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ABSTRACT

The brown trout (*Salmo trutta*) is a freshwater fish found in habitats ranging from small streams to rivers, lakes, estuaries and the coastal marine waters. The anadromous form, often termed sea trout, exhibits large variation in migratory strategies and habitat use. Many major estuaries in Norway are highly affected by human activity, as cities are often built around larger river outlets. This can potentially have negative consequences for the sea trout, as estuaries are the transition zone for their migrations between freshwater and sea. To gain more knowledge on the importance of estuaries as a habitat for sea trout, a two-year study was conducted in Gaulosen estuary in the Trondheimsfjord, Central Norway. This estuarine area has a relatively low level of impact from humans, making it an ideal place to study the sea trout's natural use of estuaries. From March 2018 through September 2019, 43 sea trout were tagged and tracked using acoustic telemetry in order to test the following hypotheses: (i) that the sea trout utilised the estuary year-round, (ii) that individuals with smaller body lengths, higher body condition, and especially males showed a greater utilisation of the estuary than other sea trout and (iii) that swimming depth changed throughout the year, with greater depths during the summer.

The sea trout used the estuary during all months of the year, but the number of individuals varied between seasons. The number of fish was highest in the period from December to May, while only 11% of the sea trout registered in the estuary at some point stayed there during the summer months of June to September. The tendency of remaining in the estuary during summer was influenced by sex, age, condition factor and body length (L_T), where females, fish with higher body condition, larger and older fish were more likely to remain resident in the estuary throughout the summer. The swimming depths in the estuary from March 2018 to August 2019 were generally surface-oriented, with a mean of 2.4 m (range 0.1 m – 25.6 m). It was influenced by season and body length, with smaller individuals staying deeper in the water and a deeper swimming depth during spring and summer. When comparing swimming depths between the estuary and the fjord for the period December 2018 to June 2019, it was significantly shallower in the estuary (mean = 2.9 m, range 0.4 – 25.6 meter) than in the fjord (mean = 5.7 m, range 0.5 – 14.0 meter). The tagged fish were found to visit nearby watercourses, and 18% of the sea trout captured and tagged in Gaulosen estuary during the spring, moved to either River Nidelva or River Orkla during the summer.

The results from this study illustrate that estuaries are important habitats for sea trout, where some individuals utilise it all year round, while other use it only as an overwintering habitat or as a transition zone between freshwater and the marine environment. The decline in sea trout populations seen in large parts of Norway makes it crucial to conserve habitats of high value for the sea trout. Given the importance of estuarine areas, protective measures should be taken to ensure that they are kept in good condition.

SAMMENDRAG

Brunørreten (*Salmo trutta*) er en ferskvannsfisk som lever i bekker, elver, innsjøer og marine kystområder. Anadrome individer, ofte kalt sjøørret, har stor variasjon i migrasjonsstrategi og habitatbruk. De fleste større elveoser i Norge er i dag kraftig påvirket av menneskelig aktivitet siden byer og tettsteder ofte er lagt rundt elvemunningene. Elveosene brukes av sjøørreten til å vandre mellom ferskvannshabitatene og de marine beiteområdene, og menneskelig aktivitet i elvemunningene kan derfor potensielt ha negative konsekvenser for sjøørreten. For å øke kunnskapen om hvor viktig elveoser er som habitat for sjøørreten, ble en toårig studie utført i Gaulosen i Trondheimsfjorden i Midt-Norge. Dette området er relativt lite påvirket av menneskelig aktivitet, noe som gjør det til et ideelt sted å studere sjøørretens naturlige bruk av elveoser gjennom året. Fra mars 2018 til september 2019, ble 43 sjøørret merket og sporet ved hjelp av akustisk telemetri for å undersøke de følgende hypotesene: (i) sjøørreten brukte elveosen året rundt (ii) individer med mindre kroppslengde, høyere kondisjonsfaktor, og spesielt hanner, viste større utnyttelse av elveosen (iii) svømmedybden endret seg gjennom året og var dypere om sommeren.

Sjøørreten brukte elveosen gjennom alle månedene i året, men antall individer varierte mellom årstidene. Antall fisk var høyest mellom desember og mai, og lavest fra juni til september når kun 11% av sjøørreten som på et tidspunkt var registrert i elveosen oppholdt seg her. Kjønn, alder, kondisjonsfaktor og kroppslengde (L_T) påvirket om sjøørreten oppholdt seg i elveosen om sommeren, hvor hunner, individer med høyere kondisjonsfaktor, større, og eldre fisk hadde større sannsynlighet for å bli igjen i elveosen. Sjøørreten i elveosen oppholdt seg generelt nært overflaten fra mars 2018 til august 2019 og hadde en gjennomsnittlig svømmedybde på 2.4 m (variasjonsbredde = 0.1 m – 25.6 m). Svømmedybden var påvirket av årstid og kroppslengde, hvor mindre fisk svømte dypere og sjøørreten hadde en dypere svømmedybde om våren og sommeren. En sammenligning av svømmedybden i elveosen og fjorden i perioden fra desember 2018 til juni 2019 viste at svømmedybden var grunnere i elveosen (gjennomsnittsdybde = 2.9 m, variasjonsbredde = 0.4 – 25.6 meter) enn i fjorden (gjennomsnittsdybde = 5.7 m, variasjonsbredde 0.5 – 14.0 meter). Sjøørreten vandret til nærliggende elver, og 18% av individene som ble merket i elveosen om våren, vandret til enten Nidelva eller Orkla i løpet av sommeren.

Resultatene fra denne studien illustrerer at elveoser er viktige habitat for sjøørreten, spesielt i perioden fra desember til mai. Tilbakegangen av sjøørretbestander i store deler av Norge gjør det ekstra viktig å bevare de habitatene som har høy verdi for sjøørreten. Elveoser er under sterkt press for utbygging i Norge, men gitt viktigheten av disse leveområdene bør de beholdes i god stand.

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1. INTRODUCTION

The brown trout (*Salmo trutta*) is a freshwater fish in the salmonid family and a dominant component of the Norwegian freshwater fish fauna. The species is found in habitats ranging from small streams to rivers, lakes, estuaries and coastal marine habitats. They spawn in freshwater, but the individuals might either spend their entire life in freshwater or become anadromous and migrate between the marine environment and freshwater. The anadromous form, often termed sea trout, show large variation in their migration depending on the type of watercourse they originate from, sex, food availability and their fitness (Eldøy, In review, Solomon, 2006, Wysujack et al., 2009). Marine migrations will maximize the sea trout's feeding opportunities which ultimately can lead to enhanced fitness and a reproductive advantage compared to the resident trout (Hendry, 2004). However, migration has its costs, in the form of higher energy expenditures of swimming and osmoregulation, as well as increased risk of predation, parasitism and diseases (Jonsson and Jonsson, 1993). The anadromous strategy is therefore only advantageous for the sea trout if the benefits of migration outweigh the costs. Thus, the "choice" between anadromy and freshwater residency is based on a risk-benefit trade-off, likely affected by a combination of genes and environmental factors (Chapman et al., 2012, Jonsson, 2006, Nevoux et al., 2019).

Estuaries are the transition zone between freshwater and the marine environment, and they are important habitats for sea trout. However, most estuaries from larger rivers in Norway are heavily affected by human activity as cities are often built around the river outlet. These urban areas have high economic value, and the estuaries of such rivers are therefore often prone to destruction or being channelized (Ulsund, 2017). Increased human activity can lead to significant habitat losses, and it can also decrease the quality of the remaining habitat (Courrat et al., 2009). Because of the value in these areas, there is a continuous pressure to start exploiting the remaining untouched estuaries. Gaulosen is one of a few relatively natural estuaries in Norway and is considered the only larger estuary in the southern and central part of Norway that is not highly affected by human activity (Ulsund, 2017). Because of the very low impact-level from anthropogenic activities, it is an ideal place to study the sea trout's natural use of estuaries year-round.

Sea trout rarely migrate far into the open ocean, instead they utilize the coastal habitat (Thorstad et al., 2016). Previous studies on sea trout and habitat use have found that some sea trout prefer the innermost parts of the fjords and stay closer to the river mouth year-round, while others may stay there during parts of the year and spend more time further out in the fjord (Bordeleau et al., 2018, Eldøy et al., 2015, Honkanen et al., 2020). Remaining in the inner parts of the fjord might have its advantages, including feeding opportunities, less risk from some marine predators as well as less risk of salmon lice (*Lepeophtheirus salmonis*) parasitism (Thorpe, 1994, Thorstad et al., 2015). Previous studies have shown that sea trout with poorer relative body condition in the spring prior to the seaward migration, are more likely to migrate to the outer parts of the fjord (Bordeleau et al., 2018, Eldøy, In review). In comparison, the fish that remain in the inner fjord tends to have a better overall condition. It has also been found that females are more likely to migrate to the outer-fjord, probably because a larger size means higher fecundity-at-age for female sea trout (Bordeleau et al., 2018, Eldøy, In review, Jonsson and Jonsson, 1993). Studies have found that sea trout spends more time in littoral habitats than it does in pelagic (Eldøy et al., 2015, Jensen et al., 2014), which might be linked to feeding behaviour with the sea trout's main prey found in shallow areas close to the shore (Knutsen et al., 2001). There might however be a size-dependent niche selection, with the smaller fish feeding more on brackish or freshwater invertebrates in the estuaries, while the larger individuals feed mainly on marine fish in the pelagic zone (Davidsen et al., 2017a).

Previous studies have shown considerable variability in the degree to which sea trout populations utilize the estuarine habitat (Honkanen et al., 2020, Moore and Potter, 1994). With some just passing through to get to the sea, while others spend more time in this habitat throughout the year. Sea trout have been found to overwinter in the river estuary as well as in freshwater habitat (Jonsson and Jonsson, 2002). In a study done on high northern latitude populations of sea trout, 91% of the individuals were found overwintering in estuarine or marine waters, and it was documented that the estuarine habitat played an important role during the winter months (Jensen and Rikardsen, 2012). In populations from rivers with lakes or deep pools, these areas might be the preferred wintering area as it is a stable environment with ice cover and less risk of predation. However, in riverine populations where this type of habitat is missing, it might be more advantageous to move to the estuary (Jensen and Rikardsen, 2008). During summer, it has been observed that some sea trout feed in the estuary while others migrate further out (Eldøy et al., 2015, Honkanen et al., 2020).

Sea trout are generally surface-oriented and utilizes the upper part of the water column, with occasional deeper dives (Eldøy et al., 2017, Rikardsen et al., 2007). In one study of swimming depths, the mean depth was found to be 1.8 meters, and the sea trout spent 93% of the time no deeper than 3 m (Rikardsen et al., 2007). This seems to also be true for the estuary, where studies have shown that the sea trout prefers to stay closer to the surface and spends most of the time at shallower depths (Eldøy et al., 2017, Kristensen et al., 2018). In one of the studies, the swimming depths were shallower in the estuary than in other habitats, including pelagic, nearshore with and without cliffs (Eldøy et al., 2017). Here, the swimming depth of sea trout was furthermore found to be influenced by habitat, time of day (day *vs* night), season, seawater temperature and the body length at the time of tagging.

Over the past two decades, there has been observed a decline in the sea trout populations in large parts of Norway (Anon, 2015) as well as in other European countries (ICES 2013). A recent report on the conditions of 430 Norwegian sea trout populations found that almost half of the populations were in a poor or very poor state (48%) (Anon, 2019). The report concluded that sea trout are negatively impacted by several anthropogenic stressors, including salmon lice, agriculture, hydropower, overexploitation and habitat changes. Getting a better understanding of the habitats used by sea trout is crucial to achieve efficient management of the populations and to evaluate their vulnerability to habitat change and other anthropogenic activities.

The objectives of this study were to gain better knowledge on the importance of estuaries as a habitat for sea trout. This was done by use of acoustic telemetry to investigate the spatiotemporal use of the estuary, including swimming depth. We tested the following hypotheses: (i) that the sea trout utilised the estuary year-round, (ii) that individuals with smaller body lengths, higher body condition, and especially males showed a greater utilisation of the estuary than other sea trout and (iii) that swimming depth changed throughout the year, with greater depths during the summer.

2. MATERIALS AND METHODS

2.1 Study area

The study was conducted during 2018 and 2019 in a branch of the Trondheim fjord, located in Trøndelag county in central Norway (Figure 1). Gaulosen estuary (63°20'18"N 10°12'16"E) consists of large tidal flats and shallow areas with sand and mud beds. Maximum water depth in the study area was 200 m. The River Gaula, with a catchment area of 3668 km^2, is the main river that drains into the estuary, and it is this river outlet and the tide that mainly control the currents in Gaulosen. In the estuary, the freshwater from River Gaula meets the saltwater from the ocean and mixes. This forms a layer of brackish water at the surface, while the more marine waters stay deeper in the water column.

Gaulosen is a larger river outlet and estuary in relatively good natural condition and is therefore of high ecological value. It has been a marine protected area since June 2016, and the protected zone covers an area of about 11 km^2. The conservation value of this area is linked to its ecological functions, the benthic environment and the chemical composition which gives rise to a rich and diverse plant and animal life and makes it an important area for birds and fishes. Especially the large shallow soft bottom areas are important living and nursery grounds for many species of fish (Ulsund, 2017).

In addition to Gaulosen estuary and the Trondheim fjord system, the study area also included nearby watercourses connected to the fjord (the rivers Gaula, Vigda, Orkla and Nidelva).

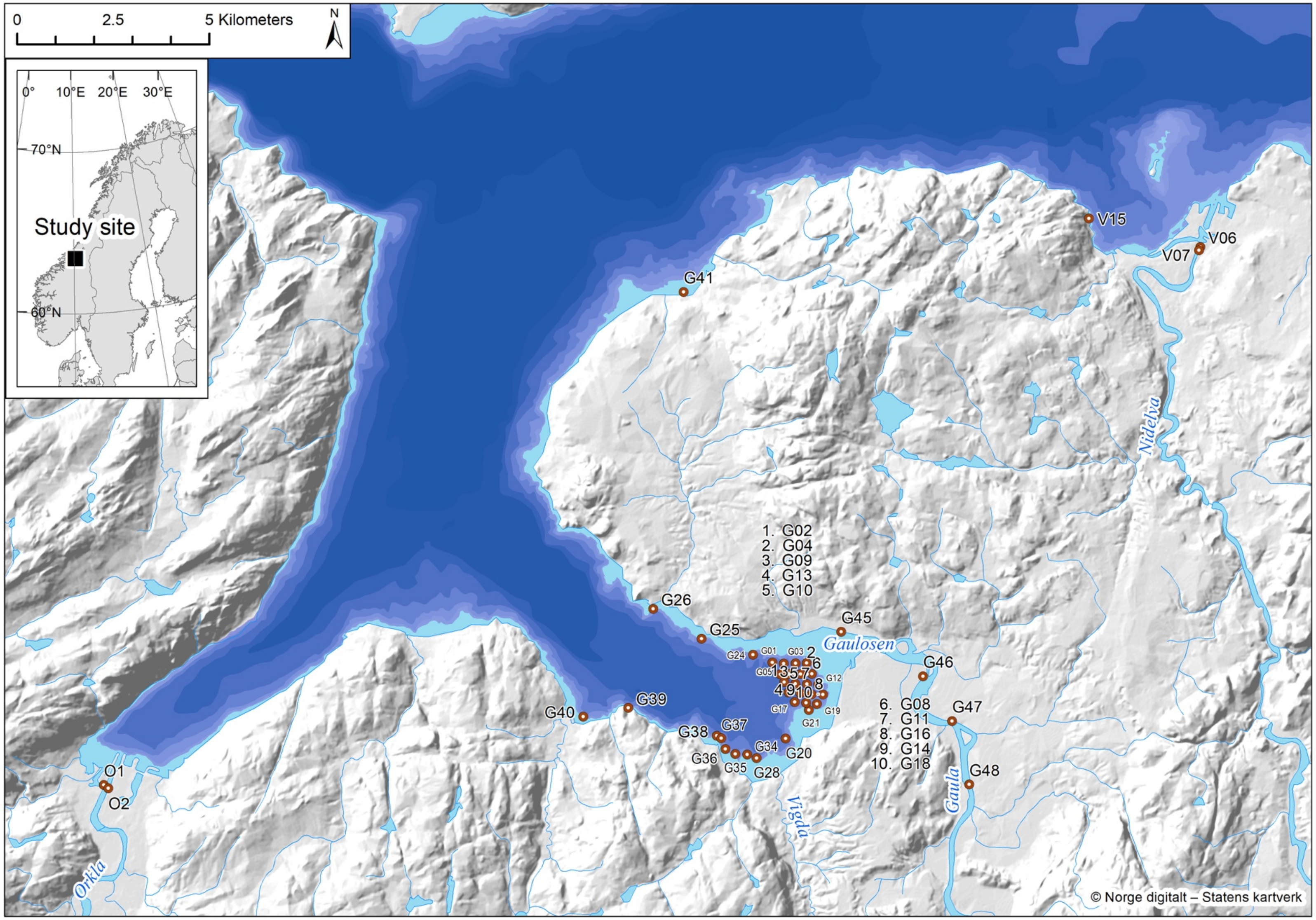

FIGURE 1. Map of study area showing the positions of the deployed acoustic receivers (red circles) used in the study. Showing Gaulosen estuary, River Gaula, River Vigda, River Orkla and River Nidelva.

2.2 Tracking of sea trout

2.2.1 Fish capture and tagging

Three groups of sea trout were captured and tagged with acoustics transmitters from the spring of 2018 to the autumn of 2019 (Table 1). The first group (GS18) consisted of 23 fish and were caught in Gaulosen estuary during March and April 2018. The second group (VA18) had ten fish and were caught in River Vigda in October 2018. The third and last group (GS19) consisted of ten fish and were caught in Gaulosen estuary from February to April 2019. In total, 43 sea trout were caught and tagged. Total body length (L_T) for the individuals in the study varied from 260 – 650 mm, and the mean body length for the fish was 429 mm (SD = 107 mm) (Table 1). Body mass of the sea trout varied from 130 – 2270 g with an average body weight of 801 g (SD = 617 g). The age of the sea trout, estimated by scale-reading, varied from 3 – 8 years. However, the age could not be determined for seven individuals.

The fish were caught using fishing rods and line (Gaulosen estuary) or flashlights and landing nets for capture at night (River Vigda). After capture, the fish were kept in holding nets until the tagging process (< 4 hours). The sea trout were implanted with individual coded acoustic transmitters that recorded their presence in the study area. In addition to presence, 33 sea trout had tags that also recorded swimming depth (Thelma Biotel model D-HP9L; diameter: 9 mm, length: 39 mm, weight in air: 6.8 g, estimated battery life: 315 days).

TABLE 1. Tagging group, date, watercourse, number of individuals, total body length, body mass and age of tagged sea trout. Each tagging group were given a name based on tagging location; G for Gaulosen and V for River Vigda, season; S for spring and A for autumn, and year.

Tagging group	Date	Watercourse	n	L_T (mm)		Body mass (g)		Age (years)	
				Mean ± S.D.	Range	Mean ± S.D.	Range	Mean ± S.D.	Range
GS18	20.03 - 05.04 2018	Gaulosen estuary	23	378 ± 94	260 - 620	550 ± 518	130 - 2150	4,5 ± 0,8	3 - 6
VA18	10.10 2018	River Vigda	10	515 ± 65	450 - 650	1255 ± 499	750 - 2270	5,7 ± 0,5	5 - 6
GS19	25.02 - 04.04 2019	Gaulosen estuary	10	458 ± 109	355 - 640	954 ± 695	340 - 2000	5,6 ± 1,6	3 - 8
		Total	43						

The following procedure was used in the tagging process of all the fish used in the study. The fish were transferred from the holding nets and into a container with a solution of phenoxy-ethanol (EEC No 204 589-7, 0.5 mL per L of water) that sedated the fish after approximately four minutes of exposure. Once anaesthetized, the fish was transferred to a plastic tube with water. The total body length (L_T) of the fish was measured, from the tip of the snout to tip of the longest caudal fin, as well as the weight. A two cm incision was made in the body cavity, and a disinfected transmitter was carefully placed inside before the incision was closed with two or three independent sutures. The size of the transmitter used was adjusted to the size of the fish to reduce tagging effects. A small sample of the fin was cut off and stored in alcohol for future molecular analyses, and five to ten scales were collected from the fish for later analyses of age. In addition, a carlin tag with a phone number for reporting of recapture was attached to the fish, below the dorsal fin. After the tagging procedure, which lasted between three to five minutes, each fish was kept in a container with water, until normal swimming behaviour and breathing frequency was obtained. The fish was then released into a calm part of the river or estuary, as close to the capture site as possible.

2.2.3 Acoustic tracking

The tagged sea trout were tracked using a total of 41 acoustic receivers (Thelma Biotel model TBR 700; Vemco model VR2-AR and VR2W). Out of the total, 33 of the receivers were placed in the main study area in the estuary and fjord, while the remaining eight were placed in other watercourses in the area (Figure 1). In the main study area, 20 receivers were placed in the estuary and 13 were placed along the shore on both sides of the fjord. The receivers placed in the estuary were deployed in a closer grid than in the other part of the fjord in order to get more detailed information about the locations of the fish. The groups of receivers were operating at different time periods during the study (Table 2). The depth of deployment varied from 30 – 120 meters. The receivers deployed in the fjord were mounted on a 14 mm rope five meters below the buoys at the sea surface. To keep the receivers at the correct position and prevent them from drifting, 140 kg anchors were attached at the bottom. During the two-year study period, the receivers were checked every 2 – 4 months to download data, check the battery and to make sure they were in good condition.

TABLE 2. Operating period for the acoustic receivers used in the study, with the watercourse where the receivers were placed, the number of receivers and the operating period.

Watercourse	Number of receivers	Operating period
Estuary	20	01.03.18 – 30.09.19
Fjord	13	01.11.18 – 30.09.19
River Orkla	2	18.12.18 – 30.09.19
River Nidelva	2	01.03.18 – 30.09.19
River Gaula: Station 1	1	23.03.18 – 19.04.18 and 18.12.18 – 30.09.19
River Gaula: Station 2	1	06.04.18 – 19.04.18 and 28.02.19 – 30.09.19
River Gaula: Station 3	1	05.04.18 – 19.04.18 and 20.03.19 – 30.09.19
River Gaula: Station 4	1	20.03.19 – 30.09.19

2.2.4 Receiver performance

The transmitter detection range of the receivers placed in Gaulosen was measured on 12.01.2018 in good weather conditions. This was done by placing a receiver (Thelma Biotel AS, model: TBR 700) on a buoy two meters down and lowering two tags down in the water at different distances from the receiver. The detection range was generally 300-350 meters, with a measured maximum detection distance of 615 meters. The detection range of receivers are, however, known to vary with the hydrological conditions in the study area (Kessel et al., 2014), and especially in estuaries with mixing water layers of freshwater and brackish waters, detection ranges may be highly variable.

2.3 Genetic sex determination

A small sample taken from the adipose fin of each tagged fish were genetically analysed to determine the sex of each individual. At the NTNU University museum DNA lab, the DNA was extracted from ethanol-preserved fin clips with the QuickExtract kit (Epigen), according to manufacturer's protocol with the exception for the extraction volume, which was reduced to 150 µL. Sex was determined by PCR amplification of a 200 base pairs (bp) fragment situated in the first intron of the male-specific SDY gene, using the Salmo-sdY-F and Salmo sdY-R primers (Quéméré et al., 2014). The PCR was performed in 10 µL reactions using the Qiagen

Multiplex PCR kit. The following PCR profile was used: 95 °C for 15 min, 11 cycles of touchdown PCR, 94 °C for 30 s, 63–52 °C for 30 s, 72 °C for 1 min, followed by 25 cycles of 94 °C for 30 s, 52 °C for 30 s, 72 °C for 1 min, with a final extension at 72 °C for 10 min. Sex was scored by running the PCR products on 1% agarose gels. Sex could be determined with confidence for all but one fish, so this individual had to be excluded from final models including sex as an explanatory variable.

2.4 Scale sample analysis

During the tagging procedure, five to ten scales were collected from each fish and stored in paper envelopes. The scales were collected from the area past the dorsal fin and above the lateral line on the fish. The scales were used for age determination of each individual.

The analyses of each scale sample were done with a stereoscopic microscope. From the scales collected from each fish, the most suitable scales for age determination were retrieved and copied onto 1 mm Lexan plates using a pressing iron. When choosing scales to press, replacement scales and scales with substantial damages were avoided as they are challenging to read accurately. Lastly, the Lexan plates with scale imprints were analysed with a computer-controlled stereoscope (Leica M165C with camera Leica MC170 HD) and its connected software, LAS V4.5 (Leica, 2014). The results from the analyses were checked by a person with long experience in reading sea trout scales.

2.5 Environmental parameters

To be able to describe the specific conditions preferred by the sea trout, measurements of the salinity and temperature were taken every fourth hour in the estuary during the study period. This was done by temperature and salinity recorders (Star Oddi dataloggers model DST milli-TD and DST milli-CT) placed at the location of two of the receivers in the estuary. The recorders were attached underneath the buoys of the acoustic receivers, at approximately 1,5 meters depth, which was the expected mean swimming depth of the sea trout.

2.6 Data analyses

2.6.1 Condition factor

Individual condition factor (K) was calculated using the formula

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

Where W is the mass (g) of the fish, and L is the total body length (cm).

2.6.2 Data filtering

Registrations of tagged fish were collected from 26.01.2018 – 30.09.2019. The initial number of registrations from the 44 receivers was 963 264. When using acoustic telemetry, false registrations can occur from tag collision, which is when signals from different acoustic transmitters happen at the same time and the receiver interprets this as a new separate signal. Although it is not possible to completely eliminate all registration errors (Pincock, 2012), filtering the data can reduce the number of false registration. The filter that was used required at least two registrations from the same fish ID at the same receiver within the time span of ten minutes to accept the registration as true. This filter removed 35 636 registrations from the data set.

In R, negative depths were removed from the data as they were thought to be false registrations as well, and this removed 4 419 registrations from the data. Furthermore, depths below 30 meters were removed to get rid of registrations from dead fish that were manually found in the data set. This removed 71 964 registrations, and the final dataset used for analyses thus contained 851 245 registrations.

2.6.3 Statistical analyses

All statistical analyses and plotting of data were conducted with R studio (RStudio Team, 2019) and R version 3.3.3 (R Core Team, 2019). To-way analyses of variance were done between the tagging groups to test for differences in body length (L_T), weight, and age. For this, Wilcoxon rank sum tests were conducted as the assumption of normality was not met. To test for differences in swimming depth between the estuary and the fjord, an ANOVA test was done. For all the models and tests, a statistical significance level of $p = 0.05$ was used.

To test for possible differences in body length, Fulton's condition factor, age and sex between the sea trout that stayed in the estuary during summer and the sea trout that left, a generalised linear model was used. It included a binomial response variable (stayed or did not stay) and length, body condition, sex, age and the interaction between length and age as explanatory variables. An overview of the model results was found using the inbuilt "summary" function in R.

For analyses of factors possibly influencing the swimming depth of the sea trout, a mixed effects model was made using the "lme" function from the "nlme" package in R (Pinheiro, 2018). To see if the swimming depth was influenced by the changing conditions throughout the year, the variable "season" was made by dividing the months in the study into four groups; winter (December to February), spring (March to May), summer (June to August), and autumn (September to November). The full model included log-transformed swimming depth as a response variable as well as age, sex, season, body length and the interaction between length and age as fixed explanatory effects. The transmitter ID for the individual fish was used as a random effect. Akaike's information criterion (AIC) was used to identify the best fitting model with the "dredge" function in the MuMIn R package (Barton, 2018). The model selection gave support for multiple alternative models (Δ AIC < 2), so conditional model averaging was applied for calculating model parameter estimates for these models.

3. RESULTS

3.1 Environmental parameters

The temperature and salinity loggers placed at approximately 1,5-meter depth at two receiver locations gave a temperature and salinity profile of the estuary during 2018, as shown in figure 2. The water temperature was low, between 2 and 8 °C, from January until May, when the water temperature increased towards August. It reached the highest daily mean temperature of 19 °C on the 27 of July and thereafter decreased. The salinity was relatively high in the winter months from January to April. It varied around 30‰, almost full seawater. In April, the spring flood combined with the tide created large fluctuations in the salinity, with variations from 2 to 30‰. In June it became more stabilised, and the rest of the year the salinity mostly stayed between 10 to 20‰.

There was generally low variation in temperature between the loggers placed at receiver fifteen (mean = 10.37 °C, SD ± 4.24 °C) and receiver nine (mean 10.13 °C, SD ± 4.48 °C). The salinity was also very similar at receiver fifteen (mean 19.09 °C, SD ± 8.92 °C) and receiver nine (mean 19.03 °C, SD ± 8.81 °C). Both of these receivers were placed in the estuary, but receiver fifteen was placed closer to land (Figure 1).

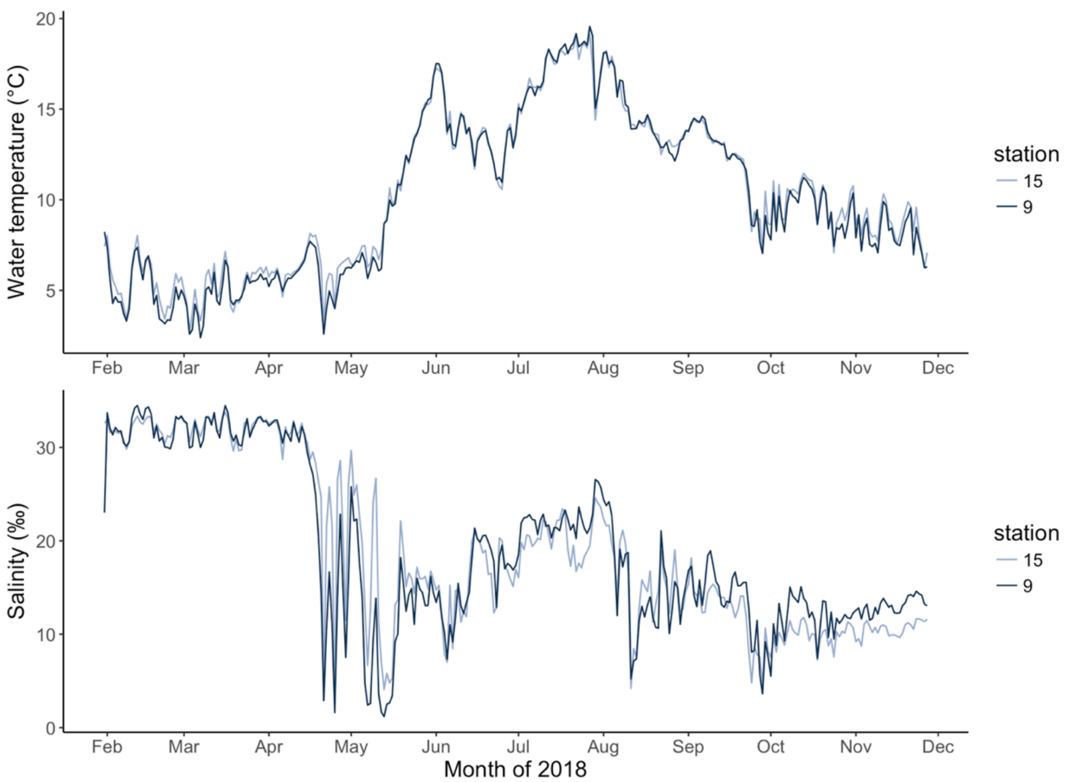

FIGURE 2. Mean daily water temperature (upper plot) and mean daily salinity (lower plot) at ~1,5 m depth from two receivers placed in Gaulosen estuary, during the period 31.01.2018 to 27.11.2018.

3.2 Study population

In total, 43 fish were captured and tagged to be used in this study. The total length (LT) of the individuals varied from 260 to 640 mm, with a mean average of 429 mm (SD = 107, figure 3.a). The body mass was obtained for 41 of the 43 fish caught and varied from 130 to 2270 g (mean = 801 g, SD = 617, figure 3.b).

Comparison of the length between the tree tagging groups (Wilcoxon rank sum test, $n = 43$) showed that fish from the tagging group VA18 had a higher LT than fish caught in GS18 (p-value < 0.001), but there was no significant difference between VA18 and GS19 (p-value = $\geq$ 0.05). Fish caught in GS19 had a higher LT than the fish caught in GS18 (p-value < 0.05). When testing for variation in body mass between the tagging groups (Wilcoxon rank sum test, $n = 41$), it was found that fish in group VA18 had a higher mass than the fish from GS18 (p-value < 0.001). There was, however, no significant difference between VA18 and GS19 (p-value ≥ 0.05) or between GS18 and GS19 (p-value ≥ 0.05).

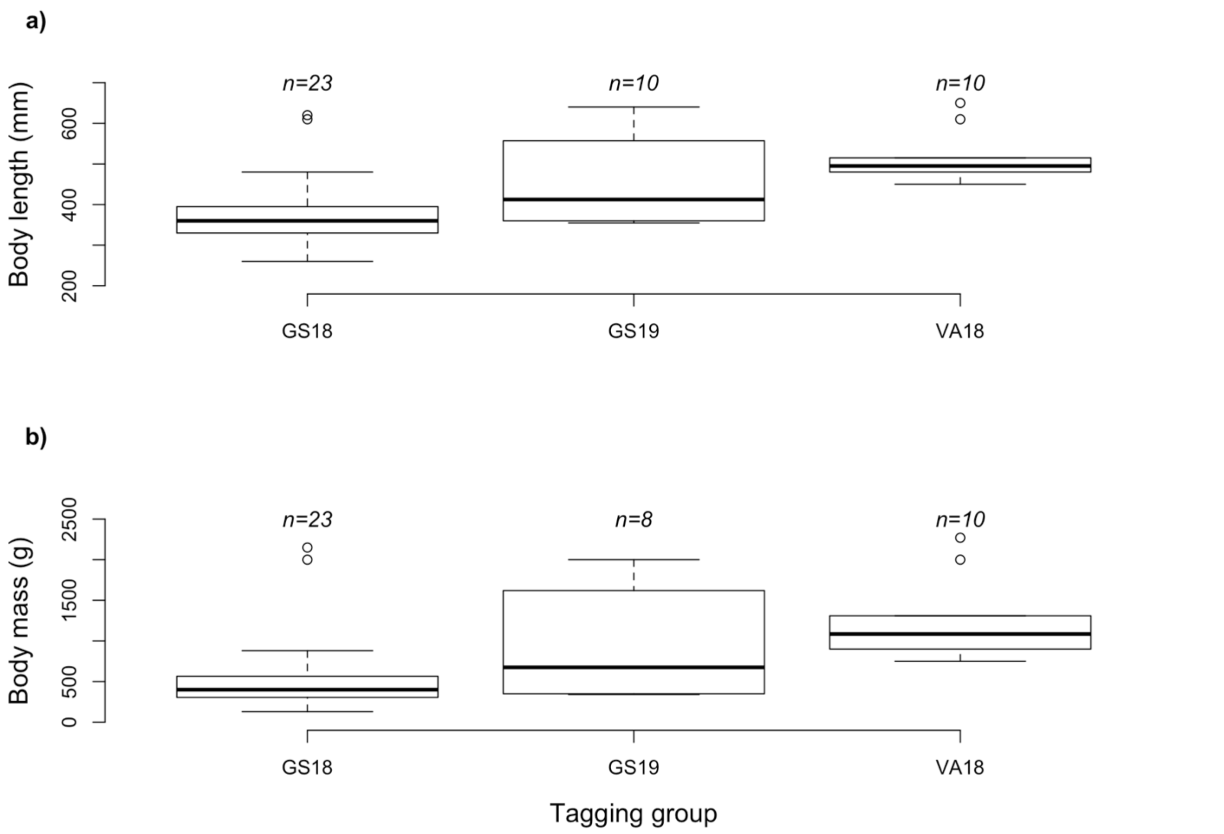

FIGURE 3. Body length (a) and body mass (b) of the different tagging groups used in the study. The box-and-whisker plots display the median values (bold lines), the interquartile ranges (boxes), the 5th and 95th percentiles (whiskers), as well as outliers (dots). Numbers above each plot indicate sample size of each tagging group.

The mean Fulton's body condition factor for the 41 fish with a measured body mass was 0.8 (SD = 0.1, figure 4) The back-calculated age of the fish at the time of tagging varied from 3 to 8 years (mean = 5 years, SD = 1 year). Out of the 43 sea trout tagged in the study, 24 (56%) where females and 18 (42%) were males. For one fish, the genetical analyses failed to confidently determine the sex.

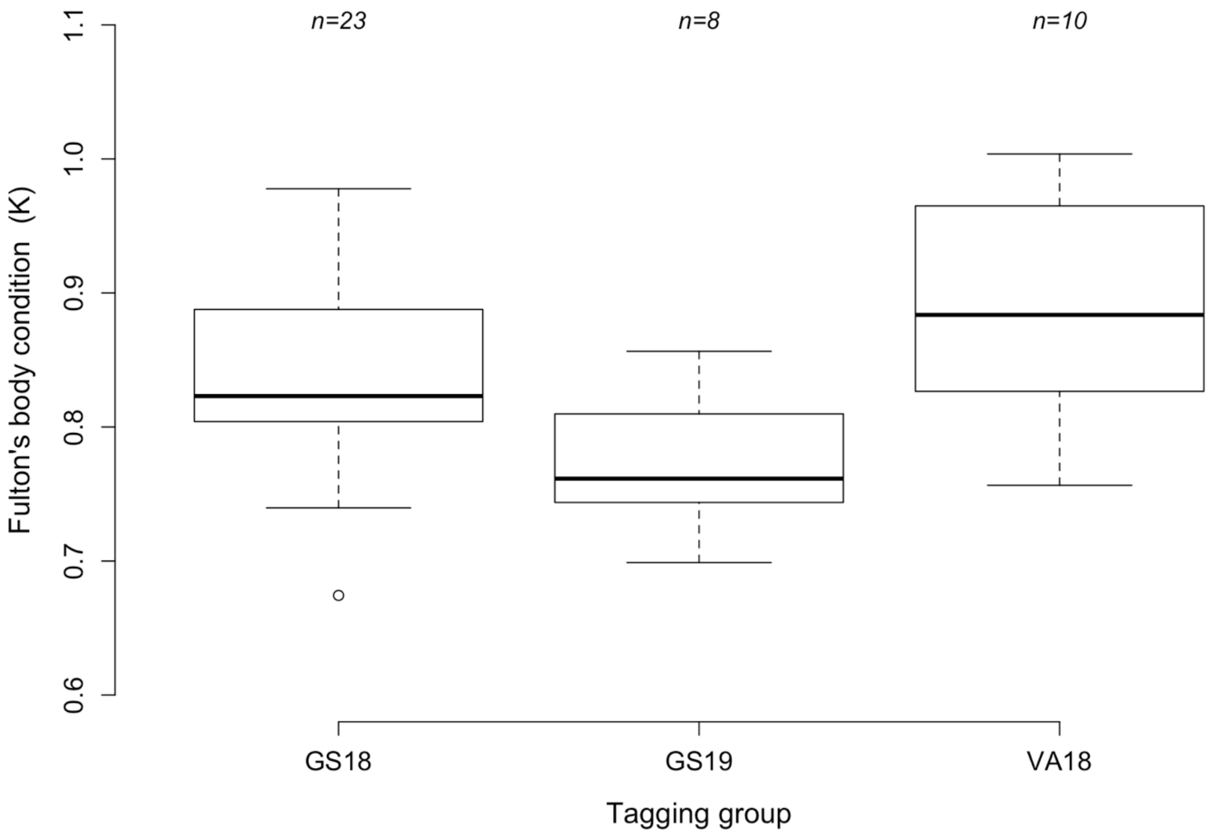

FIGURE 4. Fulton's body condition for the sea trout in the tree tagging groups at the time of tagging.

No significant variation in Fulton's body condition (Wilcoxon rank sum test, $n = 41$) was observed between the fish from tagging group VA18 and GS18 (p-value ≥ 0.05). Tagging group VA18 did, however, have a significantly higher body condition at tagging than GS19 (p-value < 0.01). Fish from GS18 had a significantly higher body condition than the fish from GS19 (p-value < 0.05).

Test of age between the tree tagging groups (Wilcoxon rank sum test, $n = 36$) showed that there was a significant difference between VA18 and GS18 (p-value < 0.01), where VA18 had a higher average age than GS18. No significant variance was found between VA18 and GS19 (p-value ≥ 0.05), or between GS18 and GS19 (p-value ≥ 0.05).

3.3 Acoustic tracking of sea trout

Of the 43 fish tagged for telemetry analyses, 40 individuals (93%) were recorded at some point at one of the acoustic receivers in the study system, including the receivers placed in River Nidelva, River Orkla and River Gaula. The remaining three individuals were never recorded at all. At the receivers in the estuary and fjord, 37 of the fish were recorded at some point. However, several fish only had a few registrations, including four fish that only had one registration in Gaulosen throughout the whole study period. In general, there was a large variation in the number of days each fish was registered in the fjord (Figure 5).

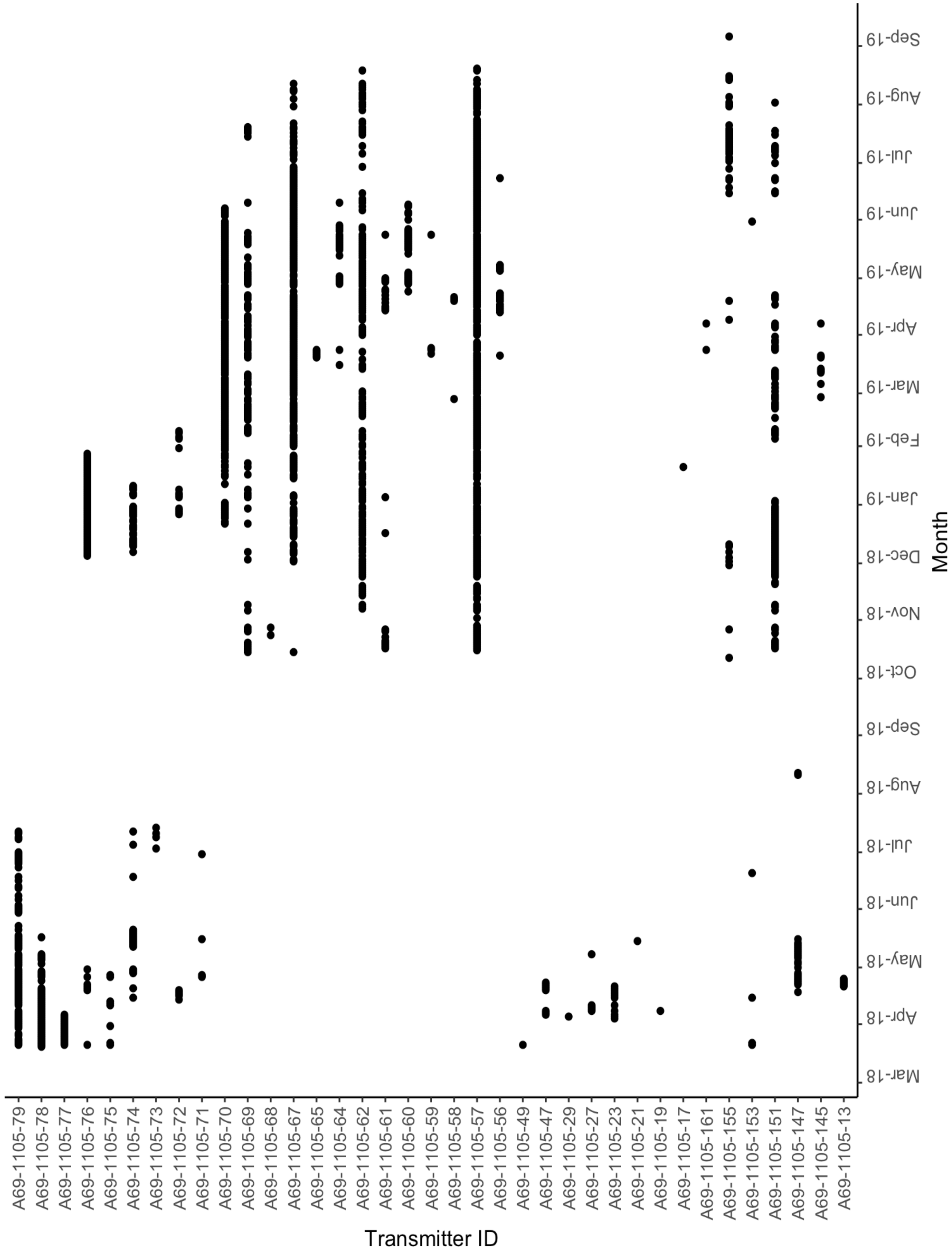

FIGURE 5. Registrations of fish at the receivers placed in the estuary as well as the ones along the coast. Each transmitter ID on the Y-axis represents one individual fish.

3.4 Characteristics of the estuary as a habitat

3.4.1 Time spent in the estuary

During the study, 37 (86%) sea trout were registered in the estuary at some point, but the number of fish residing here varied throughout the year (Figure 6). Mean number of days registered in the estuary was 33 days (SD = 59 days, range = 1 – 271 days). The estuary was found to be more frequently used during winter and spring (December to May), where the monthly average was ten individuals. There was a clear decrease of sea trout present in the estuary between June and September, with a monthly average of only four (11%) individuals.

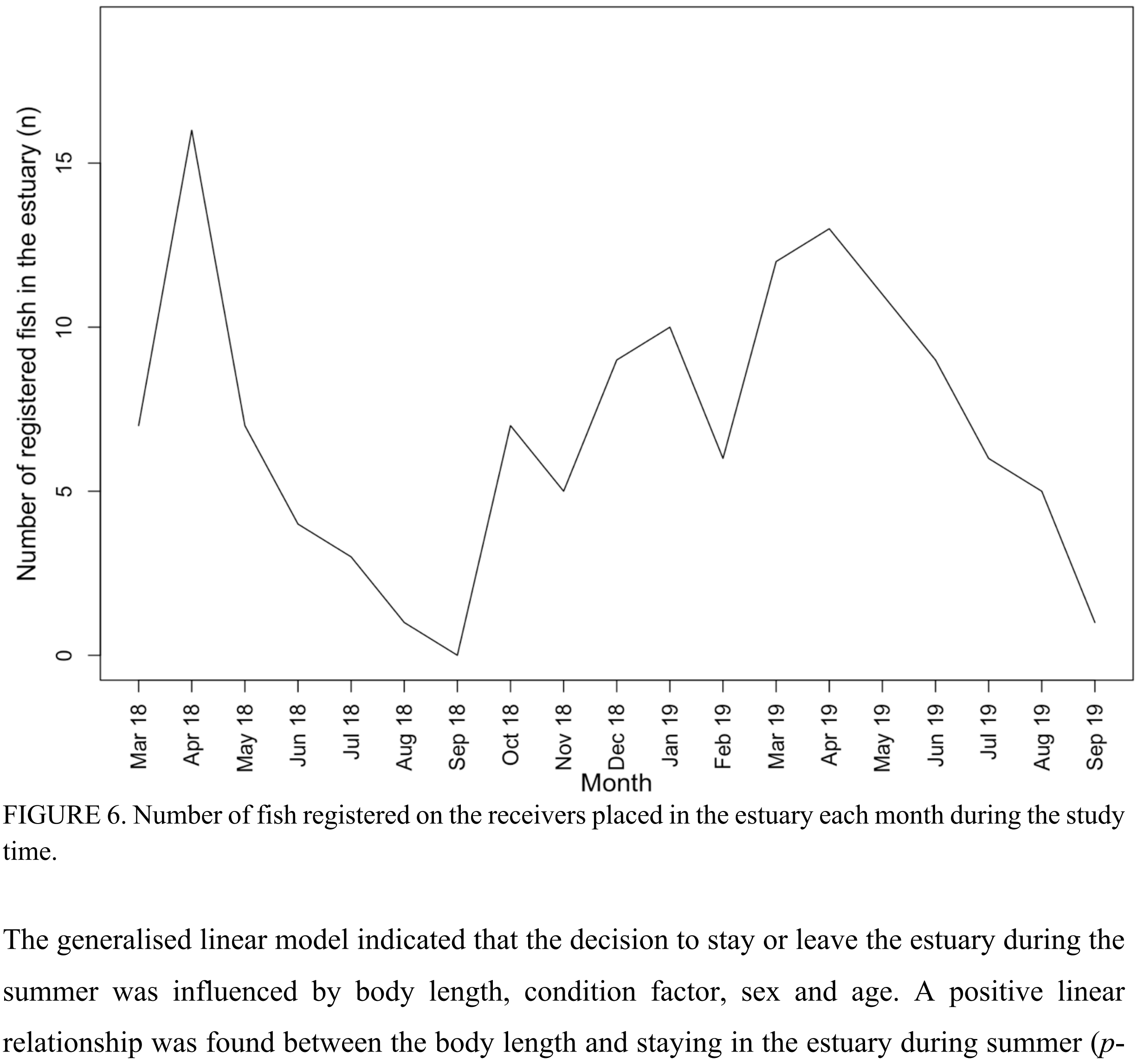

FIGURE 6. Number of fish registered on the receivers placed in the estuary each month during the study time.

The generalised linear model indicated that the decision to stay or leave the estuary during the summer was influenced by body length, condition factor, sex and age. A positive linear relationship was found between the body length and staying in the estuary during summer (p-value < 0.001), and the same was found for body condition (p-value < 0.001). Larger fish with better body condition were more likely to stay in the estuary during summer. Age was positively correlated with staying (p-value < 0.001) with older fish more likely to stay during summer.

The interaction between length age had a negative relationship with staying (p-value < 0.001), so faster growing individuals were more likely to wander to the outer fjord. It also showed that males were more likely to leave the estuary during summer than females (p-value < 0.001).

3.4.2 Swimming depth in the estuary

In total, 33 (77%) of the tagged fish had a depth sensor that recorded during the study time. Of these 33 fish, 29 of them were registered in the estuary at some point. The mean swimming depth in the estuary during the study period was 2.4 m (SD = 3.1 m, range = 0.1 m - 25.6 m), and the median swimming depth was 1.6 m. There was some variation in the average swimming depth from month to month, but the sea trout mostly utilized the top surface layer of the water column in the estuary (Figure 7). The deepest mean swimming depth was found in July 2018 (mean = 3.1 m, SD = 2.8 m), March 2019 (mean = 4.6 m, SD = 8.0 m) and June 2019 (mean = 3.5 m, SD = 4.1 m). None of the individuals with a depth sensor were present during August or September 2018 so these months are not shown in the figure.

There were three equally well fitted mixed effects models for the mean swimming depth of sea trout, indicating that it was influenced by season, body length, sex and age (Δ AIC < 2, table 3). Season and length seemed to be the best indicators of swimming depth. Model conditional averaging showed that smaller individuals had a deeper swimming depth (p-value < 0.05), and that the swimming depth was deeper during spring and summer (March to August) (p-value < 0.05). It also showed that males and older fish were negatively correlated with swimming depth, but these variables did not have significant p-values.

TABLE 3. Model selection for the influences of swimming depth, with the variables season (SN), length (L), sex (S) and age (A).

Model	AIC	ΔAIC	AIC weights	df
1 (SN, L)	1247	0.00	0.29	5
2 (SN, L, S)	1247	0.42	0.24	6
3 (SN, L, A)	1249	1.99	0.11	6

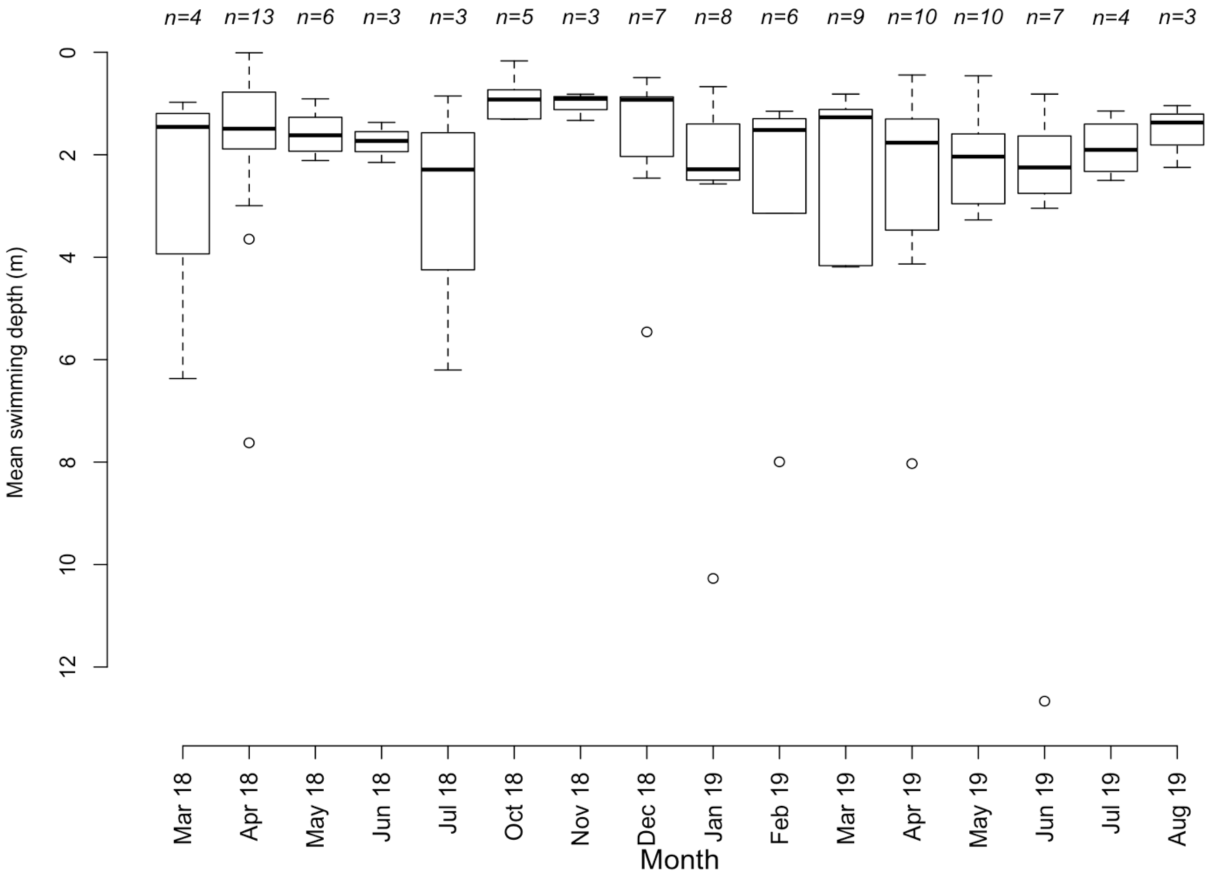

FIGURE 7. Monthly average sea trout swimming depth in estuarine habitat from 2018 to August 2019.

3.4.3 Differences in swimming depth between the estuary and the fjord

A comparison of the swimming depths recorded at the receivers in the estuary and the fjord was made from December 2018 to June 2019, since this was the period the receivers in the fjord were active and had depth registrations. During these months, 15 fish were registered in the estuary, and 12 fish were registered on the receivers further out in the fjord.

In the estuary, the sea trout mainly stayed in the upper part of the water column (Figure 8). During this period the mean swimming depth in the estuary was 2.9 m (SD = 3.9 m, range = 0.4 - 25.6 meter). On the receivers outside the estuary, there was more variation in the swimming depth, and the fish spent more time deeper in the water column. Here, the average swimming depth was 5.7 m (SD = 4.5 m, range = 0.5 - 14.0 meter). The first two months (December and January), the median swimming depth was between ten and fifteen meters. From February to April the fish stayed slightly higher in the water column, and in the last two months, May and June, the fish stayed in the top part of the water column with the median depth above three meters.

To see if there were any significant differences between the swimming depths in the estuary and the fjord, a two-way ANOVA test was done. This test showed that there was a significant difference between the two habitats, with swimming depths being deeper in the fjord than in the estuary ($n = 27$, p-value < 0.01).

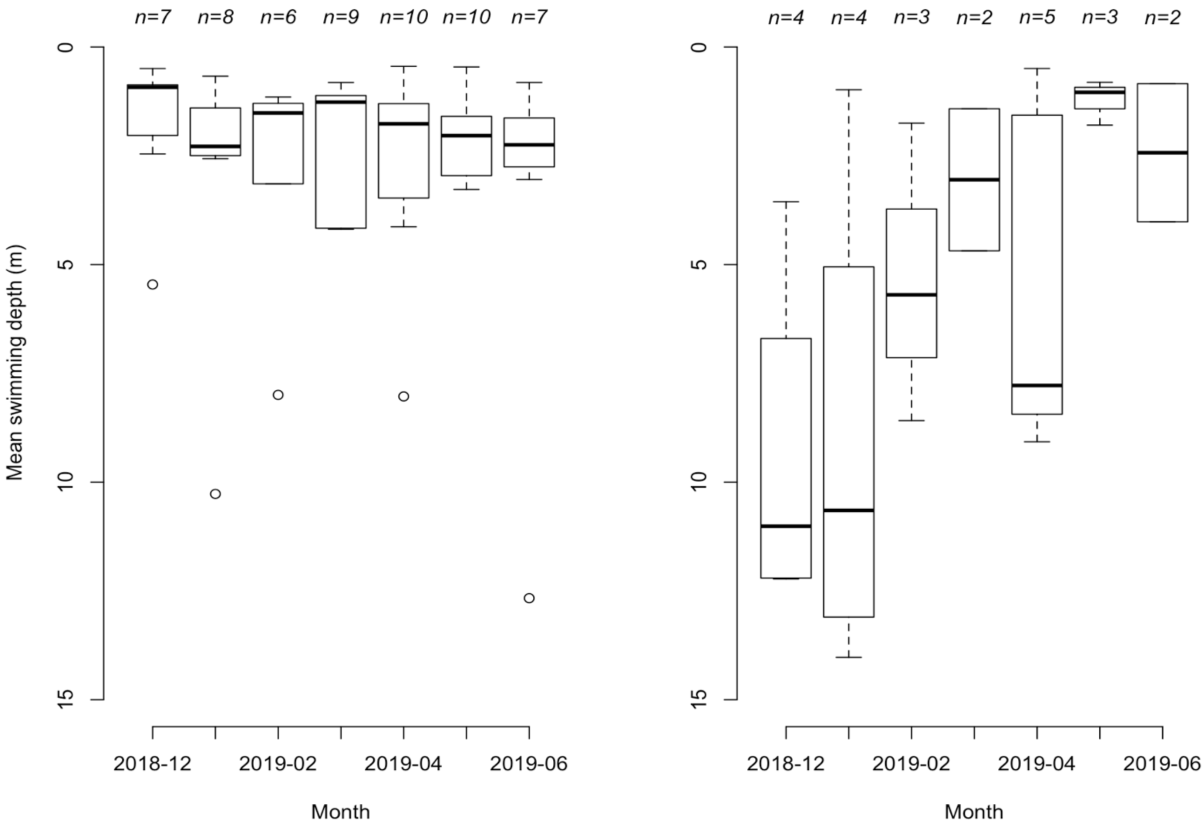

FIGURE 8. Monthly average sea trout swimming depth inside the estuary (a) and in the fjord (b) from December 2018 to June 2019.

3.4.4 Movement between watercourses

The acoustic receivers placed in the different rivers (Nidelva, Gaula, Orkla) were used to observe the movement between the estuary and freshwater habitats. In total, 18% ($n = 6$) of the sea trout captured and tagged in Gaulosen estuary during the spring, later moved to either River Nidelva or River Orkla during the summer.

Many fish also moved between the receivers deployed in the estuary and the receiver deployed upstream in the lower part of River Gaula. In total, 16 fish were registered in the river at some point. River Gaula had four receivers placed at different locations to be able to see what parts of the river the sea trout utilized (Figure 1). Most of the registrations were at the first receiver closest to the estuary, but several fish were also registered at the other receivers throughout 2019 (Figure 9). In general, the sea trout were registered in River Gaula during spring and summer (March to August). Receiver 1 had registrations every week from January to October, but there was a larger amount of fish present from March to August. Receiver 2 had registrations from February to August, while receiver 3 had registrations from March to August. Receiver 4, placed furthest up in the river, only had registrations during June and August. However, receiver 2 was not operating in January or at the start of February, and receiver 3 and 4 were not operating during January, February or March of 2019, potentially missing some registrations.

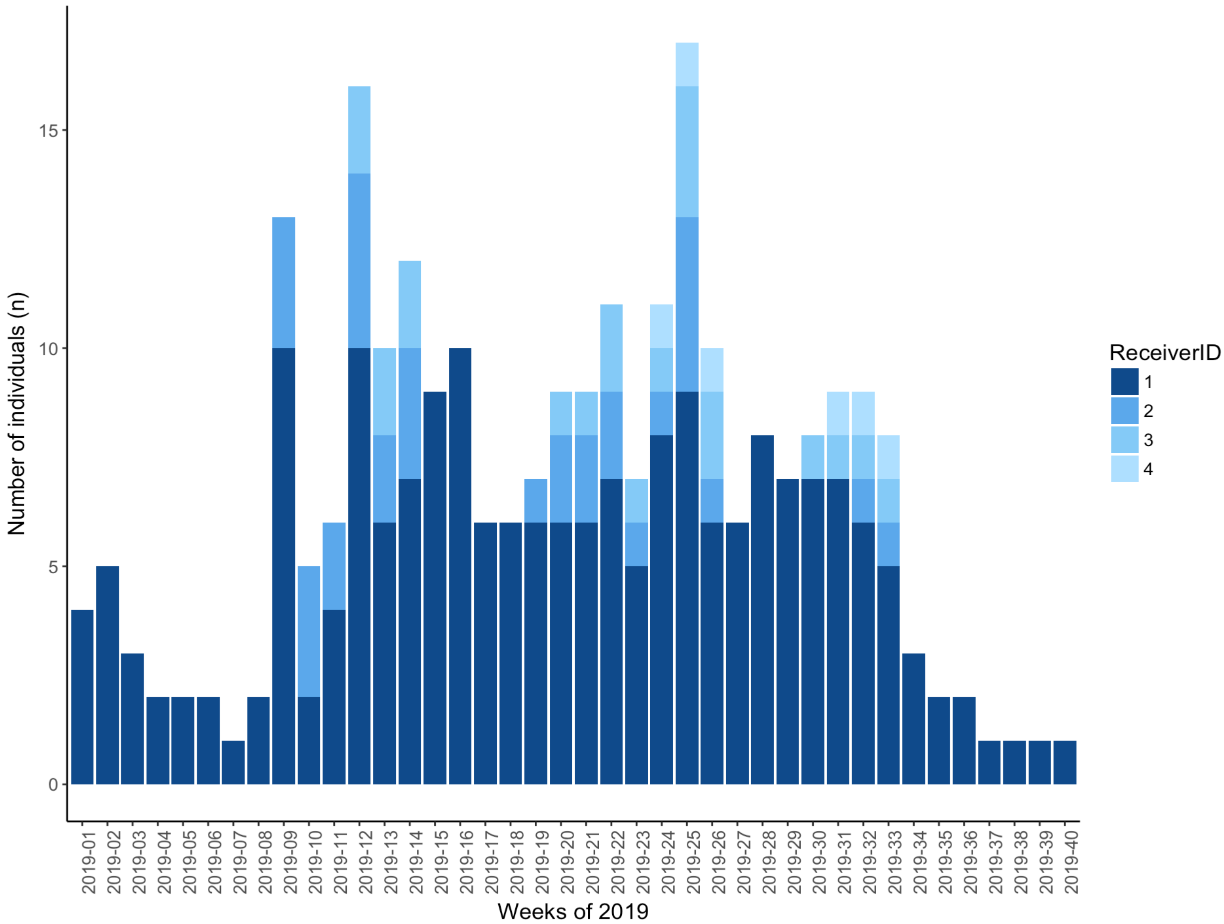

FIGURE 9. Number of fish at the different receivers in River Gaula, where 1 is the receiver closest to the estuary and 4 is the receiver furthest up in the river. Receiver 2 was not operating in January and the start of February and receiver 3 and 4 were not operating during January, February or March of 2019.

4. DISCUSSION

Estuaries are important habitats for sea trout, and the results from this study further describe how the tagged individuals used the estuarine areas throughout the year. The study was conducted over a two-year period, and acoustic telemetry was used to examine how the sea trout utilised the estuary and the fjord. Sea trout were found in the estuary during all months of the year, with an increased use during winter and spring and less use during summer. Individuals with higher condition, females, larger and older fish were more likely to remain resident in the estuary throughout the summer. In the estuary, the sea trout utilised the upper part of the water column with mostly brackish water, and the swimming depth was found to be deeper for smaller individuals and in the period from March to August.

Today, many of the major estuaries in Norway are highly affected by city development and have high levels of anthropogenic disturbances. The remaining natural estuaries are under high pressure from development, but given the importance of this habitat for sea trout and other wildlife, it will be important to continue to protect these areas (See e.g. Davidsen et al., 2017b).

4.1 The use of estuaries during winter

During the study, sea trout were present in the estuary during all months, but the number of individuals varied throughout the year. The number of fish was highest from December to May, and lowest in the period from June to September. The reason for the increased use of the estuary from December to May might be because the sea trout are using the estuary as an overwintering area, in combination with this being a transitioning area between habitats. The estuary is a natural transitioning zone between the marine environment and the freshwater habitat and is likely often used by the sea trout during feeding and spawning migrations.

Similar observations of sea trout overwintering in the marine environment were seen in a population in northern Norway, where most of the fish overwintered in the estuary for extended periods, and the estuarine habitat was found to play an important role during winter months (Jensen and Rikardsen, 2012). In a previous study by Jonsson et al. (2002) one part of a population was found to overwinter in the river while the other stayed in the estuary or the marine environment, possibly because there were limited suitable overwintering habitats in the river. It has previously been shown that sea trout may overwinter in estuaries or marine areas if their home rivers are smaller streams without deeper pools or lakes that the sea trout can reside in during winter (Jensen and Rikardsen, 2008, Rikardsen et al., 2006). Smaller rivers might have harsher overwintering conditions, with lower water levels and challenging ice conditions. The freshwater habitat is generally thought to be a more stable environment during winter, with a lower risk of predation. However, in smaller rivers with harsh conditions, the advantages of the freshwater habitat might be outweighed by the benefits of feeding in the estuary. The estuary has a higher prey availability than freshwater, making it more nutritionally beneficial for the sea trout during winter (Jensen and Rikardsen, 2012, Knutsen et al., 2004).

4.2 Summers in estuaries

During the summer months, from June to September, only 11% of the sea trout stayed in the estuary. The tendency to remain in the estuary during these months was influenced by sex, age, body condition and body length (L_T). Individuals that were larger, older, had a higher body condition, and females, were more likely to remain resident in the estuary throughout the summer.

Moving to the outer-fjord during summer can give better feeding opportunities for sea trout, which can lead to enhanced growth and reproductive capacity (Hendry, 2004). This does, however, come with higher energy use and an increased risk from predators and diseases, which can prevent the sea trout from reproducing again (Jonsson and Jonsson, 1993). In this study, individuals that had a lower body condition were more likely to leave the estuary during summer and migrate to sea, indicating that they are more willing to take the risks of migration in order to increase their growth. A study by Eldøy et al. (2020) found that sea trout with a low nutritional condition were more likely to leave the river and estuary and migrate to sea. Similar results were observed in a study where hatchery smolt with no access to food were likely to migrate to the sea, while the well-fed smolt tended to remain in the river or estuary (Davidsen et al., 2014). The findings in this study are also supported by Bordeleau et al. (2018) who found that the sea trout migrating to the outer-fjord were in poorer condition and that the variation in the nutritional state of the fish influenced the spatio-temporal use of the marine habitat.

The results also showed that smaller and younger individuals were more likely to leave the estuary in favour of the outer fjord in the period from June to September. In some previous studies, individuals of all size classes have been found to migrate longer distances, with no difference in body length between the short- and long-distance migrants (Berg and Berg, 1987, Eldøy et al., 2015). A previous study on another salmonid fish, Dolly Varden (*Salvelinus malma*) in Alaska, found that older, larger individuals were less likely to migrate to sea as the size benefits of marine foraging declined in older individuals (Bond et al., 2015). It has been suggested that this could also be a possible strategy for some sea trout populations (Thorstad et al., 2016). However, in many previous studies, it has been found that larger and older individuals are more likely to migrate to sea (Davidsen et al., 2017a, Eldøy, In review), which contradicts with the results found in this study. A previous study showed that the likelihood of finding sea trout in the outer fjord increased with increasing body length (Knutsen et al., 2001). Larger individuals are thought to migrate further out than the smaller fish as they need to find larger prey (Klemetsen et al., 2003). Previous studies have found a size-dependent selection in feeding, where smaller individuals are more likely to feed on brackish or freshwater invertebrates in the estuary, while the larger individuals move to the outer fjord to feed more on pelagic fish (Bordeleau et al., 2018, Davidsen et al., 2017a).

The results also showed that faster-growing individuals were more likely to leave the estuary and wander to the outer fjord areas. Fast-growing sea trout have been shown to shift habitat and change to a more piscivorous diet at a younger age and smaller size than slow-growing individuals (Klemetsen et al., 2003). This could possibly explain why the smaller individuals in this study were more likely to leave the estuary than the larger individuals. It could also be possible that the younger, smaller individuals are still feeding in nearshore habitats located outside the range of the receivers in this study. There is, furthermore, a possibility of sampling bias in this study, as most of the sea trout were captured and tagged in the estuary during spring. There is a chance that the larger fish found in the estuary during spring also are more likely to stay there during summer. It has been shown in previous studies that sea trout can have an inter-annual consistency in their marine area use (Eldøy et al., 2019).

In this study, males were more likely to migrate to sea than females, instead of remaining in the estuary from June to September. This contradicts with previous studies that mainly have found that females, during the summer, are more likely to migrate to the outer-fjord than males (Bordeleau et al., 2018, Eldøy, In review, Jonsson and Jonsson, 1993). This is likely because female reproductive success is more dependent on body size, so they have a greater benefit of the increased feeding opportunities at sea compared to the males (Jonsson and Jonsson, 1993). The number of individuals included in the dataset in this study varied from month to month, and especially during the summer months, the number was quite low. When n is low, it can make the results more susceptible to individual variation. This might have been the case in this model and could explain why the result differs from what has been found in previous studies. A varying number of individuals is one of the limitations with acoustic telemetry since data is only collected when the fish is registered at one of the receivers. In areas with highly varying detection range like estuaries, this might mean fewer registrations during some periods with challenging hydrological conditions.

4.3 Swimming depth

In this study, the swimming depth in the estuary was found to be generally surface-oriented, with a mean of 2.4 meters. The swimming depth varied through the year and was influenced by the season of the year and the body length of the fish. The shallow swimming depth in this study aligns well with what has been observed in previous research (Eldøy et al., 2017, Kristensen et al., 2018) and indicate that the sea trout prefers the upper part of the water column in the estuarine habitat.

The swimming depth in the estuary was found to be influenced by season, and the sea trout was found to stay deeper in the spring and summer months (March to August). This could indicate that during months when the water temperature increases, the sea trout stay deeper to seek a more preferred temperature. Previous studies have found that sea trout reside deeper in the water when the water temperature increases during summer (Eldøy et al., 2017, Kristensen et al., 2018). However, there were considerable variations in the average swimming depth throughout the year (Figure 7), as well as some individual variation within the months. This study did also have a fairly low number of sea trout with recorded depth for several of the months, and especially between June and August, which could make the results more sensitive to individual variation.

The mean swimming depth of sea trout was also found to be influenced by body length, with smaller individuals staying deeper in the water. This indicates that there could be some individual morphological variation in swimming depth. In a study by Eldøy et al. (2017), body size was also found to influence the swimming depth of the sea trout during summer. The difference in depth could possibly be because sea trout of different sizes feed on different prey, however previous studies have mainly found that the larger fish feed on prey in deeper waters

(Davidsen et al., 2017a). It is, therefore, a possibility that the depth differences found in this study, mainly are individual variations.

There was a significant difference between the swimming depth in the estuary and the fjord, with the swimming depth being considerably deeper in the fjord. This could partly be influenced by the fact that estuarine areas naturally are shallower than the outer fjord. The shallow swimming depth in the estuary might indicate that the sea trout are actively using the brackish water layer, or that the sea trout are feeding in the shallow near-shore areas. This could indicate a shift in prey between the estuary and the fjord area, with the fish in the estuary mainly feeding on surface insects and other brackish or freshwater invertebrates, while in the fjord the fish feeds on marine fish in deeper water. This is consistent with previous studies that have shown that smaller and younger fish feed on inshore and shallow water prey communities in the estuary, while larger fish fed mainly on marine fish in the pelagic zone (Davidsen et al., 2017a, Knutsen et al., 2001). It has also been seen that water transparency can play a part in determining the vertical distribution of sea trout, as they are visual feeders (Langeland et al., 1991). The study showed that sea trout stay deeper in the water when it was clear, while in more turbulent water, they stayed at shallower depths. The estuary might be a more turbulent area than the fjord, with the mixing of freshwater and saltwater combined with the tide, and this could potentially influence the sea trout to stay at shallower depths in the estuary.

4.5 Conclusion

The results from this study further illustrate that estuaries are important habitats for sea trout. The sea trout was found in the estuary frequently during the year and especially between December and May. Clearly, some individuals use the estuary all year round, while others only utilise it is as an overwintering habitat or a transition zone between freshwater and the marine environment. During summer, the estuary was mainly used by females, fish with higher body condition, larger and older fish. In the estuary, the sea trout were found to use the upper part of the water column, possibly utilising the brackish water or feeding in the shallower parts. They were also found to stay deeper in the water during spring and summer, possibly as a response to higher water temperatures. A decline in sea trout populations has been seen in large parts of Norway, and the populations are negatively impacted by several anthropogenic activities, including habitat change. Because of this, it is necessary to protect the habitats with high value for the sea trout. Estuaries are clearly important as a habitat for sea trout and should be kept in good condition. There is generally limited knowledge on how human activity in estuaries affect the sea trout, both in terms of their behaviour and survival, and this could be a potential focus for future studies.

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