present study, the body condition was evaluated in the autumn prior to the individual's spawning migration and might not have been strictly correlated to post-spawning nutritional state, as there may be individual differences in energetic investment in spawning. It is also possible that the downstream migration in the present study was merely driven by the need for suitable overwintering habitat rather than seeking better feeding opportunities. The clearer trends of sex and body condition affecting migration timing in other studies (Berg & Berg, 1989; Birnie-Gauvin *et al.*, 2019; Eldøy *et al.*, 2021), might be attributed to that the transition from estuary to the fjord more clearly denotes a shift from overwintering to initiation of the prey search and feeding. In these studies, it also appears that fjord entry occurs in spring more than in autumn. Hence, based on the limited effects of body length, condition factor and sex on the freshwater residence time and the timing of downstream migration, it can be speculated that



estuary residence is a beneficial strategy for sea trout between August and December, regardless of individual physiological status. However, it is possible that sea trout recorded in the tidal zone moved between the fjord and the tidal zone, as reported for sea trout in a north Norwegian river (Jensen & Rikardsen, 2012), but this was not possible to assess in the present study as data from fjord receivers were not available.

In conclusion, the present study suggest that the tidal influenced stretch of River Beiarelva offers a favourable habitat for sea trout between August and December, but that most sea trout in the size range included in the present study (37 cm – 86 cm) perform upstream migrations to the freshwater stretch above the tidal zone. The decision to migrate upstream is likely linked to spawning and followed by a return to the tidal zone of the river. In a management perspective, the knowledge provided by this study is of great value as river mouths and tidal influenced stretches of larger rivers often are canalized or exposed to anthropogenic interventions such as acidification, aquatic pollution and river flow alternations (Thorstad *et al.*, 2016). The continuous pressure from coastal development threatens sea trout populations on a spatial and temporal scale, calling for mitigation measures focused on the critical phases in sea trout life-history. The river migration during autumn is essential for population recruitment and unsuccessful river migration could threaten the viability of populations. In Norway, northern populations are expected to face a shift in anthropogenic impacts induced by the northwards expansion of warmer water and aquaculture bringing increased pathogen pressures (Vollset *et al.*, 2021). As sea trout may return to estuaries and rivers to escape high pathogen pressures in the marine habitat (Birkeland & Jakobsen, 1997), it is important to ensure that the river habitat offers suitable conditions to reside in. This thesis suggest that the tidal zone might confer an optimal habitat for residence between August and December, compared to upstream freshwater habitats and marine waters. In a river management perspective, this highlights the need for preventing tidal influenced river stretches from being subject to anthropogenic interventions and suggest that sea trout may be especially susceptible for fishing pressure in the lower parts of rivers.

## 5 References

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# Appendix 1

**Table A1:** Biological characteristics of the 50 tagged sea trout at the time of capture in August 2020. Sex was determined by DNA-analysis of an adipose fin sample.

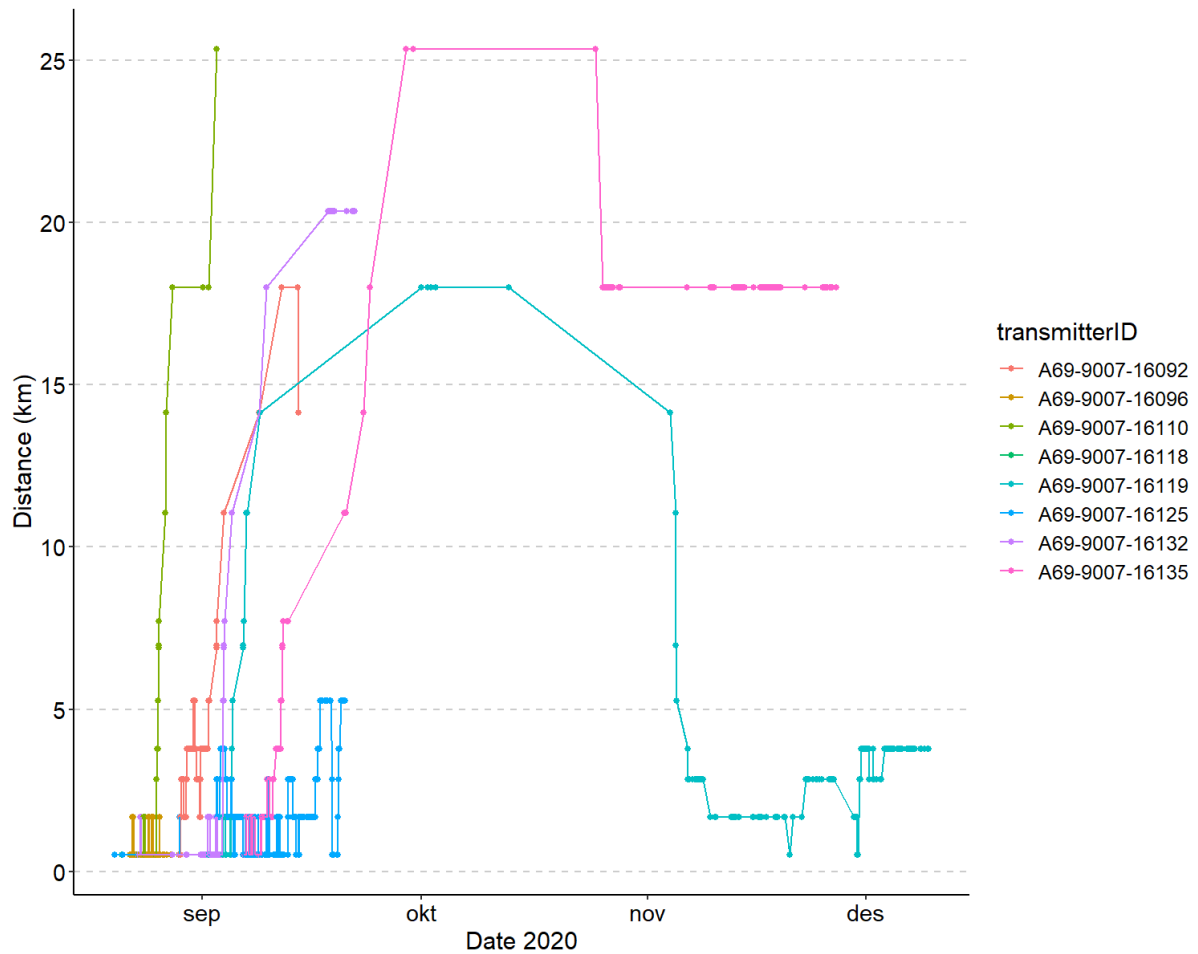
<b>Transmitter ID</b>	<b>Total body length (mm)</b>	<b>Fulton's condition factor (K)</b>	<b>Sex</b>	<b>Seasons at sea</b>	<b>Adjusted condition factor</b>
A69-9007-16113	450	0.99	Male	5	1.78
A69-9007-16114	420	1.05	Female	4	1.87
A69-9007-16115	490	1.00	Female	4	1.83
A69-9007-16116	390	1.08	NA	3	1.90
A69-9007-16125	740	1.06	Female	7	2.06
A69-9007-16138	550	0.91	Male	6	1.69
A69-9007-16122	460	1.27	Male	1	2.30
A69-9007-16128	480	1.01	Male	4	1.84
A69-9007-16121	710	1.02	Male	6	1.96
A69-9007-16126	370	1.26	Female	1	2.20
A69-9007-16117	470	1.08	Female	3	1.95
A69-9007-16118	410	0.96	Female	3	1.70
A69-9007-16107	370	1.24	Female	3	2.17
A69-9007-16108	470	0.98	Male	5	1.78
A69-9007-16109	530	0.86	Male	6	1.58
A69-9007-16110	750	1.05	Female	6	2.05
A69-9007-16111	440	1.17	Male	6	2.10
A69-9007-16112	580	1.25	Female	4	2.34
A69-9007-16101	370	0.99	Male	3	1.72
A69-9007-16103	400	1.00	Male	3	1.76
A69-9007-16096	395	1.01	Female	4	1.77
A69-9007-16104	390	1.21	Male	3	2.13
A69-9007-16106	495	0.89	Male	5	1.62
A69-9007-16095	380	1.09	Female	3	1.91
A69-9007-16097	430	0.88	Male	3	1.57
A69-9007-16102	590	1.09	Female	5	2.04
A69-9007-16105	780	0.95	Female	7	1.85
A69-9007-16098	650	0.84	Female	6	1.61
A69-9007-16099	540	1.11	Male	5	2.04
A69-9007-16100	620	0.99	Female	4	1.87
A69-9007-16089	470	1.06	Male	3	1.92
A69-9007-16090	390	1.05	Female	3	1.84
A69-9007-16091	390	1.15	Female	4	2.02
A69-9007-16092	440	0.96	Male	3	1.72
A69-9007-16093	480	1.09	Male	3	1.97
A69-9007-16094	375	1.25	Male	2	2.19
A69-9007-16130	490	0.99	Male	3	1.80
A69-9007-16136	550	0.99	Male	5	1.83
A69-9007-16127	460	1.09	Female	4	1.96
A69-9007-16133	480	0.87	Female	3	1.58
A69-9007-16132	370	1.03	Male	1	1.79
A69-9007-16124	420	1.05	Male	3	1.87
A69-9007-16131	740	0.98	Female	7	1.91
A69-9007-16129	710	0.98	Female	6	1.90
A69-9007-16135	860	0.90	Female	8	1.79
A69-9007-16119	750	1.02	Male	7	1.98
A69-9007-16134	740	0.93	Female	7	1.81
A69-9007-16120	370	1.07	Male	2	1.86
A69-9007-16123	720	1.00	Female	5	1.93
A69-9007-16137	715	1.00	Male	6	1.93

**Table A2:** Deployed receivers in River Beiarelva. The table shows receiver number, deployment date, deployment latitude, deployment longitude, instrument depth, model type, serial number, and distance from river mouth (station 64) for each receiver.

<b>Receiver no.</b>	<b>Deploy. date</b>	<b>Deploy. lat.</b>	<b>Deploy. long</b>	<b>Instrument depth (m)</b>	<b>Model</b>	<b>Serial no.</b>	<b>Distance (km)</b>
30	10.08.2020	67.03145	14.5725	2	VR2W	119078	0.516
31	10.08.2020	67.00126	14.62294	1	VR2W	119136	6.971
50	10.08.2020	67.02221	14.56467	2	VR2W	125086	1.676
51	10.08.2020	67.01597	14.5703	2	VR2W	125087	2.846
52	10.08.2020	67.00932	14.57074	2	VR2W	119953	3.771
53	10.08.2020	67.00195	14.58394	2	VR2W	119945	5.251
54	10.08.2020	66.99747	14.7006	1	VR2W	119952	11.045
55	10.08.2020	67.00072	14.63907	1	VR2W	119961	7.705
56	10.08.2020	66.99332	14.7511	1	VR2W	100968	14.145
57	10.08.2020	66.97494	14.80555	1	VR2W	102919	17.995
58	10.08.2020	66.91004	14.79588	1	VR2W	113507	28.351
59	10.08.2020	66.96584	14.82323	1	VR2W	122428	20.345
60	10.08.2020	67.00177	14.62125	2	VR2W	108573	6.881
61	10.08.2020	66.99682	14.64084	1	VR2W	102904	8.255
62	10.08.2020	66.92133	14.78164	1	VR2W	105703	26.575
63	10.08.2020	66.92054	14.78285	1	VR2W	107232	26.701
64	10.08.2020	67.03482	14.5807	3	VR2W	129608	0.000
66	10.08.2020	66.91214	14.76692	1	VR2W	122436	27.495
68	10.08.2020	66.92813	14.77675	1	VR2W	119947	25.335

**Table A3:** Table of 11 sea trout that were excluded from some analysis on river migratory behaviours based on their last detection within the study period (August 2020-August 2021). For each sea trout, transmitter ID, the last detection, the analyses it was excluded from and the reasons for being excluded from the particular analyses is given.

<b>TransmitterID</b>	<b>Last detection</b>	<b>Excluded from</b>	<b>Reason for being excluded</b>
A69-9007-16089	2020-09-17 00:07:43	All analyses	Never entered river
A69-9007-16101	2020-09-23 01:04:02	All analyses	Never entered river
A69-9007-16094	2020-09-23 08:02:30	All analyses	Never entered river
A69-9007-16118	2020-08-24 05:08:10	All analyses	Disappeared from receiver recordings shortly after tagging and only detected in river mouth
A69-9007-16125	2020-09-20 14:44:27	All analyses	Disappeared from receiver recordings shortly after tagging and never migrated upstream
A69-9007-16096	2020-08-31 03:27:31	All analyses	Disappeared from receiver recordings shortly after tagging and never migrated upstream
A69-9007-16110	2020-09-02 22:52:10	Migratory distance in the river, timing of downstream migration, residence time in freshwater	Disappeared from receiver recordings shortly after tagging, but migrated upstream
A69-9007-16132	2020-09-21 22:28:09	Migratory distance in the river, timing of downstream migration, residence time in freshwater	Disappeared from receiver recordings shortly after tagging, but migrated upstream
A69-9007-16092	2020-09-11 20:34:45	Migratory distance in the river, timing of downstream migration, residence time in freshwater	Disappeared from receiver recordings shortly after tagging, but migrated upstream
A69-9007-16135	2020-11-26 21:37:20	Timing of downstream migration	Disappeared from receiver recordings in November
A69-9007-16115	2021-05-19 02:45:32	Timing of downstream migration	Only one detection in spring



**Figure A1:** Plot of distance migrated in River Beiarelva over time for eight sea trout that were last detected between 11 August and 9 December 2020. The coloured dots and lines correspond to an individual given as the transmitter ID of the acoustic transmitter. Three individuals (A69-9007-16096, A69-9007-16125, A69-9007-16118) were excluded from all analyses on migratory behaviour as they disappeared from receiver recordings in August or September, four (A69-9007-16110, A69-9007-16132, A69-9007-16092, A69-9007-16135) was included in some analyses and one (A69-9007-16119) was included in all analyses. See Table A3 for the details on which analyses the individuals were excluded from and why.



