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Migration and habitat use of sea trout *Salmo trutta* in relation to a marine protected area

A study conducted in Beiarfjorden national salmon fjord

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Science and Technology

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ABSTRACT

Coastal areas are important habitats for anadromous brown trout (sea trout, *Salmo trutta*), but vulnerable to anthropogenic activities, such as aquaculture, due to the free movement of pathogens between the net pen and the surrounding water masses. The Norwegian government has designated 29 fjords for protection of important Atlantic salmon populations. Fish residing in these protected areas, known as “national salmon fjords” are expected to have lower levels of salmon lice and thus be less affected by the negative effects by lice infestations. Investigating the sea trout’s migration in relation to a national salmon fjord is important to evaluate to what extent the sea trout utilizes the protected habitats. The aim of this thesis was to investigate individual sea trout migratory behavior in relation to the location and coverage of Beiarfjorden national salmon fjord. The study was conducted over a two-year period, and acoustic telemetry was used to examine how the sea trout originating from river Beiarelva utilized the fjord system.

Tagged sea trout were recorded in all parts of the fjord system. More time was spent in the protected area (63%) compared to the non-protected areas. Two different migratory behavioral traits were observed: sea trout either stayed in Beiarfjorden (medium-distance migrants, < 17 km) or migrated out of Beiarfjorden (long-distance migrants, > 17 km). Of the fish entering the fjord, 84% were classified as long-distance migrants. No individuals remained close to the river where they were tagged (< 4 km) throughout the summer. Individuals of a greater body length were more likely to leave Beiarfjorden to more open sea habitats and stayed a lower proportion of time in the protected area compared to smaller individuals. Body condition, sex, and age had limited influence on the decision on whether to stay in Beiarfjorden, and also limited effect on the proportion of time spent within versus the non-protected areas. Sea trout tended to use greater proportions of their time at sea within the protected area in 2020 than in 2019.

The results indicates that Beiarfjorden national salmon fjord includes habitats that are important for sea trout, although there was variation among individuals in the proportion of time resided within the protected area. The degree of protection given did not seem random, but depended on the length of the fish, where larger individuals appeared to be less protected than smaller individuals. Beiarfjorden national salmon fjord is one of the smallest national salmon fjords in Norway, but is a fjord with many long-distance migrating sea trout. Hence, to protect the entire sea trout population, the protected area should be of a larger size. Knowledge of how well national salmon fjords protects sea trout from potential negative impact from aquaculture will be important when evaluating the function of these marine protected areas.

SAMMENDRAG

Kystområder er viktige leveområder for anadrom brun ørret (sjøørret, *Salmo trutta*), men også sårbare for menneskeskapt påvirkning, slik som oppdrettsanlegg, på grunn av den frie bevegelsen av patogener mellom oppdrettsmær og vannmassene rundt. Regjeringen har utpekt 29 fjorder for spesiell beskyttelse av viktige laksebestander. Fisk som oppholder seg i slike beskyttede områder, kjent som "nasjonale laksefjorder", forventes å ha lavere nivåer av lakselus og dermed være mindre påvirket av de negative effektene forbundet med påslag av selus. Det å undersøke sjøørretens vandringer i relasjon en nasjonal laksefjord er viktig for å evaluere i hvilken grad sjøørret bruker habitatene som er beskyttet. Målet med denne oppgaven var å undersøke sjøørretens atferd i forhold til plasseringen og dekkningen av Beiarfjorden nasjonale laksefjord. Studien ble utført over en toårsperiode, hvor akustisk telemetri ble brukt til å undersøke hvordan sjøørret fra Beiarelva benyttet fjordsystemet.

Merket sjøørret ble registrert i alle deler i fjordsystemet. Totalt brukte sjøørreten mer tid i det beskyttede området (63%) sammenlignet med det ikke-beskyttede fjordområdet utenfor. To forskjellige vandringsatferder ble observert: sjøørret som oppholdt seg kun i Beiarfjorden (mellomdistansevandrer) og sjøørret som forlot Beiarfjorden (langdistansevandrer). Av fisk som ble registrert i fjorden, gjennomførte 84% lang-distansevandring (> 17 km). Ingen individer holdt seg kun i nærhet til Beiarelva (< 4 km) gjennom hele sommeren. Individer med en lengre kroppslengde forlot Beiarfjorden til mer åpen sjø og oppholdt seg en kortere tid i det beskyttede området sammenlignet med mindre individer. Kondisjonsfaktor, kjønn og alder hadde en begrenset påvirkning i beslutningen på å bli i Beiarfjorden, og i forhold til tiden brukt i det beskyttede området versus det ubeskyttede området. Sjøørret hadde en tendens til å bruke en høyere andel tid i det beskyttede området i 2020, enn i 2019.

Resultatene viser at den nasjonale laksefjorden Beiarfjorden inkluderer viktige habitat for sjøørreten, selv om det er variasjon blant individer i andelen tid de oppholder seg i det beskyttede området. Graden beskyttelse gitt av den nasjonale laksefjorden virker ikke tilfeldig, men å avhenge av lengden på fisken, hvor lengre individer ser ut til å være dårligere beskyttet enn kortere og mindre individer. Beiarfjorden nasjonale laksefjord er en av de minste nasjonale laksefjordene i Norge, men har mange langdistansevandrere. Derfor, for å beskytte hele bestanden, bør det beskyttede området være større. Kunnskap om hvor godt nasjonale laksefjorder beskytter sjøørret mot potensielle negative påvirkning fra opprett, vil være viktig når man skal vurdere funksjonen til disse marine verneområdene.

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1. INTRODUCTION

Atlantic salmon (*Salmo salar* L.) farming in Norway has had a large growth since the production started in the 1970s (Statistics Norway, 2020). Norway is the largest production country, with a production share of 55% of the global production (Iversen *et al.*, 2020). In 2019, more than 1.3 million tons of Atlantic salmon were produced in Norway, distributed in approximately 1000 fish farms along the coastline (Norwegian Directorate of Fisheries, 2020b; a). Open caged farming is the most widespread production form in Norway, a production method with challenges regarding free movement of pathogens between the net pen and the surrounding water masses (Grefsrud, 2021). This free movement can have negative effects on wild salmonids, in regards to lice and other diseases (Grefsrud, 2021).

Open cage salmon farming is known to considerably increase the number of salmon lice (*Lepeophtheirus salmonis* K.) infecting wild salmonids in sea areas with salmon farming (Bjørn *et al.*, 2001; Costello, 2009; Jansen *et al.*, 2012; Thorstad *et al.*, 2015). When farming of Atlantic salmon was established, salmon lice quickly developed as a concern (Heuch *et al.*, 2005). During the last decades, the marine parasite has become one of the most serious pathogens on migrating wild salmonids (Thorstad *et al.*, 2015; Grefsrud *et al.*, 2018; Grefsrud, 2021), and is considered the greatest threat to wild anadromous brown trout (*Salmo trutta* L., hereafter referred to as sea trout) along the coastline in Norway (Anon, 2019). Salmon lice feed on host mucus, skin and underlying tissue (Costello, 2006; Thorstad *et al.*, 2015). As a result, the host may experience physiological stress or death due to disturbances in osmoregulation, in addition to sub lethal effects, such as reduced feeding and growth (Costello, 2006; Thorstad *et al.*, 2015). Moreover, increased susceptibility to secondary infections, and therefore a reduced disease resistance is also a risk, leading to a higher mortality in heavily infected hosts (Bjørn *et al.*, 2001; Wells *et al.*, 2007; Thorstad *et al.*, 2015).

Sea trout are especially vulnerable to salmon lice, because most individuals stay in fjords and coastal waters where salmon farms are situated during their marine migration (Thorstad *et al.*, 2015). In Norway, sea trout are usually not observed far from their native river (Thorstad *et al.*, 2016), and only occasionally found in the open ocean (Birnie-Gauvin *et al.*, 2019). Some sea trout prefer the innermost parts of the fjords and stay close to the river mouth year-round, while others spend more time further out in the fjord (Jensen *et al.*, 2014; Eldøy *et al.*, 2015). Studies on sea trout have previously demonstrated a large individual variation in behavior regarding

migration timing (Berg & Berg, 1987; Jonsson & Jonsson, 2002) and migration distance (Berg & Berg, 1987; Eldøy *et al.*, 2015). Such variation may be due to different biological characteristics among individuals, such as body length, age, sex and body condition (Eldøy *et al.*, 2015; Bordeleau *et al.*, 2018; Eldøy *et al.*, 2021). Furthermore, the time spent at sea varies from only a few weeks, during the summer only, to two or more years at sea before returning to their origin river to spawn (Klemetsen *et al.*, 2003; Thorstad *et al.*, 2016).

The ultimate goal of the marine migration among salmonids is most likely to improve fitness, such as through increased growth, and avoidance of unfavorable environmental conditions (Jonsson, 1985; Gross *et al.*, 1988). Good feeding opportunities at sea results in a larger body size and gonadal production, and the reproductive success is therefore increased (Jonsson, 1985). However, the life history strategy that provides the opportunity for increased fitness may also involve disadvantages, such as higher energetic cost due to smoltification, osmoregulation and swimming (Klemetsen *et al.*, 2003). In addition, marine migration also increases risks of predation, diseases and parasites (Bjørn *et al.*, 2001; Klemetsen *et al.*, 2003).

Studies have demonstrated that sea trout tend to return to brackish or fresh water if heavily infected with salmon lice (Birkeland, 1996; Bjørn *et al.*, 2001; Halttunen *et al.*, 2018). Salmon lice have a low tolerance for low levels of salinity and die or shed if their host remains in brackish or fresh water for a longer period (Hahnenkamp & Fyhn, 1985; McLean *et al.*, 1990). However, compared to the individuals spending a longer growth season at sea, the returned fish will have a reduced growth, which may result in a reduced fecundity and reproductive success (Birkeland, 1996; Wells *et al.*, 2007). A recent report classifying the status of sea trout in 430 Norwegian rivers concluded that almost half of the stocks were in poor or very poor state (48%), with declines in population abundance. The reasons included hydropower, agriculture, overexploitation, habitat changes, and salmon lice, where salmon lice had by far the most negative impact on sea trout (Anon, 2019).

The Norwegian authorities have implemented several measures in order to reduce the infection pressure of salmon lice to wild salmonids. One of these measures was the establishment of "national salmon fjords" (NOU, 1999:9; DKMD, 2002; 2006). In 2007, 52 rivers and 29 fjords were designated as national salmon rivers and national salmon fjords (Aasetre & Vik, 2013). The aim of the protection regime, is to rebuild the Atlantic salmon stocks to a size and composition that ensures diversity within the species (DKMD, 2006). In a national salmon fjord, no new fish farms are allowed to be established. In addition, existing fish farms will have

stricter requirements for escape prevention and control of salmon lice (NOU, 1999:9; DKMD, 2002; 2006). Thus, wild salmonids in a national salmon fjord are expected to have lower levels of salmon lice and consequently be less affected by them, than fish outside a protected area (Bjørn *et al.*, 2011). The national salmon fjords were established to protect important Atlantic salmon stocks (NOU, 1999:9; DKMD, 2002; 2006), but they will also affect sea trout populations.

As of today, only salmon are included in some management measures, such as the traffic light system and national salmon fjords (DKMD, 2006; Nilsen *et al.*, 2019a). Due to the sea trout's unique use of fjord system as habitat, these management measures may be different if sea trout were included (Nilsen *et al.*, 2019b). One of the challenges when establishing a protection regime for sea trout is the spatial conflict with aquaculture. Even so, it is important to aim towards a sustainable coexistence between aquaculture and other interests, (NFD, 2015) such as sea trout. Thus, it is essential to investigate how the sea trout utilize the fjord system to be able to preserve them. Information regarding the movements and residency of sea trout within and outside a national salmon fjord may be of importance to see if, or to what extent, the sea trout's behavior allows them to be protected by these national salmon fjords. This information can further be used when assessing the functions of these national salmon fjords. Furthermore, gaining a greater knowledge of habitat used by sea trout in relation to aquaculture is needed to achieve efficient management of populations and to evaluate how implemented management measures may be improved.

The main aim of this thesis was to investigate individual sea trout migratory behavior in relation to the location and coverage of a national salmon fjord. The objectives were to investigate migration patterns inside and outside the protected fjord area in terms of: (1) timing of sea entry and freshwater return, and return rate, (2) migration distance from the river mouth, (3) potential differences in marine residence time between protected and non-protected areas, and (4) individual repeatability in marine migration behavior between two years of tracking. This was done by using acoustic telemetry with individually coded transmitters. Sea trout were captured in Beiarelva national salmon river and were tracked within, and outside Beiarfjorden national salmon fjord in Northern Norway.

2. MATERIALS AND METHODS

2.1 Study area

The present study was conducted in a fjord system within the three municipalities Beiarn, Gildeskål and Bodø in Nordland county in Northern Norway (figure 1). The innermost fjord Beiarnfjorden proceeds into the fjord system consisting of the Holmsundfjorden, Morsdalsfjorden and Nordfjorden. The Beiarelva watercourse (67.0693°N 14.5328°E) flows northward from the mountain area Saltfjellet, and river Beiarelva drains to the innermost part of Beiarnfjorden. The watercourse has several tributaries and streams, but no anadromous stretch connecting to a lake. The catchment area is about 1065 km², and the watercourse is the fifth largest in Nordland with an average water flow of 33 m³/s (Sjursen *et al.*, 2018). The river Beiarelva is affected by glaciers, causing cold water temperatures in the river and estuary, and snow melt influences much of the water flow in spring and early summer (Hellen *et al.*, 2016).

In 2007, parts of the present study area was designated as a national salmon fjord, with an area of approximately 38 km², to protect the Atlantic salmon population in river Beiarelva. Beiarnfjorden national salmon fjord includes areas in the municipalities of Gildeskål and Beiarn, and consists of Beiarnfjorden and Holmsundfjorden (DKMD, 2006). Within the fjord system, but outside the protected area, seven open caged Atlantic salmon fish farms (figure 1) were operated during the study period. During the study period, May 2019-October 2020, the number of salmon lice per fish was above the legal lice per salmon limit at two of the aquaculture facilities (<https://www.barentswatch.no/fiskehelse/>, table 1). Furthermore, the fish disease ISA (infectious salmon anaemia) was suspected, but later disproved, at the localities Mulnesodden and Mulnesodden S (figure 1), between 23.01.2020-23.01.2021 and 21.08.2020-23.01.2021 respectively (<https://www.barentswatch.no/fiskehelse/>).

TABLE 1: Overview of aquaculture facilities and week numbers when the mean number of salmon lice per fish counted at the facilities in the study area was above the lice limit (0.5 adult female lice per fish). Mean number of lice in moving stages and attached lice per fish is also given. Lice in moving stages move freely over the host skin to feed, while attached lice feed on the host skin around their point of attachment (Costello, 2006).

Week	Year	Facilities	Adult female lice (<i>n</i>)	Lice in moving stages (<i>n</i>)	Attached lice (<i>n</i>)	Sea Temperature (°C)
43	2019	Hammarvika	1.00	0.25	0.0	9.5
44	2019	Hammarvika	0.75	0.55	0.0	9.5
43	2020	Kjervika	0.92	1.00	0.1	9.5

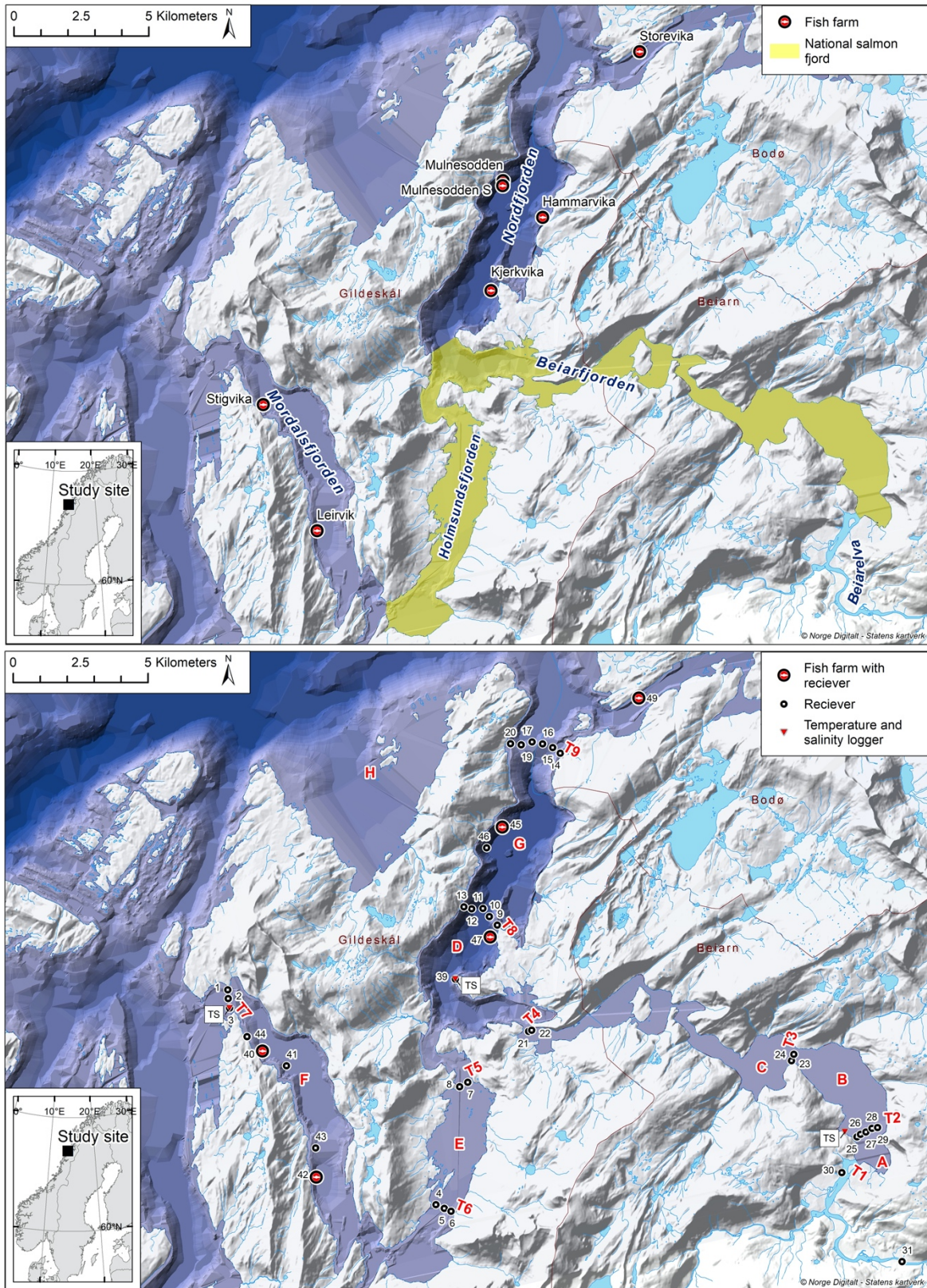


FIGURE 1: Map of the study area. The upper panel shows Beiarfjorden national salmon fjord, names and location of operating fish farms, location of the river Beiarelva and names of fjords in the fjord system. The lower panel indicate the position of deployed acoustic receivers, distribution of transect lines (T1-T9) with receivers and division of the zones (A-H). The locations of temperature and salinity loggers, as well as fish farms with acoustic receivers, are also included.

2.2 Collection of data with use of telemetry

2.2.1 Fish capture and tagging

Fish were tagged in the spring of 2019 and 2020 (table 2). In total, 59 sea trout were caught, and an acoustic transmitter was implanted in the abdominal cavity. All fish were caught by using fishing rod and line in the lower part of river Beiarelva. Hooks used were barbless to ensure minimal damage to the fish. After capture, the fish were kept in keep nets located in parts of the river with relatively low current until tagging (< 4 hours).

The fish were placed in a tarpaulin-covered tub containing a solution of Benzoak (15-20 mL per 100 L water) for approximately four minutes. When anesthetized, the total body length (*LT*) and weight of the fish were measured. A 1.5-2.0 cm incision was made on the side of the *linea alba* and a sterilized acoustic transmitter was inserted into the body cavity. The incision was closed with two or three independent sutures (Resolon 3/0). In 2019, but not in 2020, a Carlin tag was attached to the fish with steel wires just below the dorsal fin using two cannulas, to recognize the fish in the event of recapture. Lastly, approximately 15-20 scales were sampled from each fish for age determination and a small piece of the adipose fin was clipped for DNA sex determination and to verify the specie.

Throughout the operation, water was poured over the gills to keep them wet. After tagging, fish were kept in holding tanks for recovery until normal behavior was regained (approximately 3-5 minutes). The fish were then released back into the river close to the capture site. The experimental procedures were approved by the Norwegian National Animal Research Authority (permission number 19/23443).

TABLE 2: Dates and year of tagging, number of sea trout tagged, sex, and mean, standard deviation (SD) and range for total body length and body mass are given for each tagging group.

Tagging group	Date tagged	<i>n</i>	Male:Female (<i>n</i>)	Total length (mm)		Body mass (g)	
				Mean ± SD	Range	Mean ± SD	Range
2019	30.04-06.05	34	25:9	516 ± 110	340-730	1261 ± 829	240-3320
2020	20.04-22.04	25	15:10	600 ± 124	380-840	1948 ± 1130	420-5240

Fish tagged in 2020 had a had a longer *LT* (Welch two-sample t-test, $n = 59$, $P < 0.05$) and larger body mass (Wilcoxon rank sum test, $n = 59$, $P < 0.05$), than fish tagged in 2019.

2.2.2 Acoustic transmitters

The fish were, depending on total body length, tagged with one of two sizes of cylindrical 69 kHz acoustic transmitters from Thelma Biotel AS (Trondheim, Norway). Model ID-MP9L (29.4 x 9.0 mm, 5.2 g in air, 0.2-2.2% of fish total body mass; estimated battery life of ~13 months; output 146 dB re 1uPa @1m) was used for fish $LT > 340$ mm and model ID-MP13 (12.7 x 33.3 mm, 11.5 g in air, 0.2-2.7% of fish total body mass; estimated battery life of ~26 months; output 153 dB re 1uPa @1m) was used for fish with $LT > 380$ mm. Each tag had a unique ID-code. The tags transmitted an acoustic signal with a random delay between consecutive signals of 30-90 seconds to minimize the risk of signal collision if two or more tagged fish were within the receiver range at the same time.

2.2.3 Tracking of tagged fish

The fish were tracked by using 40 automatic receivers (Vemco Inc., Halifax, Canada, model VR2W and VR2W-AR). Of these, 38 were deployed in the fjord system and two in the river. The receivers were either attached to land, moored to buoys, submerged to the seabed with an acoustic release system (Sub sea sonic model AR60, Sub Sea Sonic inc., San Diego, USA or Vemco Ascent Acoustic Release, Vemco inc., Halifax, Canada), or chained to existing infrastructure at different fish farms located in the fjord system. The depth of the receivers in the river were approximately two meters, while most of the receivers in the fjord system were moored five meters below sea surface. The exception was the acoustic release stations, where the receivers were placed 15-150 meters below surface, depending on the depth in the fjord where they were placed and which acoustic release system used. The receivers attached to the moored ropes on buoys were attached to 40-80 kg anchors at the bottom, preventing them from drifting. Fish passing receivers were registered and the data were automatically stored. Receivers were regularly inspected throughout the study period to check battery and download data. The receivers in the river were removed in late autumn and deployed back in the river in spring due to ice formation in the river during the winter.

2.2.4 Receiver performance

To ensure reliability of the receiver lines, the receiver performance was checked. Firstly, the ID-codes of tagged fish registered at the outermost line of receivers (in the north, line T9, and in the south, line T7) were compared to the ID-codes of fish recorded at all transects in route

from T2 to the outermost receiver (figure 1). All fish that were detected at the outermost receiver line were also detected when passing the transects further in the fjord system. Secondly, receiver performance was investigated at T1 in the river by checking if fish tagged were registered at T1 before being registered in the fjord system. In 2019, 21% of tagged individuals were registered in the fjord without being registered at T1. Fish tagged in 2020 were not included in this analysis as they were tagged before the receiver at T1 was deployed in the river after the winter. In addition, 21 of the acoustic receivers in the fjord system had built-in pinger tags (Vemco model VR2W-AR), which were programmed to transmit signals similar to those of the tagged fish once every ten minutes. When analyzing the pinger tag signals, overlap between signals from adjacent receivers was found, indicating that fish passing through the transect lines would have been recorded by a receiver. However, two of the receivers on line T8 (station 9 and station 13) were out of service during summer and fall of 2019, hence the receiver performance has likely been reduced in this period.

2.3 Age determination by scale analysis

The scales collected from the fish during tagging were taken past the dorsal fin and above the lateral line with use of forceps. The scales were stored in paper envelopes until analysis in the laboratory and was examined at the NTNU University Museum by using a light microscope. Favorable scales for age analysis were selected and imprinted onto a 1 mm Lexan plate using a pressing iron. The Lexan plate was pictured and analyzed with a computer-controlled stereoscope (Leica M165C with camera Leica MC170 HD, Sankt Gallan, Switzerland) and its connected software, LAS V4.5. Scale readings were completed by using the method described by Dahl (1910) and Lea (1910). To avoid subjective results, the results were discussed, and quality checked by an experienced scale reader.

2.4 Genetic sex and species determination

To determine the sex and verify specie of the tagged fish, a small sample of the adipose fin of each individual was genetically analyzed at the NTNU University Museum DNA lab as described in Eldøy *et al.* (2021). In addition to sex determination, the method described in Eldøy *et al.* (2021) also verifies the specie.

2.5 Environmental parameters

Salinity and water temperature were measured every sixth hour with temperature and salinity data loggers (Star Oddi model DST centi-CT, Reykjavik, Iceland) placed at the location of two of the receivers in the fjord and one in the estuary. One data logger was attached to the rope with the acoustic receivers, at approximately 5 meters depth (receiver line T7, figure 1). The two other loggers were attached to two different docks (by receiver line T2 and receiver 39) at between 2-4 meters depth, depending on the tide. When analyzing these data, a measurement error was observed. Therefore, no salinity data from station 39 during the period 10.06.2019 to 02.10.2019 was available. Furthermore, mean temperatures and salinities for 2020 are not calculated and compared due to technical problems with the equipment.

2.6 Data analyses

2.6.1 Calculation of condition factor

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

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

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

2.6.2 Filtration of telemetry data and removal of registrations

Registrations of tagged fish spanned a period of one and a half year (two migration seasons, 02.05.2019-12.09.2020). Registrations were last downloaded 14.10.2020. The initial number of registrations from individuals tagged on the 40 receivers during this period was 1 043 937 (not including pinger tags from VR2W-AR receivers). All data was stored and managed in VUE [version 2.6.0, VEMCO, 02.2019].

There are two main sources of error by means of registrations when using acoustic telemetry: sound pollution and tag collision. Sound pollution occurs when sound from other sources, such as wind and waves, are interpreted as a tag signal by a receiver. Since these signals seldom match any of the fish ID-codes, they are often negligible when filtering the data. Tag collision occurs when signals from different acoustic tags reaches the receivers simultaneously, creating a separate signal. Tag collision have a higher risk of being identical to another fish ID-code, as they derive from similar codes. Although use of data filtration and removal of registrations will

reduce some of these false registrations, it is not possible to eliminate all registration errors (Pincock, 2012). However, they are reduced by filtering the data. The filter used in the present study required at least two registrations from a fish unique ID-code within a time span of 30 minutes to accept the registrations as true. The registrations defined as false were excluded from further analyses. During visual inspection of the data, four registrations (all at line T8) that were filtered out by the time filter were kept for the analyses. These registrations were considered realistic due to the overall tracks of the fish and were of importance for the residence time analyses. The final data set used in the analysis consisted of 1 038 084 (99.4% of the initial number) registrations.

2.6.3 Timing and duration of marine migration

The following procedures were used to calculate the duration of marine migrations of the fish. The beginning of the marine migration phase was set at the first registration of the fish in the innermost line in the fjord (T2). When the last registration of a fish occurred at line T2, the fish was assumed to have returned from the marine migration.

In some cases ($n = 15$), fish moved back and forth between the estuary and the river after tagging. In such cases, the first registration at T2 after the shifting between habitats, was used as the start of the marine migration to reduce risk of including adverse behavior caused by tagging and handling. In a few cases ($n = 5$), sea trout were recorded in the estuary after residency in the river. In these cases, the last registration at T2 before the residency in the river was used as the end of migration.

2.6.4 Defining short-, medium- and long-distance migrants

Each individual fish registered in the fjord was classified as either a short-, medium- or long-distance migrant, depending on which transect lines they were registered at during the study period. The distances each fish was measured (from Kartverket) to travel should be considered a minimum estimate of the true marine migration distance, as the distance was measured as the shortest possible swimming distance.

- Fish that were recorded at, but never beyond, the closest line to the river (line T2, figure 1) were classified as short-distance migrants (< 4 km).

- Fish recorded at line T4, but never beyond, were classified as medium-distance migrants (< 17 km).
- Fish that were recorded past line T4 were classified as long-distance migrants (> 17 km).

Fish classified as short- or medium-distance migrants that did not return from migration, were excluded from the analysis if the number of days they had been tracked in the fjord did not exceed a set minimum threshold. The exclusion of fish disappearing was done to ensure that fish were not classified as short- or medium-distance migrants only because they disappeared from the study before they had time to perform a potential long-distance migration. The minimum threshold was defined as the average time long-distance migrating fish from the same year and tracking group (see chapter 2.2.6), spent from their first day of migration until they fulfilled the criteria for long-distance migration, added to the standard deviation (SD). The minimum threshold for fish tagged in 2019 to be included was 39 days ($n = 26$, mean = 20 + SD = 19 days) in 2019 and 13 days in 2020 ($n = 12$, mean = 7 + SD = 6 days). For fish tagged in 2020, the minimum threshold was 25 days ($n = 20$, mean = 13 + SD = 12 days).

2.6.5 Geographic use of the fjord system

The number of individual fish registered at each line in the fjord was summarized to get an overview of the individuals' use of the fjord system. To evaluate the time spent in the different parts of the fjord, residence times in eight zones were calculated based on the receiver's geographic location (figure 1). The eight zones were the estuary (A), central Beiarfjorden (B and C), the central fjord (D), Holmsundfjorden (E), Morsdalsfjorden (F), Nordfjorden (G) and the open sea (H). To estimate the residence times in each zone, the sum of all timespans between subsequent registrations in each zone was calculated for each fish. The following criteria were used to assign the timespans when fish transitioned between zones:

- For transitions between zone A and B, the time span between the registrations were assigned to zone B.
- For transitions between zone B and C, the time span between the registrations were assigned to zone C.
- For transitions between zone C and D, the time span between the registrations were assigned to zone D.
- For transitions between zone D and E, the time span between the registrations were assigned to zone E.
- For transitions between zone E and F, the time span between the registrations were assigned to zone F.
- For transitions between zone F and E, the time span between the registrations were assigned to zone E.
- For transitions between zone E and D, the time span between the registrations were assigned to zone D.
- For transitions between zone D and G, the time span between the registrations were assigned to zone G.

- For transitions between zone G and D, the time span between the registrations were assigned to zone D.
- For transitions between zone D and C, the time span between the registrations were assigned to zone C.
- For transitions between zone C and B, the time span between the registrations were assigned to zone B.
- For transitions between zone B and A, the time span between the registrations were assigned to zone A.
- The fish were considered to reside in the outermost fjord zone (zone H) if the fish were registered at receiver 49. The residency in this zone was calculated from the previous registration in any fjord zone until the next registration in any fjord zone. Fish were also considered to reside in zone H if the fish had subsequent recordings on receiver array T7 or T9 with time spans between registrations of > 7 days. Fish were also considered to reside in zone H if the fish transitioned from receiver line T7 to T9 or *vice versa*.
- In six cases, fish passed transect line T8 without being detected. In those cases, the residence time was split and shared equally between zone D and G.
- Time spent in zone A was calculated by subtracting time spent in all other zones from the total duration of marine migration

To investigate the trout's use of the national salmon fjord, the zones were divided into four sections, the protected area (A, B, C and E), mixed zone (D), non-protected fjord area (G and F) and open sea (H). Furthermore, the non-protected fjord area and sea were combined to non-protected area (G, F and H) for statistical analyses. The proportion of time spent for each individual in the protected area was calculated. This was done by dividing the number of days spent in the protected area by the number of total days spent at sea, except for number of days spent in mixed zone (D), as it was unknown whether the individuals were residing in the protected area or not.

2.6.6 Tracking groups

In addition to tagging group 2019 and tagging group 2020, some of the fish tagged in 2019 that migrated to the fjord and returned to the river in the fall, were also tracked during the marine migration in 2020. The behavior of these individuals could be compared between two marine migration seasons. Thus, to separate the different tracking groups from the tagging groups, individuals tracked for two seasons were named the following:

- Fish tagged in 2019 and tracked during 2019: 2019A
- Fish tagged in 2019 and tracked during 2020: 2019B

2.6.7 Statistical analyses

RStudio (Rstudio Team, 2018) with R version 3.6.3 (R Core Team, 2018) was used for all statistical analyses. The statistical significance level was set to $P < 0.05$. The two tagging groups were not merged, except in the two models where year of tagging was included as an independent variable, because different environmental variables between the two years could affect migratory behavior. When comparing fish tagged in 2019 and 2020, Welch two-sample t-test was used if the assumption of normality was met, and the Wilcoxon rank sum test was used if the assumption of normality was not met. For fish tagged in 2020, comparison between medium- and long-distance migrants was not conducted due to a low sample size of medium distance migrants ($n = 2$). Normality was tested for with functions `shapiro.test` and `ggqqplot`, required package `ggpubr` (Kassambara, 2018). Paired Welch two-sample t-test and Wilcoxon signed-rank test were conducted to compare data from the same individuals tracked during two seasons. To test for differences in the proportion of medium- and long-distance migrants, proportion of fish staying only within Beiarfjorden and return rates between the two tagging groups, a χ^2 -contingency test was conducted with the function `chisq.test`.

To test for possible differences in biological characteristics between sea trout that stayed in Beiarfjorden during the marine migration (medium-distance migrants) and the sea trout that left Beiarfjorden (long-distance migrants), a binomial regression model was used. To compare the variables with each other, all variables were standardised prior to modelling using the ‘scale’ function in the R ‘base’ package. Because the increase in weight and length of an individual is not linear (Le Cren, 1951), the body condition factor for individuals used in this analysis were adjusted using the regression coefficient of the mass-length relationship for the included fish (3.105776). Hence, the adjusted body condition was calculated using the formula $K = 100 \times \text{mass (g)} \times \text{total length (cm)}^{-3.105776}$. Adjusted condition factor was used to avoid collinearity with body length and condition factor, as these variables were used to calculate the condition factor. Collinearity within the model was checked using the ‘check_collinearity’ function in the ‘performance’ R package (Lüdecke *et al.*, 2020), and collinearity was found to be low ($VIF \leq 1.81$). The binomial regression model included a binomial response variable (stayed or did not stay) and the predefined independent variables body length, adjusted body condition, age, sex and year of tagging. Akaike’s information criterion (AIC) was used to identify the best fitting model(s) with the ‘dredge’ function in the ‘MuMIn’ R package (Barton, 2018). The model selection gave support for multiple alternative models ($\Delta AIC < 2$, Anderson *et al.* 2001).

Conditional model averaging was therefore applied to calculate model parameter estimates for these models.

For analyses of biological characteristics possibly influencing the proportion of time spent in the protected area, a generalized linear model (GLM) was used. The generalized linear model was done by using the ‘GLM’ function from the ‘base’ package in R with a gaussian distribution. To compare the variables with each other, all variables were standardised prior to modelling using the ‘scale’ function in the R ‘base’ package. Only individuals utilizing both the protected area and the non-protected area were included in this analysis. The body condition factor was therefore adjusted again, using the regression coefficient of the mass-length relationship for the included fish (3.207948). Hence, the adjusted body condition was calculated using the formula $K = 100 \times \text{mass (g)} \times \text{total length (cm)}^{-3.207948}$. Collinearity within the model was checked using the ‘check_collinearity’ function in the ‘performance’ R package (Lüdecke *et al.*, 2020), and collinearity was found to be low ($\text{VIF} \leq 2.37$). The model included proportion of time at sea spent in the protected area as the response variable. The predefined independent variables in the model were body length, sex, year of tagging, age and adjusted condition factor. Akaike’s information criterion (AIC) was used to identify the best fitting model(s) with the ‘dredge’ function in the ‘MuMIn’ R package (Barton, 2018). The model selection gave support for multiple alternative models ($\Delta \text{AIC} < 2$, Anderson *et al.* 2001). Conditional model averaging was therefore applied to calculate model parameter estimates for these models.

3. RESULTS

3.1 Environmental parameters

During the summer of 2019, the mean daily water temperature in the inner part of the fjord system, T2, (estuary in Beiarfjorden, figure 1) was 9.2 °C (SD = 1.6 °C, range: 5.5-11.5 °C) based on data from the temperature and salinity data logger (figure 2). The mean daily temperature in the outer part was 12.3 °C at T7 (SD = 1.7 °C, range: 8.4-14.7 °C), and 9.7 °C at station 39 (SD = 1.7 °C, range: 7.1-12.6 °C), respectively. The salinity in the inner fjord (T2) fluctuated considerably during the summer months, with a mean daily salinity of 18.9‰ (SD = 7.3‰, range: 0.0-25.5‰). The salinity in the outer part of the fjord system (station 39 in 2020 and T7 in 2019) fluctuated also, but were generally higher (T7; mean = 28.2‰, SD = 1.8‰, range: 22.8-31.8‰).

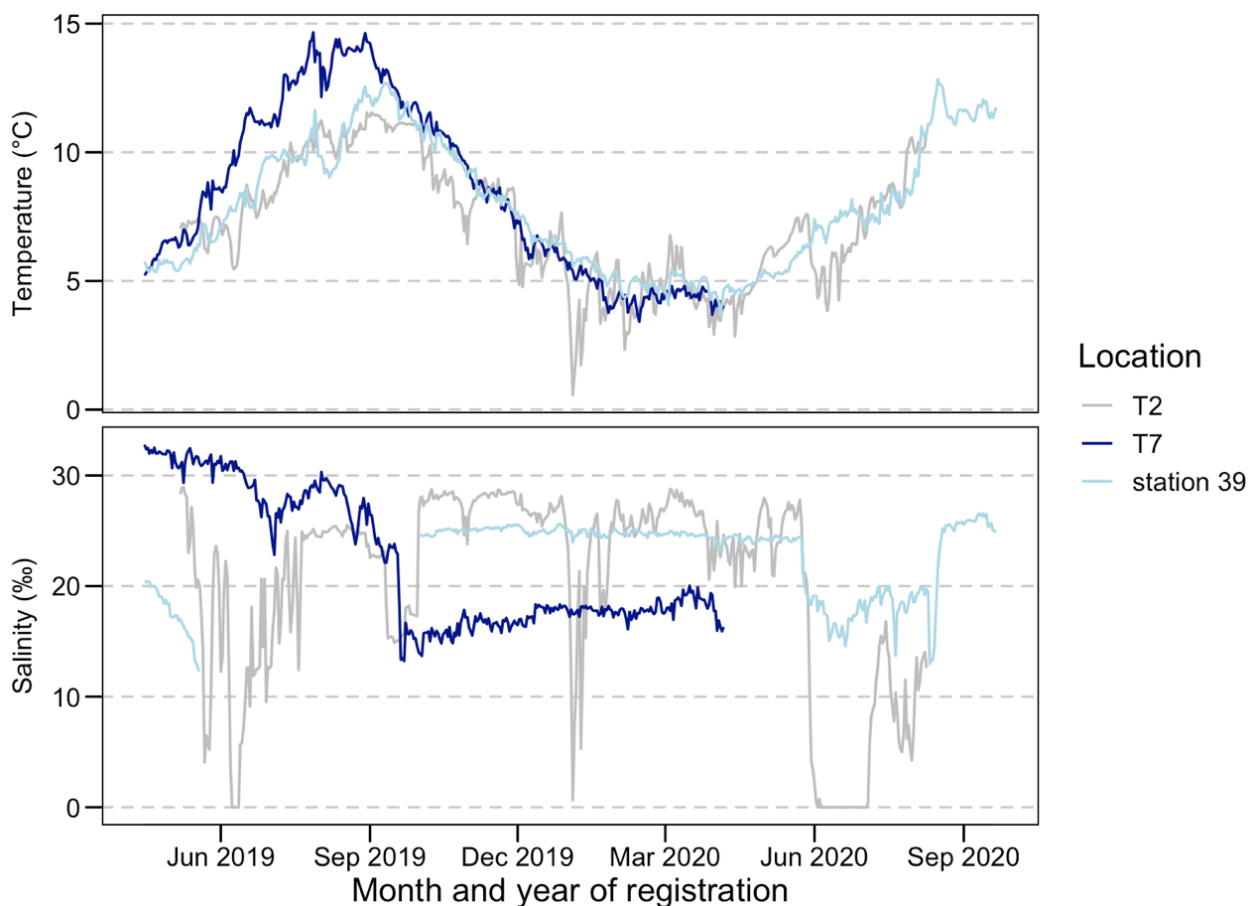


FIGURE 2. Mean daily water temperature (upper panel) and mean salinity (lower panel) at ~3 m depth at three receivers (T2, T7 and station 39) placed in fjord system, during the period 15.04.2019 to 21.09.2020.

3.2 Study population

Individuals in tagging group 2019 and 2020 did not differ in age at the time of tagging (Wilcoxon rank sum test, $n = 59$, $P > 0.05$, table 3) or in number of previous marine migration seasons (Wilcoxon rank sum test, $n = 59$, $P > 0.05$, table 3).

TABLE 3: Sample size (n) for each tagging group, mean and standard deviation (SD) for age at tracking (in years), and mean and SD for number of previous marine seasons of individuals tagged in 2019 and 2020.

Tagging group		2019	2020	Total
	n	34	25	59
Age at tracking	Mean	8.4	8.5	8.4
	SD	1.8	1.3	1.6
Previous number of marine seasons	Mean	3.8	4.5	4.2
	SD	1.9	1.6	1.8

Mean Fulton's body condition factor at capture for all tagged individuals was 0.8 (SD = 0.1). The condition factor did not differ between the fish tagged in 2019 and 2020 (Wilcoxon rank sum test, $n = 59$, $P > 0.05$, figure 3).

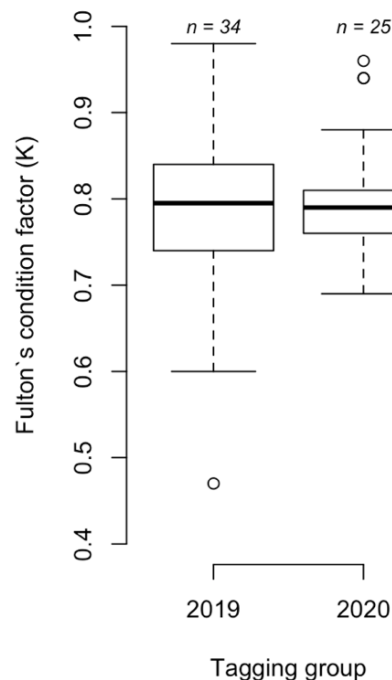


FIGURE 3. Fulton's condition factor at capture for fish tagged in 2019 and 2020. The box-and-whisker plots show median values (bold lines), the interquartile ranges (boxes) and the 5th and 95th percentiles (whiskers). Circles indicates outliers. Numbers above each plot gives sample size (n) of each tagging group.

3.3 Migratory behavior

3.3.1 Overview of telemetry results

Of the total 59 tagged fish, 57 individuals (97%) were recorded by receivers in the fjord during the study (table 4). Of the two remaining fish, one fish was never recorded and one fish was only recorded in the river. In total, 34 individuals were recorded in the fjord in 2019 (tagging group 2019), while 24 individuals were recorded in the fjord in 2020 (tagging group 2020). Among those recorded in the fjord, two fish tagged in 2020 (two of 57 fish, 4%) were excluded from further analysis because they disappeared before estimated threshold time (see chapter 2.6.4, one and three days after first recording at T2). In addition, 13 individuals tagged in 2019 were also recorded in the fjord in 2020 (tracking group 2019A, tracked in 2019 and 2019B, tracked in 2020).

TABLE 4: Overview of telemetry data, including aspects of the marine migration phase for the individuals that were recorded in the fjord (number of individuals, return rates, timing of migration, duration of marine migration for returnees, migration distance and residence time in the protected area). Individuals that disappeared from the study within the calculated minimum threshold after entering the fjord were excluded from classification as short-, medium- and long-distance-migrants.

Group	Migrating to fjord (<i>n</i>)	Returning to watercourse (<i>n</i>)	Timing of migration (dates)		Duration of marine phase (days)	Migration distance in fjord (<i>n</i>)			Residence time (days) Protected area
			Outward migration	Return migration		Short	Medium	Long	
Tagging group									
2019	33	24 (73%)	04.05-08.06	09.07-12.11	95 (±28)	–	7	26	58 (±30)
2020	24	16 (67%)	22.04-23.05	21.08-23.09	121 (±13)	–	2	20	69 (±26)
Tracking group									
2019A	13	13 (100%)	11.05-08.06	17.07-09.10	89 (±20)	–	1	12	47 (±21)
2019B	13	9 (69%)	21.04-22.05	12.07-18.09	109 (±19)	–	1	12	45 (±27)

3.3.2 Migration timing and duration

Typically, the tagged sea trout entered the fjord in May ($n = 47$), but some entered in late April ($n = 6$) and early June ($n = 4$, table 5). The time span between first and last migrating sea trout stretched across approximately one month for both tagging groups (2019 and 2020). Furthermore, the time span for returning sea trout stretched across more than four months during the two years. Some fish returned in July ($n = 4$), October ($n = 1$) and November ($n = 1$), while the majority of fish returned in August ($n = 16$) and September ($n = 18$).

TABLE 5: Tagging groups and tracking groups, number of individuals, mean, range and standard deviation (SD) date for outward and return migration.

Group	Outward migration				Return migration			
	<i>n</i>	Mean	Range	SD	<i>n</i>	Mean	Range	SD
Tagging group								
2019	33	20.05.2019	04.05-08.06	9	24	23.08.2019	09.07–12.11	27
2020	24	06.05.2020	22.04-23-05	9	16	06.09.2020	21.08-23.09	10
Tracking group								
2019A	13	23.05.2019	11.05–08.06	9	9	19.08.2019	17.07–09.10	26
2019B	13	06.05.2020	21.04-22.05	9	9	23.08.2020	12.07–18.09	22

For individuals tracked during two seasons, the average timing between the first and second year of tracking for marine entry was 15 days ($n = 13$, $SD = 9$, range: 1–39 days). The average difference in the timing of return to river between the consecutive years was 6 days ($n = 9$, $SD = 21$, range: 6–45 days). The timing of marine entry was earlier the second year of tracking than the first year of tracking. (Wilcoxon signed-rank test, $n = 13$, $P < 0.01$). However, the timing of return to river did not differ (Wilcoxon signed-rank test, $n = 9$, $P > 0.05$).

The overall return rate to the river for fish entering the fjord was 70% (2019; 73%, 2020; 67%), and there was no difference between the years (χ^2 contingency test, $\chi^2 = 0.244$, $df = 1$, $P > 0.05$). Duration of marine migration could be assessed for the 40 individuals that returned after the marine migration. The mean total migration duration was 105 days ($n = 40$, $SD = 27$, range: 39-183 days). Duration of marine migration was longer for fish tagged in 2020, than in 2019 (Wilcoxon rank sum test, $n = 40$, $P < 0.001$). Sea trout tagged in 2019 spent an average of 95 days in the fjord ($n = 24$, $SD = 28$, range: 39-183 days) while sea trout tagged in 2020 spent 121 days in the fjord (2020, $n = 16$, $SD = 13$, range: 94-144 days).

For individuals tracked during two consecutive seasons, mean duration of the marine migration was 89 days ($n = 9$, $SD = 20$, range: 55–125 days) the first year and 109 days ($n = 9$, $SD = 19$, range: 72–134 days) the second year. Migration duration was longer the second year of tracking compared to the first year of tracking (Wilcoxon signed-rank test, $n = 9$, $P > 0.05$).

3.3.3 Migration distance

Of the 55 individuals included for classification of distance migrated, 46 (84%) were classified as long-distance migrants, nine (16%) as medium-distance migrants, and none as short-distance migrants (figure 4). Of the 33 fish migrating into the fjord in 2019, 26 (79%) qualified as long-distance migrants and seven (21%) as medium-distance migrants. Of the 22 fish in 2020, 20 (91%) qualified as long-distance migrants and the remaining two (9%) as medium-distance migrant. The proportion of medium- and long-distance migrants did not differ between 2019 and 2020 (χ^2 contingency test, $\chi^2 = 1.417$, $df = 1$, $P > 0.05$).

Of the 13 fish tagged in 2019 that migrated out in the fjord again in 2020, all except one fish (92%) qualified as long-distance migrants the second year. The last one qualified as a medium-distance migrant (8%) the second year. All 13 fish tracked during two seasons maintained their same classification as medium- and long-distance migrants in the second year as the first year.

The Fulton's condition factor did not differ between medium and long-distance migrants (Wilcoxon rank sum test, 2019; $n = 33$, $P > 0.05$, figure 4) However, long-distance migrants were longer than medium-distance migrants (Wilcoxon rank sum test, 2019; $n = 33$, $P < 0.01$)

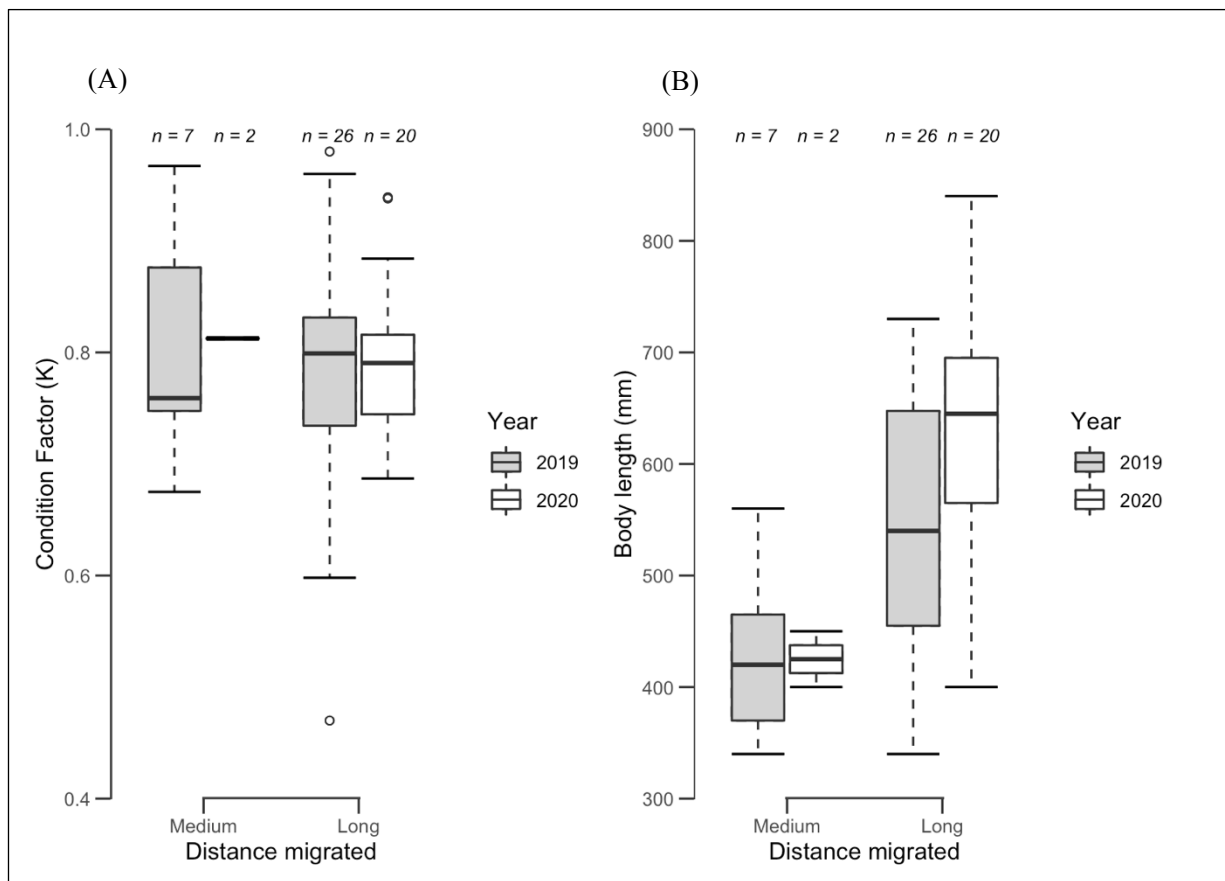


FIGURE 4: Fulton's condition factor (A) and total body length (B) in spring of 2019 and 2020 prior to migration for medium- and long-distance migrants. The box-and-whisker plots show median values (black lines), the interquartile ranges (boxes) and the 5th and 95th percentiles (whiskers). Circles indicate outliers. Numbers above each plot gives sample size (*n*) of each group.

3.3.3.1 Regression models for staying or leaving Bearfjorden

There were seven equally well fitted regression models exploring the decision to stay or leave Bearfjorden. These models indicated that the decision was influenced by a combination of body condition, body length, age, sex and year of tagging ($\Delta AIC < 2$, table 6). Total body length was found to be the best indicator for staying only in the protected area, being included in all of the best alternative models. Model conditional averaging showed that smaller individuals were more likely to remain in Bearfjorden, and thus, being fully protected by the nation salmon fjord (table 7). Further, the model conditional averaging indicated that year of tagging, sex, age and condition factor were less important variables for the choice of staying or leaving Bearfjorden.

Table 6: Model selection for estimating the determinants of residence only in Beiarfjorden versus leaving Beiarfjorden. The models estimated the relative contributions to residency of the parameters adjusted condition factor (C), total body length (L), sex (S), age (A) and year of tagging (Y). AIC is the score based on Akaike's information criterion.

Model	AIC	Δ AIC	AIC weights	d.f.
[L]	39.9	0.00	0.155	2
[L, C, S]	40.5	0.62	0.145	4
[L, C]	40.6	0.76	0.099	3
[L, S]	40.0	0.97	0.080	3
[L, A]	41.1	1.22	0.076	3
[L, Y]	41.7	1.84	0.070	3
[L, C, A]	41.8	1.95	0.063	4

Table 7: Summary of intercept and independent variables from model conditional averaging from binomial regression models on determinates for residence only in Beiarfjorden versus leaving Beiarfjorden ($n = 55$). The asterisk mark show significant values

Effect	Estimate	Std. Error	z value	<i>P</i>
(Intercept)	-2.2508	0.8485	2.602	< 0.01 *
Total length	-2.0843	0.7196	2.832	< 0.01 *
Sex (Male)	-1.2250	1.0246	1.169	> 0.05
Condition factor adjusted	0.5740	0.5011	1.120	> 0.05
Age	0.5843	0.6460	0.883	> 0.05
Tagging group (2020)	-0.3846	0.9732	0.386	> 0.05

3.3.4 Residence time in different parts of the fjord system

Utilization and residency of the different parts of the fjord system during marine migration could be determined for 40 individuals (figure 5). All fish tagged were registered in the estuary (T2) and further out in Beiarfjorden (T3). For tagging groups 2019 and 2020, a small number of fish were registered on lines T5, T6 and T7, meaning few fish used Morsdalsfjorden and Holmsundfjorden in the south-western part of the fjord system. There was a large number of fish registered in the outer fjord system at line T8, meaning most fish migrated in a northward direction. In total, there were twice as many individuals registered at line T8 ($n = 32$) compared to T5 ($n = 16$), indicating that most fish moved north and thus out of the national salmon fjord when they exited Beiarfjorden. In addition, all but one fish in tagging group 2019 and 2020, were registered at line T9 ($n = 30$) if they were registered at line T8.

For individuals tracked during two marine migration seasons, there was only some differences in the number of individuals registered in southward direction between the years, with a slightly fewer registrations the second year compared to the first year.

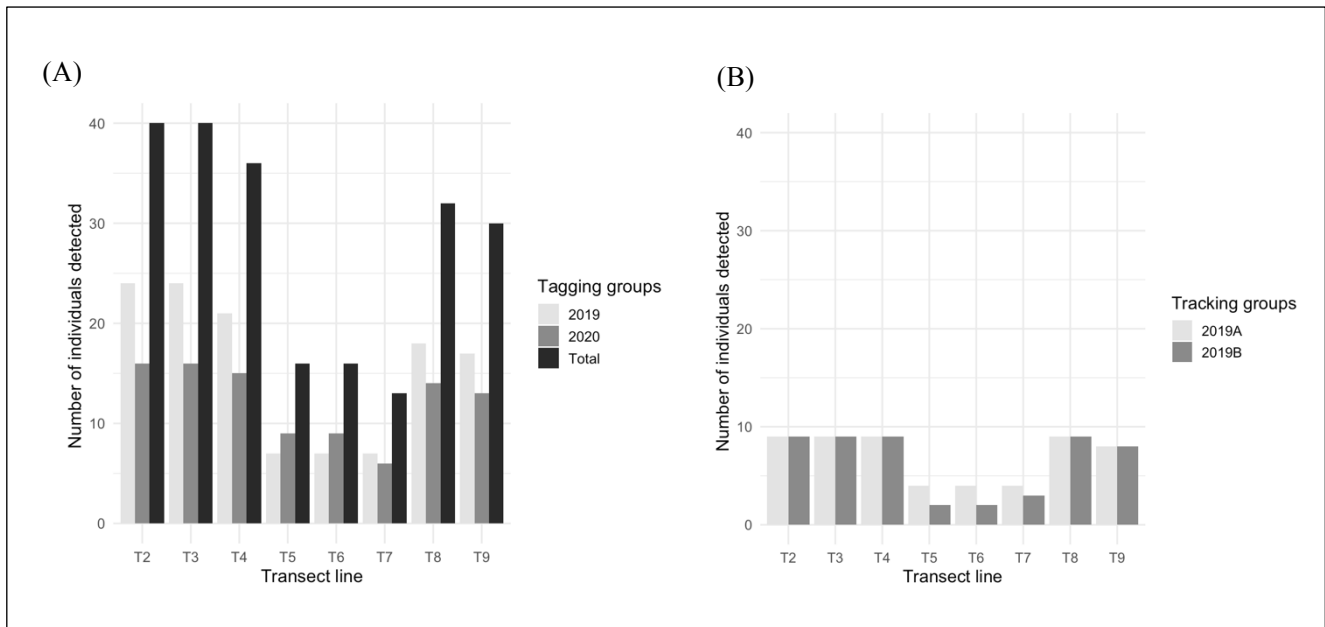


FIGURE 5: Number of individuals detected at each transect line during marine migration among fish that returned from marine migration for tagging groups (A) and tracking groups (B).

In total, six (12%) individuals stayed only within the protected area of the fjord, while 34 (88%) migrated further, to the outer, non-protected area (figure 6). The proportion of fish staying only within protected area did not differ between 2019 and 2020 (15% vs 8%, χ^2 contingency test, $\chi^2 = 1.601$, $df = 1$, $P > 0.05$).

Among all individuals included in residency analysis, more time was spent in the protected area than the non-protected area (Wilcoxon rank sum test, 2019; $n = 24$, $P < 0.01$, 2020; $n = 16$, $P < 0.01$). Fish tagged in 2019 and 2020 spent on average 63% of total marine migration time in the protected area. Individual residence time in the protected area varied widely, ranging from 7 days to 121 days for fish tagged in 2019 (mean = 58, SD = 30, figure 6), and from 16 days to 119 days for fish tagged in 2020 (mean = 69, SD = 26).

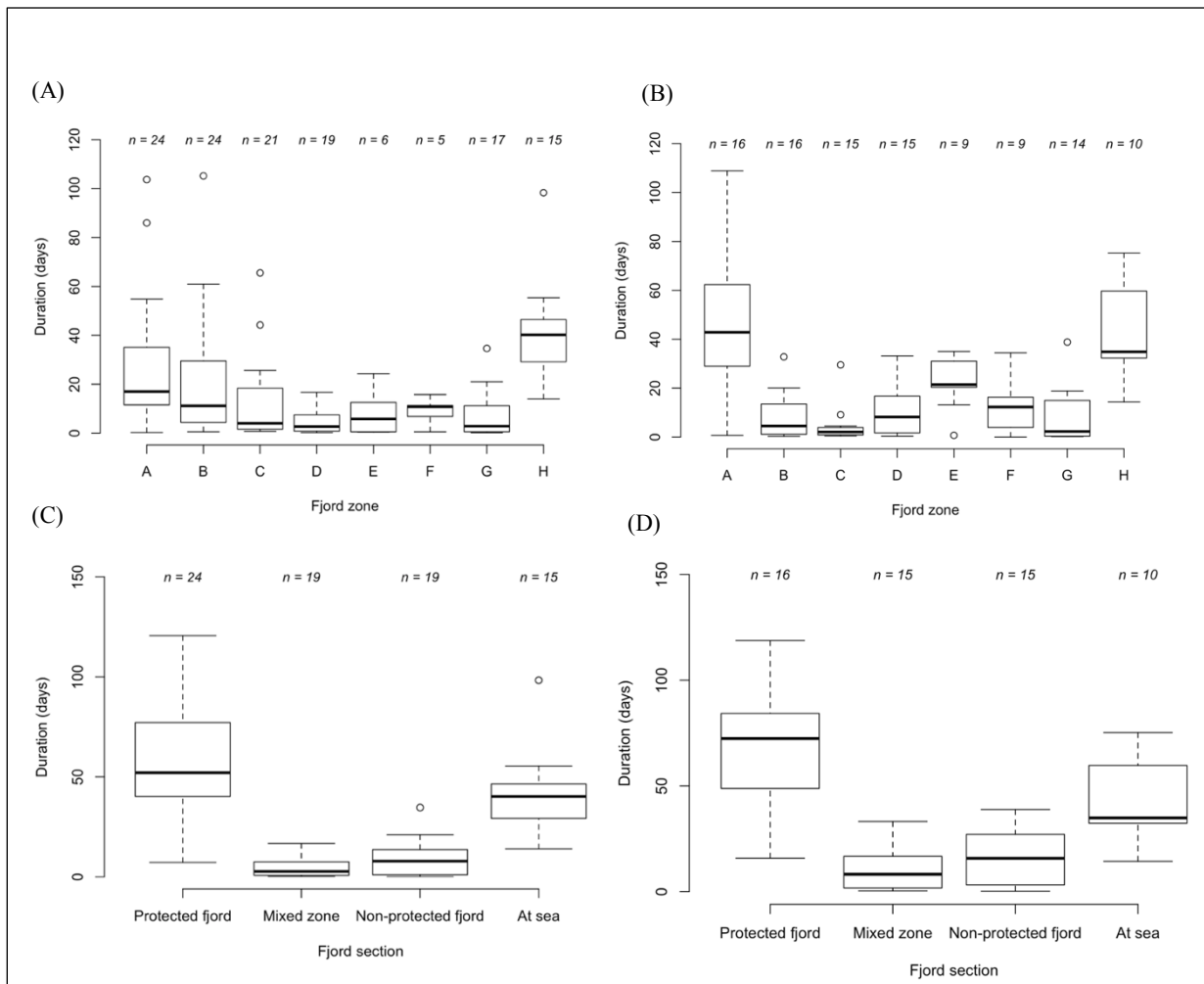


FIGURE 6. Residence time in fjord zones (figure A and B) and fjord section (figure C and D) during marine migration for returning individuals for tagging group 2019 (figure A and C) and 2020 (figure B and D). The box-and-whisker plots show median values (bold lines), the interquartile ranges (boxes) and the 5th and 95th percentiles (whiskers). Circles indicate outliers. Numbers above each plot gives sample size (n) of individuals resided in the fjord zones and fjord sections.

For individuals tracked for two seasons, mean residency in the protected area was 47 days ($n = 9$, $SD = 21$, range: 7-84 days) for the first year of tracking and 45 days ($n = 9$, $SD = 27$, range: 8-94 days) for the second year of tracking. The number of days spent in the protected area did not differ between the two years (Wilcoxon signed-rank test, $n = 9$, $P > 0.05$). Furthermore, the proportion of time spent in the protected area between the two years of tracking did not differ (Paired Welch two-sample t-test, $n = 9$, $P > 0.05$).

3.3.4.1 Generalized linear models of time spent in the protected area

There were four equally well fitted generalized linear models exploring the proportion of time spent in the protected area. The models indicated that the time spent in the protected area was influenced by body condition, body length, age, sex and year of tagging ($\Delta AIC < 2$, table 8). Total body length and year of tagging was the best indicator for proportion of time spent in the protected area, and was included in all of the best models (table 8). The estimates from the conditional model averaging (table 9) indicated that smaller individuals spent a higher proportion of time in the protected area compared to longer individuals, that the fish tagged in 2020 tended to spend higher proportions of their time inside the protected area and that fish in good body condition tended to spend less time in the protected area. The sex and age of the fish seemed to have limited effect on the proportion of the time used in the protected area, as the estimated standard errors exceeded the estimates in the conditional model averaging (table 9).

Table 8: Model selection for estimating the determinants on the proportion of time spent in the protected area. The models estimated the relative contributions to residency of the parameters adjusted condition factor (C), total body length (L), sex (S), age (A) and year of tagging (Y). AIC is the score based on Akaike's information criterion.

Model	AIC	ΔAIC	AIC weights	d.f.
[L, Y, C]	96.3	0.00	0.177	5
[L, Y]	98.0	1.74	0.074	4
[L, Y, C, S]	98.2	1.88	0.069	6
[L, Y, C, A]	98.2	1.90	0.068	6

Table 9: Summary of intercept and independent variables from model conditional averaging from generalized linear model on the proportion of time spent in the protected area during summer ($n = 34$). The asterisk mark show significant values

Effect	Estimate	Std. Error	z value	P
(Intercept)	-0.26520	0.25255	1.034	> 0.05
Total length	-0.40094	0.18836	2.043	< 0.05 *
Sex (Male)	-0.12491	0.39501	0.303	> 0.05
Condition factor adjusted	-0.29910	0.16367	1.753	> 0.05
Age	0.06883	0.23207	0.284	> 0.05
Tagging group (2020)	0.65515	0.34646	1.815	> 0.05

4. DISCUSSION

Coastal areas are important habitats for sea trout, and the results from the present study supplement knowledge of how this species utilizes marine areas within and outside a national salmon fjord during the summer. Relatively few (12%) of the individuals tagged remained only in the protected area throughout the migration season. Although some individual variation, approximately 63% of the duration of the total marine migration time was spent inside the marine protected area. Longer fish stayed shorter times in the protected area compared to smaller fish, and were more likely to leave Beiarfjorden and migrate further out in the fjord system.

The time span between marine entry of first and last sea trout was about one month while the timespan of freshwater return stretched across several months. Generally, from May until September, Beiarfjorden national salmon fjord may have importance for protection of sea trout, because it was during this time period sea trout from river Beiarelva generally were found at sea. Thus, there is seasonal variation in its importance.

The average duration of marine migrations both years (2019; 95 days, 2020; 121 days), was longer than recorded in previous studies in Northern Norway, which have found a duration between 45 and 70 days to be common (Berg & Berg, 1989; Klemetsen *et al.*, 2003; Davidsen *et al.*, 2018; Davidsen *et al.*, 2019). In contrast to the present study, studies in Tosenfjorden and Skjerstadjorden (Davidsen *et al.*, 2018; Davidsen *et al.*, 2019) found an average marine migration to be only 52 and 63 days, respectively. However, the individuals studied in these two fjords had rivers accessing lakes, while individuals in river Beiarelva had no access to lakes. Jensen and Rikardsen (2008) suggested that individuals may exploit different migratory strategies in rivers with and without access to lakes. If stable lake environments are absent, advantages of residing in freshwater compared to residing at sea might be reduced. A longer marine duration may therefore be an advantageous behavioral strategy for individuals from rivers without access to lakes (Davidsen *et al.*, 2014b; Aldvén & Davidsen, 2017). Hence, the lack of stable lake environment in river Beiarelva may partly explain the relatively long duration of marine migration in this fjord system. The duration of marine migration differed between fish tagged in 2019 and 2020. Several factors influence the duration of migration in individual fish, such as body condition, body length, sex, maturity and age (Jonsson, 1985; Berg & Berg, 1989; Eldøy *et al.*, 2015; Thorstad *et al.*, 2016). In addition, external factors such as

temperature (Berg & Berg, 1989) and salmon lice infestation (Birkeland, 1996), may affect time spent at sea. Hence, differences between years may occur (Berg & Berg, 1989).

The return rate, i.e., the number of tagged fish returning from the marine migration, was 70%, and did not differ between fish tagged in 2019 and 2020. The return rates are within the range of what other tagging studies in Northern Norway have found (50%-86%) (Berg & Jonsson, 1990; Jensen *et al.*, 2014; Bordeleau *et al.*, 2018). The reasons why the remaining individuals did not return were in most cases not known. Two fish were reported recaptured and killed by fishers (Davidsen *et al.* unpublished data). No tagging mortality was detected during tagging, but it is possible that some tagged fish died later due to tag effects. Other reasons why fish were not registered to return to the river could include unreported recaptures, tag malfunctioning, tag expulsion, restricted battery life on tags, or death due to natural causes. Furthermore, tagged fish could have returned to the river after the last data were downloaded from the receivers in mid-October 2020. In 2019, one fish returned in October and one fish returned in November, indicating that some, but not many fish may have returned after the data were last downloaded in 2020. In addition, fish may have strayed into other rivers (Berg & Berg, 1987) or stayed at sea during the winter (Jensen & Rikardsen, 2012).

The probability of migrating to the outer fjord (long distance migration) increased with total body length. Other studies have also found larger fish to be more likely to migrate to sea and migrate a greater distance at sea than smaller fish (Jensen *et al.*, 2014; Eldøy *et al.*, 2021). Furthermore, among the individuals utilizing both protected and unprotected areas, longer fish spent a lower proportion of time in the inner, protected area compared to smaller individuals. This may be explained by the ability of larger fish to exploit prey of a larger size (L'Abée-Lund *et al.*, 1992; Davidsen *et al.*, 2017). Migration further out in the fjord may increase the opportunities for more energy efficient feeding (Davidsen *et al.*, 2017). A previous study found differences in feeding strategies in the marine environment depending on the size of the fish, where smaller individuals fed on a mixture of invertebrate and fish in estuaries, and larger individuals mainly fed on marine pelagic fish (Davidsen *et al.*, 2017). Larger individuals might therefore be more likely to perform long-distance migrations.

Although longer fish were more likely to leave Beiarfjorden, some of the smaller fish (< 340 mm) were also found to be long-distance migrants. Since 84% of the fish migrated further out in the fjord system, the results may indicate that the inner fjord area is not the only favored

habitat, and that conditions may be better further out in the fjord system. Telemetry studies conducted in other fjords have found different results regarding proportion of long-distance migrants. Eldøy *et al.* (2015) found that 42% of sea trout tracked in Hemnfjord and Snillfjord (Trøndelag, Norway) were long-distance migrants (> 13 km), while Bordeleau *et al.* (2018) found that 52% of sea trout tracked in Tosenfjorden and Bindalsfjorden (Nordland, Norway) were long-distance migrants (> 21 km). Different migratory distance among populations can be found, due to both genetic and environmental differences (Klemetsen *et al.*, 2003; Ferguson *et al.*, 2019).

In the present study, the condition factor had little importance for the sea trout being medium- or long-distance migrants. In comparison, it has previously been reported that individuals completing a long-distance migration, often have a poorer body condition at the beginning of migration than individuals performing a short-distance migration (Eldøy *et al.*, 2015; Bordeleau *et al.*, 2018). Lower body condition in long-distance migrants is likely reflected by a greater need to maximize feeding compared to individuals with a better body condition (Davidsen *et al.*, 2014a; Eldøy *et al.*, 2021). The possibility to investigate the importance of condition factor between medium- and long-distance migration in the present study was restricted, since almost all fish were classified as long-distance migrants. Even so, fish in good body condition tended to spend less time in the protected area compared to fish with poorer body condition. This is contradictory to arguments that fish with poorer body condition may have a riskier migration behavior, such as migrating longer distances, and staying longer at sea, due to increased feeding opportunities (Eldøy *et al.*, 2021). The reason for the finding in the present study is not known, but may be explained by good feeding opportunities in the protected area, making it a suitable habitat for both fish in poor and good initial body condition.

In the present study, sex had limited influence on distance migrated and on the proportion of time spent in the protected area. This result differs somewhat with previous studies, which have found that females are more likely to migrate than males, instead of remaining in freshwater and the estuary (Jonsson, 1985; Bordeleau *et al.*, 2018; Eldøy *et al.*, 2021). Females' tendency to migrate is likely caused by a greater reproductive success with increased body size compared to males, and therefore a greater benefit of increased feeding opportunities (Elliott, 1995). The result in the present study may be influenced by a low sample size, skewed distribution between the sexes and all individuals had performed previous marine migrations. In addition, age had limited effect on migration distance and the proportion of time spent in the protected area, which

might illustrate that body length was more important than age. Body length being more determining than age has previously been shown in terms of timing of smolt migration (Bohlin *et al.*, 1996). However, a previous study from Hemnfjord and Snillfjord found that long-distance migrants were older than short- and medium-distance migrants (Eldøy *et al.*, 2015).

Fish tagged in 2020 tended to spend higher proportions of their time inside the protected area than fish tagged in 2019. However, year of tagging had little importance on distance migrated. Differences in environmental conditions, such as temperature and food availability, can affect migration behavior (Dill, 1983; Jensen *et al.*, 2014). However, this information was not available in the present study.

As a poikilothermic animal, the metabolism of sea trout is highly affected by the water temperature surrounding the fish (Angilletta *et al.*, 2002). Previous studies have demonstrated that the optimal temperature for growth in trout is 12-17 °C (Elliott & Hurley, 2000a; b; Larsson, 2005). The distribution of the tagged sea trout might therefore be influenced by the seawater temperature (Rikardsen *et al.*, 2007; Jensen *et al.*, 2014). Rikardsen *et al.* (2007) found that sea trout mostly resided in inner and warmer parts of the fjord, likely because of the more optimal temperature for growth in the inner parts of the fjord compared to further out in the fjord system (Rikardsen *et al.*, 2007). Jensen *et al.* (2014) found that with large temperature differences within the fjord system, the probability of finding sea trout was higher in the inner, warmer parts of the fjord. The estuary in Beiarfjorden is highly affected by glacial runoff, making the estuary cold for large parts of the summer, and probably colder than the study area of Rikardsen *et al.* (2007) and Jensen *et al.* (2014). Thus, the low temperatures in the estuary may lead to slow growth rates, prompting sea trout from river Beiarelva to seek warmer areas further out in the fjord system. However, in the present study, sea trout resided a long period in the inner, protected area, especially in the inner part of Beiarfjorden. The water temperatures in the estuary in Beiarfjorden and further out in the fjord correlated considerably during summer months. The mean temperature between the areas during these months did not differ much. Jensen *et al.* (2014) found that with minimal temperature differences in adjacent fjord sections the probability of finding sea trout in these areas were the same. Thus, the approximately similar temperatures in the neighboring areas in the present study may partly explain why the observed residence time in the inner area was high, as in the study of Jensen *et al.* (2014).

One main route was preferred for individuals leaving Beiarfjorden, even though the fjord system has two different migration routes out of the fjord system. The reason why sea trout mainly used this route is unknown, but it could be due to better habitat or conditions in the northern Nordfjorden compared to the southwestern Holmsundfjorden and Morsdalsfjorden.

Beiarfjorden national salmon fjord covers only Beiarfjorden and Holmsundfjorden, while sea trout tagged utilized all parts of the fjord system. Although fish resided in all fjord parts during the marine migration season, approximately 63% of the time was spent in areas protected by the national salmon fjord. However, there are some limitations with the setup of the receivers for this fjord system. With only one transect line, one can tell when a fish was present within the receiver range, but not in which direction the fish was swimming or whether it was crossing the transect line or not. For instance, much time in the present study was spent in the estuary. A long time spent in the inner parts of fjords are common for sea trout (Eldøy *et al.*, 2015; Davidsen *et al.*, 2018), but because of poor coverage in the lower part of the river, this time could be overestimated as fish might be residing in the river instead. One can therefore not rule out the possibility that fish in periods reside in other zones than assumed, affecting the result of residence time in the zones and in the protected area. Hence, the calculations are only an estimation of time spent in each zone.

All individuals tracked during two marine migration seasons ($n = 9$) maintained their same medium- and long- distance migrants' classification. The number of days and proportion of time spent in the protected area did not differ between the two marine migration seasons, which may indicate consistency in area use between the two marine migration seasons. This interpretation is supported by Eldøy *et al.* (2019), who found a strong and significant individual consistency in marine area use between marine migration seasons. Individual sea trout tracked during two migration seasons demonstrated no difference in the timing of freshwater return between the years. Consistency in the migration timing of freshwater return was also observed by Jensen *et al.* (2020) and Eldøy *et al.* (2019). However, there was a difference between the years in the timing of marine entry and in the total duration of marine migration. Differences in timing of marine entry and in the total duration of marine migration was also found by Eldøy *et al.* (2019), and could be explained by differences in environmental conditions between the years. Increased water temperatures, timing of ice melting, and increased discharge have all been found to influence the timing of migration (Thorstad *et al.*, 2016).

Evaluating management actions is vital to determine the effects of the actions taken and to use the knowledge for future decisions (Pullin *et al.*, 2013). One of the main purposes of establishing national salmon fjords was to protect wild Atlantic salmon populations against negative influences from salmon fish farms (NOU, 1999:9; DKMD, 2002; 2006). Initially, these protected areas were not intended to protect sea trout (DKMD, 2006). However, it is argued that national salmon fjords might benefit and protect the more coastal dwelling sea trout populations against salmon lice (Bjørn *et al.*, 2011; Serra-Llinares *et al.*, 2014). The protection of the national salmon fjords is expected to depend on the size and design of the protected area (Serra-Llinares *et al.*, 2014), the production from aquaculture outside the protective area (Serra-Llinares *et al.*, 2014; Karlsen *et al.*, 2018), and environmental influence (Jansen *et al.*, 2016), such as temperature and currents, which affect salmon lice and other pathogens dispersal (Serra-Llinares *et al.*, 2014; Jansen *et al.*, 2016; Grefsrud *et al.*, 2018).

Sea trout residing inside a national salmon fjord are likely to receive protection against salmon lice, viruses and other diseases from salmon farms because of a generally lower infection pressure than in areas where the salmon farms are located (Bjørn *et al.*, 2011). The situation is not necessarily the same for sea trout utilizing outer, non-protected fjord areas, or sea trout which have to pass farmed areas to reach the open sea (Bjørn *et al.*, 2011). Consequently, if a national salmon fjord, such as Beiarfjorden national salmon fjord, only covers parts of the fjord system that sea trout utilizes, it may reduce the overall protection of sea trout (Karlsen *et al.*, 2018). Since fish with longer body lengths were more likely to spend less time and more often left the protected area, they may receive less protection from the protection regime than smaller fish. Thus, the Beiarfjorden national salmon fjord may to a lower degree protect large individuals compared to smaller individuals. A similar result was found in a different protected regime, a marine protected area (MPA) in Tvedestrandfjorden (Southern Norway), where large fish was found to receive less protection from the no-take zone compared to smaller fish (Nordgård, 2016). Large individuals are regarded as important due to their high reproductive success (Jonsson, 1985). Preferably, protected areas should include all individuals, regardless of biologic characteristics, to prevent altered population behavior. Hence, to protect the entire population, including the valuable large individuals, the protected area should be of a large size.

Beiarfjorden national salmon fjord is one of the smallest national salmon fjords in Norway with its approximately 38 km² protected area (Karlsen *et al.*, 2018). In addition, the distance to the closest fish farm from the border of the national salmon fjord is less than 3 kilometers (shortest

distance at sea, measured from Kartverket). The highest infection levels of salmon lice are often found close to fish farms, especially within 30 km of the nearest farms (Bjørn *et al.*, 2011; Middlemas *et al.*, 2013; Serra-Llinares *et al.*, 2014; Thorstad *et al.*, 2015), minimizing the effect of the protective zone as salmon lice can disperse to areas inside the protective area. Hence, the impact of aquaculture close to a national salmon fjord will be greater in smaller protected areas compared to larger-farm free fjords (Bjørn *et al.*, 2011; Serra-Llinares *et al.*, 2014). Regardless of which route sea trout left the fjord system through, they must pass areas with farming. Moreover, most fish were registered leaving through Nordfjorden, the fjord with a higher number of salmon farms compared to Morsdalsfjorden. By including Morsdalsfjorden and Nordfjorden in the protected area, the entire fjord system from river Beiarelva to the open sea would be protected. Both of these fjord areas were investigated in relation to the establishment of Beiarfjorden national salmon fjord, but were not proposed to be included (DKMD, 2006).

A salmon lice count on a small sample of wild sea trout ($n = 25$) in Nordfjorden during the weeks 24-25 in 2017 illustrated a low risk (0%) of salmon lice related mortality in this period (Grefsrud *et al.*, 2018). However, in a recent comprehensive report, salmon lice were estimated to have a moderate effect on sea trout (10-30% mortality) from river Beiarelva during the weeks 26-33 in years 2012 to 2017 (Anon, 2019). The estimate in the report by Anon (2019) included salinity data, lice counts from salmon farms, and a lice dispersal model from the farms. All data in this report were collected during the same weeks as the marine migration period of fish tagged in the present study. Based on the report, salmon lice are likely to have a negative impact on the sea trout population from river Beiarelva.

In the present study, a high freshwater influence in the estuary of Beiarfjorden was found, with a mean salinity of 18‰ during the summer months. Finstad *et al.* (2021) argued that sea trout populations from rivers in inner parts of fjords were somewhat protected from salmon lice by freshwater influence, because of the salmon lice low tolerance for freshwater (>25%) (Johnson & Albright, 1991; Bricknell *et al.*, 2006). National salmon fjords including areas with brackish water, such as in inner Beiarfjorden, can therefore act as refuges where sea trout can retreat if there are high levels of salmon lice outside the protected area. This might be a better alternative than migrating to the river, which can reduce growth opportunities (Birkeland, 1996).

Two of the salmon farms located in Nordfjorden were under surveillance due to suspicion of ISA (infectious salmon anemia) and treatment of ISA in nearby areas outside the study area. ISA was disproved at both salmon farms. However, tagged fish visiting this fjord section during

the summer of 2019 and 2020 (71% and 88% of individuals migrating to fjord, respectively) were in proximity to fish farms with suspected ISA. The occurrence of pathogens on fish farms can spread to wild fish and lead to higher numbers of disease outbreaks in nature. It is probable that significant amounts of pathogens are spread to the environment from infected fish in aquaculture, and that wild fish in the proximity of the farms are exposed to these pathogens (Grefsrud *et al.*, 2018). Sea trout can be infected by the ISA virus, but they do not develop symptoms (Nylund & Jakobsen, 1995; Snow *et al.*, 2001). The risk of population-reducing effects of ISA on sea trout is therefore considered low (Grefsrud *et al.*, 2018). However, sea trout can function as a host for the ISA virus and possibly transfer the virus to salmon (Nylund & Jakobsen, 1995). Infectious diseases are a serious problem in fish farming in Norway, with 300-500 outbreaks of disease along the coast annually (Svåsand *et al.*, 2016; Sommerset *et al.*, 2019). Although diseases can be spread over long distances (Aldrin *et al.*, 2010; Kristoffersen *et al.*, 2013), the concentration is generally diluted with the distance from fish farms (Grefsrud *et al.*, 2018). Thus, farm-free areas such as national salmon fjords can reduce disease transmission to wild fish (DKMD, 2006).

Sea trout management is in many countries viewed as a by-product of Atlantic salmon management (Nevoux *et al.*, 2019). To manage and protect sea trout populations as its own specie, it is essential to have knowledge of where they are residing in the fjord system (Nilsen *et al.*, 2019a) and if the behavior is repetitive. However, such information is scarce (Eldøy *et al.*, 2019; Jensen *et al.*, 2020), but can be important for implementing management measures. If it is possible to determine consistency in area use between consecutive years, protected areas could be customized and provide better protection for wild sea trout. However, it is also important to remember that behavior can change with environmental conditions and anthropogenic factors (Berg & Berg, 1989; Birkeland, 1996). Furthermore, knowledge regarding the biological traits influencing migration distance and habitat use may increase the understanding about which traits contributes to protection by a national salmon fjord. Despite the small size of Beiarfjorden national salmon fjord, the results from the present study demonstrate that sea trout to a large extent reside in habitats that are covered by the protected area. In addition, low temperatures in the fjord system, low salinities in the inner Beiarfjorden, few cases of lice counts above lice limit from salmon farms and previous low salmon lice counts on wild fish have been found. Combined, these results may indicate that Beiarfjorden national salmon fjord also benefits the sea trout.

5. CONCLUSION

The present study indicates that Beiarfjorden national salmon fjord contains important coastal habitats for sea trout. Although sea trout migrated further out in the fjord system, individuals originating from river Beiarelva resided most of their time within the protected area of the fjord. Longer individuals spent less time in the protected area and were more likely to leave Beiarfjorden compared to smaller individuals, meaning smaller fish are likely more protected by the national salmon fjord compared to larger fish. Furthermore, the observed consistency regarding behavior and duration of marine migration between fish tagged and tracked in consecutive years supports the conclusion about the sea trout's use of Beiarfjorden national salmon fjord. The task of reducing negative human impact, especially from fish farming, must be strengthened to ensure having sea trout in Norway in the future. National salmon fjords can protect sea trout that live within the protected area to a certain extent. Nevertheless, the degree of protection will also strongly depend on the size of the protected area, the infection pressure, environmental factors, and time used in unprotected areas during migration. Including sea trout in existing management actions may be an efficient approach to mitigate salmon lice threats to the specie. Knowledge of how well national salmon fjords protects sea trout from potential negative impact from aquaculture will be important when evaluating the function of these marine protected areas. Since it is difficult to transfer results from field studies between different areas, carrying out similar studies in other national salmon fjords should be a focus in future studies. The Norwegian authorities have chosen national salmon fjords and national salmon rivers as one of the main measures to preserve wild Atlantic salmon. Hence, knowledge on possible inclusion of sea trout in national salmon fjords should be of interest for future management decisions.

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