

Marine migration and habitat use of anadromous brown trout *Salmo trutta*

Sindre Håvarstein Eldøy, Jan Grimsrud Davidsen, Eva Bonsak Thorstad, Fred Whoriskey, Kim Aarestrup, Tor Fredrik Næsje, Lars Rønning, Aslak Darre Sjursen, Audun Håvard Rikardsen and Jo Vegar Arnekleiv

S. H. Eldøy (sindre@hardware.no), J. G. Davidsen (jan.davidsen@ntnu.no), L. Rønning (lars.ronning@ntnu.no), A. D. Sjursen (aslak.sjursen@ntnu.no) and J. V. Arnekleiv (jo.arnekleiv@ntnu.no). NTNU University Museum, Norwegian University of Science and Technology, NO-7491 Trondheim, Norway.

E. B. Thorstad (eva.thorstad@nina.no) and T. F. Næsje (tor.naesje@nina.no). Norwegian Institute for Nature Research, NO-7485 Trondheim, Norway.

F. Whoriskey (fwhoriskey@dal.ca). Ocean Tracking Network, Dalhousie University, Halifax, NS B3H 4J1, Canada.

K. Aarestrup (kaa@aqu.dtu.dk). Technical University of Denmark, National Institute of Aquatic Resources, DK-8600 Silkeborg, Denmark.

A. H. Rikardsen (audun.rikardsen@uit.no). The Arctic University of Norway, NO-9037 Tromsø, Norway.

Corresponding author: Jan Grimsrud Davidsen, NTNU University Museum, Department of
Natural History, NO-7491 Trondheim; Norway. Tel.: +47 924 64314; email:
jan.davidsen@ntnu.no.

ABSTRACT:

The biology and ecology of anadromous brown trout *Salmo trutta* at sea is poorly understood. This study provided information on spatial and temporal distribution of sea trout in the ocean. The behaviour of 115 individuals (veteran migrants, 270-700 mm) was tracked by using acoustic telemetry in a fjord system during April-September in 2012-2013. Overall, fish spent 68% of their marine residence time close to river mouths (< 4 km). Most fish registrations (75%) were in near shore habitats, but pelagic areas were also used. The maximum migration distance of tagged fish was categorized as short (< 4 km from river mouth, 40% of fish), medium (4-~13 km, 18% of fish) or long (> ~13 km, 42% of fish). Long distance migrants had poorer body condition in spring prior to migration, used pelagic areas more often and returned earlier to freshwater than short and medium distance migrants. Marine residence time was 7-183 days, and was positively correlated to body length and smolt age, but negatively correlated to the date of sea entry.

Key words: acoustic telemetry; life history strategy; migratory behaviour; sea trout;

INTRODUCTION

The brown trout (*Salmo trutta* L.) is an iteroparous salmonid species with indigenous populations in Europe, North Africa and western Asia (MacCrimmon et al. 1970). It has been introduced by humans to all other continents except Antarctica (MacCrimmon and Marshall 1968). The brown trout is an opportunistic carnivore that with its large ecological variability has adapted to and found suitable niches in a variety of habitat types (Klemetsen et al. 2003). Brown trout often migrate to utilise the best suited habitat during different stages of its life cycle, moving either within freshwater systems, or repeatedly between freshwater and marine habitats, to ultimately increase their individual fitness (Jonsson and Jonsson 1993). By exploiting better feeding habitats (i.e., the sea or a lake), migration can enable individuals to attain higher growth rates, larger sizes at-age, and for females higher fecundities (Hendry et al. 2004), all of which may provide fitness benefits. The costs related to migration may include physiological adjustments, the allocation of energy for swimming, and increased probability of mortality, e.g. owing to predation, parasitism and diseases during migration (Gross et al. 1988, Jonsson and Jonsson 1993).

Brown trout populations in coastal rivers may consist of both anadromous (hereafter referred to as sea trout) and resident individuals originating from the same parents (Jonsson and Jonsson 1993). The mechanisms controlling whether an individual becomes resident or migratory are yet to be fully understood (Acolas et al. 2012), but an individual's tendency to migrate seems partly genetically determined and partly caused by phenotypic plasticity (Jonsson and Jonsson 1993). Factors such as metabolic rate, growth rate, body size, energy reserves, sex and genetics are thought to influence whether an individual adopts migratory or resident behaviour (Thorpe 1987, Forseth et al. 1999, Wysujack et al. 2009). The balance between migration and residency is influenced by environmental factors such as food availability, fish density, and interspecific

competition in combination with inter-individual differences, presumably underpinned by genetically determined reaction norms (Pulido 2011). Similar intrinsic and environmental factors may also influence individual behavioural strategies during marine migrations, determining whether to become a short or long distant migrant, and which feeding habitats to utilise. However, little is known about the inter-individual variation of migration behaviour and strategies in the marine environment, and of the factors that may influence this variation.

Previous studies of sea trout in the marine environment have revealed a large variation in migration timing, residence periods (Jensen 1968, Jonsson 1985, Jensen and Rikardsen 2008, Jensen et al. 2012), migration distance (Berg and Berg 1987, Jensen et al. 2014) and prey choice (Knutsen et al. 2001, Rikardsen and Amundsen 2005, Rikardsen et al. 2007). In Europe, sea trout can enter estuaries from fresh water during all months of the year (Went 1962, Jonsson and Jonsson 2002, Jonsson and Jonsson 2009) and the marine residence-time may differ considerably among individual fish. For instance in Irish rivers, marine residence time was found to vary between 43 and 362 days (Piggins 1964). Migratory distances may also differ significantly. In Russia, Chernitsky et al. (1995) suggested that some trout resided in the estuary of the River Varsina, while others migrated to the open Barents Sea. Intra-population variation in marine migration distance was also recorded in a Danish population, where 47% of the tagged sea trout post-smolts remained close to their home river in a coastal fjord, and 53% migrated to the open Kattegat Sea (del Villar-Guerra et al. 2013). The authors suggested that the variation in migration distance was consistent with a continuum of partial migration, in which a decision-making point existed after fjord entry on whether to stay in the fjord or migrate to the open sea. However, both smolts and sea trout kelts (repeat spawning individuals) in a nearby fjord all migrated into the Kattegat sea (Aarestrup et al. 2014, Aarestrup et al. Accepted), demonstrating a large life history variability both within and among nearby populations.

During the last decades, the abundance of sea trout has declined markedly in many regions (ICES 2013). As an example, the catches in Norwegian rivers have, except for the northernmost areas, declined by 23–66% during the last two decades (Anon. 2011). Recent findings from several other countries where sea trout occur indicate similar decreases, and for some areas it is hypothesized that this results from reduced marine survival caused at least in part by changes in food supply or increased parasite infestations related to fish farming (ICES 2013). In sea trout populations, mortality in the freshwater phase, especially during the earliest embryonic and post-emergence life stages, can have a population regulating effect, whereas mortality in the marine phase is not regulatory, but has a population reducing effect (Milner et al. 2003, Jonsson and Jonsson 2011). Hence, it is not believed that there are compensatory mechanisms for additional mortality in the marine phase, and elevated marine mortality rates can result in a proportional reduction in the number of spawning adults. Because sea trout typically are females (e.g. Knutsen et al. 2004, Jensen et al. 2012), additional marine mortality has an accentuated potential to negatively affect population recruitment by reducing the egg supply. The marine phase is therefore an important life stage of sea trout. However, their biology and ecology in the sea is poorly understood (Drenner et al. 2012, ICES 2013), and to understand the causes for the decrease in the abundance of sea trout in many regions, increased knowledge on the marine life stage is fundamental. To identify which anthropogenic or natural factors impact sea trout, and to what extent, it is essential to determine the habitats utilized by the sea trout at different times. Migration distance is also important, as short distant migrants will mainly be impacted by local factors close to a population's river mouth, whereas long distance migrants may be impacted by multiple factors acting along the migration routes and in the different feeding habitats.

Most previous marine tracking studies of sea trout have focused on post-smolt migration behaviour (e.g. Moore et al. 1998, Thorstad et al. 2004), whereas only a few studies have covered

older life stages (Bendall et al. 2005, Jensen and Rikardsen 2008, 2012, Jensen et al. 2014, Aarestrup et al. Accepted). The aim of the present study was to provide novel information on the marine habitat utilization during the summer season for sea trout that had previously performed one or more previous marine migrations, termed veteran migrants. Spatial and temporal distributions of tagged fish were recorded throughout the summer using acoustic telemetry in a marine fjord in Central Norway. Specifically, marine migration distance from the trout's putative home river mouth, marine residence time and utilisation of littoral versus pelagic habitat was examined. In order to explain individual variation in marine residence time, and possible differences between the short, medium and long distance migrants, information on individual morphometric (body length, body condition, age) and life history characteristics (back calculated smolt length, age at smolting, previous number of marine seasons) were analysed in relation to the observed migration patterns.

MATERIALS AND METHODS

STUDY AREA

The study was performed in two interconnected fjords (Hemnfjord and Snillfjord) in Sør-Trøndelag County, Central Norway. Together, the two fjords cover more than 60 km² of sea surface and have 65 km of shoreline (Fig. 1). The fjord system is connected to the open sea through a 36 km long strait.

The Sjøa watercourse has a drainage basin of 113 km² and a mean annual water discharge of 13.9 m³ s⁻¹. The freshwater section accessible to anadromous fish is 10.2 km long and includes Lake Rovatnet (surface area 7.65 km²), which offers suitable overwintering habitat and conditions for sea trout. River Sjøa drains from the lake to the sea in Hemnfjord.

The River Snilldalselva consists of two branches, Snilldalselva and Bergselva.

Snilldalselva has a drainage basin of 42.7 km², mean annual water discharge of 1.4 m³ s⁻¹ and a 4.8 km long section accessible to anadromous trout. Bergselva has a drainage basin of 69.3 km², mean annual water discharge of 2.1 m³ s⁻¹ and an accessible stretch of 1.1 km. Both branches are highly influenced by floods and have few deep pools, consequently they are considered to be poor overwintering areas for sea trout.

ENVIRONMENTAL VARIABLES

Three temperature and salinity recorders (DST milli-CT, Star-Oddi Ltd, Iceland) were deployed in the fjord system, the first 1 km from the mouth of the River Sòa in the inner Hemnfjord (Array H1, Fig. 1), a second 600 m from the river mouth of the River Snilldalselva in the inner Snillfjord (Fig. 1), and the third at the middle receiver of the outermost array (Array H3, Fig. 1). They were mounted at 1 m depth on the same moorings as the automatic acoustic receivers.

FISH CAPTURE AND TAGGING

Five groups of sea trout were captured and tagged with acoustic transmitters during 12 April 2012-12 May 2013 (Table 1). A total of 80 individuals were tagged in the Sòa watercourse, consisting of 30 fish tagged in the outlet of Lake Rovatnet during the spring of 2012 (HS12 tagging group), 21 fish tagged in Lake Rovatnet during autumn 2012 (HA12), and 29 fish tagged in the river mouth of River Sòa during the spring of 2013 (HS13). A total of 35 individuals were tagged in River Snilldalselva, consisting of 20 fish tagged during autumn 2012 (SA12), and 15 fish tagged during spring 2013 (SS13). The fish were captured using 3-5 gillnets with 35-42 mm mesh width. The nets were checked continuously, and captured fish were retrieved as soon as vibrations/visual observations indicated a fish was entangled. This reduced fish stress and

injuries. The fish were taken out of the nets by cutting net mesh with scissors to prevent damage to gills, skin and scales. Prior to tagging, the captured fish were kept up to two hours in a net cage in a calm part of the river or shoreline.

The sea trout were implanted with individually coded acoustic transmitters. Study partners contributed tags to the study, which resulted in using different models of tags having different characteristics and capabilities depending on partner resources and research interests. The different models had the same shape but differed in length and diameter which allowed adaptation of tag size to the length of the fish (HS12: $n = 15$ model MP-9-long, natural length (L_N) 335 - 440 mm, $n = 15$ model MP-13, L_N 350 - 600 mm; HA12: $n = 10$ model V9-2x, L_N 270 - 380 mm, $n = 11$ model V13-1x, L_N 370 - 700 mm; SA12: $n = 5$ model MP-9-long, L_N 310 - 400 mm, $n = 6$ model MP-13, L_N 340 - 650 mm, $n = 9$ model V13-1x, L_N 340 - 440 mm; HS13: $n = 29$ model ADT-9-long, L_N 330 - 580 mm, SS13; $n = 15$ model ADT-9-long, L_N 320 - 460 mm). Natural length of the fish was measured from the tip of the snout to the tip of the longer lobe of the caudal fin, without compressing the lobes along the midline. Estimated battery life was 246 days (MP-9-Long), 267 days (ADT-9-long), 282 days (V9-2L), 525 days (MP-13) or 622 days (V13-1L), respectively. Hence, 41 fish tagged in 2012 could also be tracked in 2013. Transmitter models MP and ADT were produced by Thelmafiotel AS, Norway, and all V models by VEMCO Inc., Canada. Tag size was chosen according to body length and condition of the fish to minimise tag size relative to fish size. Tag mass in air relative to fish body mass was on average 1.46% (range 0.30-3.09%). The tag used for any individual fish was believed to be small enough that it would not significantly affect behaviour or survival (e.g., Cooke et al. 2011).

Prior to tagging, the fish were anaesthetised with 2-phenoxy-ethanol (EC No 204-589-7; SIGMA Chemical Co., USA; 0.5 ml l⁻¹ water). A 1.5 - 2 cm incision was made in the body cavity on the ventral surface anterior to the pelvic girdle. After the tag was inserted via the incision into

the body cavity, the incision was closed using two independent monofilament sutures (RESORBA Wundversorgung GmbH & Co. KG, Germany; 5/0 Resolon). During the 3-5 min surgery, the gills were gently irrigated. After surgery, the fish were placed in a holding tank for recovery (3-5 min) before they were released in a calm part of the river or near the shoreline close to the capture site.

TRACKING OF TAGGED FISH

The tagged fish were tracked using a total of 50 acoustic receivers (Vemco Inc., Canada, model VR2W and VR2). Of these, 39 were deployed in the fjord system, while 11 were deployed in different watercourses, including those where the fish were captured for tagging (Fig. 1). All receivers deployed in the fjord were mounted on moorings 5 meters below the surface, and were operative from 20.04.2012-04.12.2013. The receivers deployed in rivers were moored on 50 mm iron pipes which were hammered into the riverbed. With exception of the four receivers in River Sjøa between Lake Rovatnet and the Hemnfjord which were in operation during the whole study period, all receivers in freshwater habitats were operative from 20.04 2012 – 02.12.2012 and from 22.04.2013 – 04.12.2013.

RECEIVER PERFORMANCE

Receivers recorded transmitter identification code (individual fish identity), detection date and time for each signal received. Receiver range was tested at the middle receiver of array H1 (Fig. 1) on 22.08.2013 (calm, clear weather, high tide) and at the Hafsmo salmon farming site (Fig. 1) on 03.12.2013 (calm, clear weather, slack tide) by deploying a transmitter (model ADT-9-long, 146 dB re 1uPa @1m) at 3 and 5 meters depth and at increasing distance from the receiver in steps of 50 meters. The maximum receiver range was on both occasions 300 - 350 meters. The

transmitter model used in the range test was expected to have the shortest range of all transmitter models used in the study, based on its technical specifications.

SCALE SAMPLE ANALYSIS

A small number of fish scales (5-7 scales) were sampled from the studied animals during the tagging procedure. Information obtained from the scales on smolt length, age at smoltification, age when studied, and numbers of previous seaward migrations were used in the analyses of the migratory behaviour. Scale growth was assumed to be proportional to length growth (Dahl 1910, Lea 1910, Závorka et al. 2014). The ages assigned by the research team to the experimental animals were verified by sending a subsample of the scales for reading by personnel at the Norwegian Institute for Nature Research and the Technical University of Denmark. Uncertain values of age, length and age at smoltification and number of previous seaward migrations were excluded from analyses.

The sea trout tagged in the river mouth of River Sjøa during spring 2013 (HS13) had uncertain river of origin, due to presence nearby (500 m) of another watercourse housing sea trout. This group of fish was therefore separated from the groups tagged in Lake Rovatnet when analysing morphology and life history of the individuals by the watercourses of tagging.

DATA ANALYSIS

DATA FILTERING

The initial number of detections (registrations) logged onto all receivers used in the study was 5 147 075. Mean number of detections of the tagged individuals was 44 745 (SD = 91 294, range 0-597 433). A total of 1 360 (0.03%) registrations with false IDs were excluded from the dataset. Data from the two receivers in the outlet of the River Sjøa and the three innermost receivers in

Snillfjord were anticipated to contain higher frequencies of false detections due to concurrent signals from high numbers of simultaneously occurring tagged fish. Concurrent signals (tag collisions) can confound receiver detections and generate false ID codes. A data filter that required at least two registrations from a tagged individual within a time span of 10 minutes was applied to these receivers, which excluded 46 223 (0.90%) registrations from further analyses.

STATISTICAL ANALYSES AND COMPUTER SOFTWARE

After sorting and extracting data using Access 2013 and Excel 2013 (Microsoft Co., USA), the statistical analyses were conducted using R version 2.15.3 (R Core Team 2014; www.r-project.org). For one and two-way analysis of variance between two groups, Welch's t-test were conducted, assuming unequal variance. For analysis of variance between three or more groups, Tukey's ANOVA was conducted using the R-package Multcomp (Hothorn et al. 2008).

The hypothesis that numbers of days spent at sea depended on some combination of fish age, body length, condition factor, previous numbers of time the fish had been to sea, time of sea entry (Julian day number), maximum distance migrated away from the home river and smolt age and length was tested using the R-package MuMIn (Barton' 2015). In total, 576 models of varying complexity were fitted for hypothesis testing. To avoid autocorrelation between body length and condition factor, residual values (resvalbc) from the linear model $\log(\text{condition}) \sim \log(\text{length})$ were used instead of the body condition *per se*. The global model included age at tagging, length (L_N), resvalbc, previous number of times the fish had been to sea, time of sea entry, short, medium or long distance migratory strategy, back calculated smolt age and smolt length and the interaction terms length*resvalBC, strategy*length and strategy*resvalbc. The other 575 models were all nested models from the global model. The

approximating models were compared using Akaike information criterion (AIC) (Anderson et al. 2001). AIC ranks the candidate models to determine which model provides the best description of the data with the fewest parameters. The hypothesis was tested for those 27 sea trout for which data on all variables were available.

DEFINING SHORT, MEDIUM AND LONG DISTANCE MIGRANTS

The fish were categorised as short, medium or long distance migrants according to the maximum distance at which they were detected from their release point during 1 April-1 October in either 2012 or 2013(see Fig. 1). Short distance migrants were only recorded at receivers up to 4 km from the river mouth. Medium distance migrants were registered up to 10 km from the river mouth for fish tagged in Søa watercourse, and up to 13 km for the fish tagged in River Snilldalselva. Long distance migrants were registered at receivers more than 10 km from the river mouth for fish tagged in Søa watercourse, and more than 13 km for fish tagged in River Snilldalselva. The slight difference in the distances which defined migrant groups for the two watercourses (10 vs. 13 km) was due to logistical concerns that resulted in different distances between the receiver arrays in the two fjords. Fish that did not return to freshwater and were not recorded by any receiver in the marine habitat after 1 July in either 2012 or 2013, were excluded from the migration distance analysis, because they potentially were lost from the study before they had reached their maximum dispersal. An exception was done for fish registered at receivers more than 10 km (Søa watercourse) or 13 km (River Snilldalselva) from the river mouths, since they already had been recorded as long distance migrants.

CALCULATING MARINE RESIDENCE TIME

The study area was divided into different zones based on geographic location (Fig. 1). Residence time was only calculated for individuals returning to freshwater or for fish recorded in the fjord after 1 October in 2012 or 2013. The calculation of residence time by tagged fish in different fjord zones was carried out using the following criteria:

1. In the case of a transition to a zone further out in the fjord, the residence time in the next zone started at the time of the last registration at a receiver in the previous zone.
2. In the case of transition to a zone further into the fjord, the residence time in the next zone started at the time of the first registration at a receiver in the inner zone.
3. For transitions into freshwater, the freshwater residence started at the time of the last registration at a river mouth receiver.
4. For transitions from freshwater to fjord zones, the fjord residence started at the first registration at a river mouth receiver.

Receivers in river mouths were considered as part of the fjord. For the fish tagged in 2013, estimated marine residence times were considered as minimums since the fish were captured in the river mouths, and it was possible that they had spent a preceding period in marine habitat before they were tagged. Nine fish tagged in Lake Rovatnet in spring 2012 conducted sea migrations during summer in both 2012 and 2013. These fish were only included in the statistical analyses of marine residence during the first year, to avoid repeated measures concerns.

USE OF PELAGIC VS LITTORAL HABITATS

The receiver arrays that contained both pelagic and near shore receivers (array H1, H2, H3 and S1, Fig. 1) were used to investigate the importance of littoral and pelagic habitats for the tagged sea trout. Receivers deployed near the shore or in areas with shallow water (< 10 meters depth) where the sea trout was likely to feed at or near the bottom or along cliff walls within the receiver

range, were defined as near shore receivers. Receivers deployed over deep water, without coastline or shallow areas (< 25 meters depth) within the receiver range were defined as pelagic receivers. The proportional numbers of littoral and pelagic registrations at the receiver arrays, corrected for the proportion of littoral (8 receivers) *versus* pelagic (9 receivers), were investigated for each fish for the period 1 April-1 October in 2012 or 2013. This was assumed to give a rough estimate of relative preference of littoral and pelagic habitats. Potential differences between littoral and pelagic habitats were tested with a Chi-square test.

RESULTS

ENVIRONMENTAL PARAMETERS

From 1 May-1 October, marine water temperatures in the study area varied from 3.8 °C to 19.4 °C . The salinity levels during the same period were brackish in the outer areas (2012: mean = 28 ‰, SD ± 1.8 ‰, 2013: mean = 21 ‰, SD ± 2.0 ‰), the inner Hemnfjord (2012: mean = 29 ‰, SD ± 2.7 ‰, 2013: mean = 23 ‰, SD ± 7.6 ‰) and the inner Snillfjord (2012: mean = 26 ‰, SD ± 4.7 ‰, 2013: mean = 24 ‰, SD ± 4.8 ‰).

MORPHOLOGICAL CHARACTERISTICS OF TAGGED FISH

Among the study animals there was considerable variation both among individuals (Table 1) and tagging groups (Table 2) regarding body size, body condition, age, back calculated smolt length, age at smoltification and number of previous marine seasons.

The two groups of fish tagged in Lake Rovatnet (HS12 and HA12) had greater mean smolt length, higher mean age at smoltification, higher mean age and a tendency towards having spent more previous seasons at sea than the groups of fish tagged in River Snilldalselva (SA12 and SS13; Table 2). Similarly, the groups of fish tagged in Lake Rovatnet had higher mean smolt

lengths, ages at smoltification, and total age than the fish tagged in the mouth of River Sjøa (HS13; Table 2).

Sea trout tagged in River Snilldalselva (SA12 and SS13) had lower mean natural length and greater mean body condition than the group of fish tagged in the mouth of River Sjøa (HS13; Table 2). The fish tagged in the mouth of the River Snilldalselva during the spring of 2013 (SS13) had a higher body condition at tagging than the fish tagged both in Lake Rovatnet in spring 2012 (HS12,) and the mouth of River Sjøa in spring 2013 (HS13; Table 1 and 2).

Fish tagged in the River Snilldalselva during autumn 2012 (SA12) had shorter body lengths at smoltification than the fish tagged in Lake Rovatnet in spring 2012 (HS12) and autumn 2012 (HA12, Table 2). Similarly, at smoltification fish tagged in Lake Rovatnet in autumn 2012 (HA12) had greater body length than individuals tagged in the mouth of River Sjøa (HS13) and in the river mouth of River Snilldalselva (SS13) during spring 2013 (Table 2).

The group of fish tagged in Lake Rovatnet during autumn of 2012 (HA12) had greater ages at smoltification than those tagged in the mouth of River Sjøa in spring 2013 (HS13), in River Snilldalselva in autumn 2012 (SA12) and in the mouth of River Snilldalselva in spring 2013 (SS13; Table 2). The fish tagged in Lake Rovatnet in autumn 2012 (HA12) had greater total age than the fish tagged in River Snilldalselva in spring 2013 (SS13, Table 2).

MORPHOLOGICAL CHARACTERISTICS OF SHORT, MEDIUM AND LONG DISTANCE MIGRANTS

In total, 100 of the 115 tagged sea trout were recorded by the acoustic receivers in the fjord system. Individual sea trout were tracked from 6-624 days. Based on the previously described criteria, a total of 88 fish were categorized as either short, medium or long distance migrants (Table 3). The proportions of short, medium and long distance migrants varied among the tagging

groups. The fish tagged in Lake Rovatnet in spring 2012 (HS12) consisted of 6 short (26%), 5 medium (22%) and 12 long distance migrants (52%). All sea trout tagged in Lake Rovatnet in autumn 2012 (HA12) were long distance migrants (11 individuals, 100%). The fish tagged in the river mouth of River Sjøa in spring 2013 (HS13) consisted of 19 short (70%), 4 medium (15%) and 4 long distance migrants (15%). The sea trout tagged in River Snilldalselva in autumn 2012 (SA12) had 4 short (31%), 2 medium (15%) and 7 long distance migrants (54%), while the those tagged in spring 2013 (SS13) consisted of 6 short (43%), 5 medium (36%) and 3 long distance migrants (21%). The body lengths of the 15 individuals that were not recorded at any receivers did not differ significantly from the rest of the individuals (t-test, $n = 115$, $P = 0.22$).

There was no difference in mean body length (L_N) among short, medium and long distance migrants (Table 3, ANOVA, $n = 88$, $P = 0.20$). However, most ($n = 7$) of the largest individuals (≥ 450 mm, $n = 12$) conducted long distance migrations, while fewer large individuals performed medium ($n = 3$) and short distance ($n = 2$) migrations. Among the smallest individuals (≤ 350 mm, $n = 18$), there were equal proportions of short ($n = 6$), medium ($n = 6$) and long distance ($n = 6$) migrants.

There was large inter-individual variation in mean body condition in spring (Table 3). Long distance migrants had significantly (Tukey ANOVA) poorer body condition in spring prior to the marine migration than short ($n = 29$, $P = 0.013$) and medium distance migrants ($n = 33$, $P = 0.018$). The body condition in spring of short and medium distance migrants did not differ ($n = 44$, $P = 0.92$).

Age, back calculated smolt length, age at smoltification and number of previous marine seasons varied among the groups of short, medium and long distance migrants (Table 3). Long distance migrants had larger smolt lengths than both short (Tukey ANOVA, $n = 57$, $P = 0.023$) and medium distance migrants ($n = 43$, $P = 0.013$). The long distance migrants had a near

significant higher age at smoltification than short distance migrants ($n = 50$, $P = 0.057$), but were similar in age to the medium distance migrants ($n = 36$, $P = 0.104$). Long distance migrants tended to have had more previous marine seasons than the medium distance migrants ($n = 38$, $P = 0.057$), but not more previous marine seasons than the short distance migrants ($n = 44$, $P = 0.255$). The long distance migrants were older than both the short ($n = 41$, $P = 0.043$) and the medium distance migrants ($n = 35$, $P = 0.032$).

Among the nine fish tagged in Lake Rovatnet in spring 2012 that were followed through their sea migration both during the summer 2012 and again in 2013, there were identical numbers of short ($n = 3$), medium ($n = 3$) and long distance ($n = 3$) migrants during 2012. In 2013, one short distance migrant from 2012 performed a medium distance migration and one medium distance migrant from 2012 performed a long distance migration. The seven other individuals repeated the migration pattern from the year before. However, this change in maximum migratory dispersal was not significant, but the sample size was low (Chi-squared; $n = 9$, $P = 0.72$).

MARINE RESIDENCE TIME DURING SUMMER

During 1 April-1 October (2012 and 2013), 51 of the 115 tagged sea trout were never registered in the marine fjord, or after an initial period of detections on the marine receivers the detections stopped and the fish were not recorded returning to freshwater. The reasons for losing track of the fish were in about half of the cases not known. However, 15 individuals were reported captured and killed by anglers, 8 individuals tagged in the Lake Rovatnet were never recorded to leave the lake, and 4 individuals migrated out of the study area and did not return. After the study

ended, two of the individuals that migrated out of the study area were recaptured by anglers 130 km southwest of their tagging location.

There was large inter-individual variation in the total residence time in marine habitats during 1 April-1 October in 2012 and 2013 (Fig. 2). Among tagged fish tracked throughout these periods, the mean marine residence time was 100 days (SD 52 days, range 7 - 183 days). The largest variation was found within the fish tagged in Lake Rovatnet in spring 2012 (HS12) which had a mean residence of 91 days (SD 59 days, range 7 - 171 days). The fish tagged in the outlet of spawning streams of Lake Rovatnet during autumn 2012 (HA12) and tracked during summer 2013, had the lowest intragroup variation with a mean marine residence time of 53 days (SD 15 days, range 27 - 72 days). When comparing marine residence times of the different tagging groups, the fish tagged in Lake Rovatnet in autumn 2012 (HA12) had shorter marine residence times than the fish tagged in the mouth of River Sjøa in spring 2013 (HS13, Tukey ANOVA, $n = 25$, $P = 0.049$) and fish tagged in River Snilldalselva in autumn 2012 (SA12, $n = 17$, $P = 0.0105$).

The four best predictive models all indicated that the number of days spent at sea was positively correlated to body length (L_N) and smolt age, and negatively correlated to the Julian day number of sea entry and migration distance (Table 3). The best model ($r^2 = 0.65$, $P < 0.001$) included age, body length (L_N), smolt age, timing of sea entry and migration distance (Table 3).

Fish from all tagging groups utilized all areas of the fjord. However, the innermost parts of the fjord, near the tagging location of the sea trout (zone 1 and 2, up to 4 km from the river mouth) were found to be especially important areas for the tagged individuals, as they spent on average 68% (SD 39%, range 0.002% - 100%) of their marine residence time in these areas (Fig. 3). Fish tagged in the Sjøa watercourse spent a significantly longer time in the innermost part of Hemnfjord (zone 1, mean 71.1 days, SD 59.1 days, range 0.2 – 170.8 days) than in inner Snillfjord (zone 2, mean 0.6 days, SD 2.0 days, range 0 – 12.1 days, Tukey ANOVA, $n = 90$, $P <$

0.001), central Snillfjord (zone 3, mean 1.87 days, SD 4.5 days, range 0 – 18.7, $n = 90$, $P < 0.001$), central Hemnfjord (zone 4, mean 11.9 days, SD 19.9 days, range 0 – 116.7 days, $n = 90$, $P < 0.001$) and outer areas (zone 5, mean 6.4 days, SD 14.8 days, range 0 – 68.2 days, $n = 90$, $P < 0.001$). Fish tagged in the River Snilldalselva spent a longer time in the innermost part of Snillfjord (zone 2, mean 92.6 days, SD 69.1 days, range 0.002 – 183.0 days) than in the inner Hemnfjord (zone 1, mean 0.3 days, SD 1.1 days, range 0 – 5.0 days, Tukey ANOVA; $n = 38$, $P < 0.001$), central Snillfjord (zone 3, mean 10.2 days, SD 29.3 days, range 0 – 124.0 days, $n = 38$, $P < 0.001$), central Hemnfjord (zone 4, mean 9.9 days, SD 28.5 days, range 0 – 121.0 days, $n = 38$, $P < 0.001$) and outer areas (zone 5, mean 7.9 days, SD 25.1 days, range 0 – 101.0 days, $n = 38$, $P < 0.001$).

When comparing the residence time in the innermost parts of the fjords (zone 1 for fishes tagged in the Sjøa watercourse and fjord zone 2 for fishes tagged in the River Snilldalselva), there was no difference between fish tagged in the Sjøa watercourse and those tagged in River Snilldalselva (Fig. 3, two-sided t -test, $n = 64$, $P = 0.25$). Nor were there differences between these two groups in their residence times in the central parts of Snillfjord (zone 3, $n = 64$, $P = 0.23$), central parts of Hemnfjord (zone 4, $n = 64$, $P = 0.78$) or the outer study area (zone 5, $n = 64$, $P = 0.81$).

MARINE RESIDENCE TIME VS MIGRATION DISTANCE

Long distance migrants had, despite large inter-individual variation, shorter mean marine residence time than both short (Tukey ANOVA, $n = 50$, $P = 0.05$) and medium distance migrants ($n = 38$, $P = 0.005$, Table 4). There was no difference between 2012 and 2013 in the mean marine residence time for long distance migrants (two-sided t -test, $n = 24$, $P = 0.99$).

Large inter-individual variation in the mean residence time in the different fjord zones was observed (Fig. 3). For long distance migrants from both Rivers Sjøa and Snilldalselva, the time spent in the inner fjord was significantly shorter than for the short distance migrants (Tukey ANOVA, Sjøa: $n = 37$, $P = 0.002$; Snilldalselva: $n = 13$, $P = 0.039$). Similar differences were evident between long and medium distance migrants from Sjøa ($n = 26$, $P = 0.008$) but not from Snilldalselva ($n = 12$, $P = 0.092$).

LITTORAL VS PELAGIC HABITAT UTILIZATION

Overall, at the receiver arrays containing both near shore and pelagic receivers the tagged fish had larger proportions of their registrations at receivers along the shoreline (mean 75%, SD 19%, range 37-100%) compared to receivers in the pelagic areas (mean 25%, SD 19%, range 0-63%, Chi-squared; $n = 73$, $P < 0.001$) (Fig. 4). The fish had larger proportions of registrations at receivers deployed near the shore than in pelagic areas at array H1 (near shore; mean 76%, range 35-100%, pelagic; mean 24%, range 0-65%; Chi-squared; $n = 64$, $P < 0.001$), array S1, (near shore; mean 80%, range 41-100%, pelagic; mean 20%, range 0-59%, $n = 29$, $P < 0.001$), and array H2 (near shore; mean 64%, range 0.04-100%, pelagic; mean 36%, range 0-96%; $n = 23$, $P < 0.001$), but not in array H3 (near shore; mean 50%, range 0-100%, pelagic; mean 50%, range 0-100%; $n = 27$, $P < 0.001$).

Long distance migrants had higher proportions of pelagic registrations than medium distance migrants (Fig. 5, Tukey ANOVA, $n = 146$, $P = 0.020$), and nearly significant higher proportions of pelagic registrations compared to short distance migrants ($n = 146$, $P = 0.052$, Fig. 4). Short and medium distance migrants did not differ in their uses of pelagic and inshore areas ($n = 146$, $P = 0.72$).

DISCUSSION

MORPHOLOGICAL CHARACTERISTICS AND LIFE HISTORY

The sea trout differed in morphology and life history both within and between the watercourses. Sea trout tagged in River Snilldalselva had better body condition than fish tagged in the Sjøa watercourse, and individuals tagged in the mouth of River Snilldalselva in the spring of 2013 had better body condition than the other groups of fish also tagged during the spring. Differences in body condition in the spring might be influenced by differences in overwintering conditions and whether an individual fish had spawned in the previous autumn (Jonsson and Jonsson 2011). For the fish tagged in the river mouth in the spring of 2013, their area of residence prior to tagging is not known, i.e. if they had been in the sea or fresh water. Marine residence during winter has been reported for sea trout in both the southern and northern parts of Norway (Knutsen et al. 2004, Jensen and Rikardsen 2008, 2012), and Jonsson and Jonsson et al. (2009) found that sea trout spending the winter at sea had better growth during the first two years after smoltification compared to sea trout that returned to freshwater for overwintering.

Fish tagged in Lake Rovatnet did not differ in natural body length (L_N) or body condition from fish tagged in the River Snilldalselva, but were older and tended (nearly statistically significant) toward having experienced more previous marine seasons. Since we tagged all fish of suitable minimum sizes (>27 cm) that we captured, this may indicate a systematic difference in the ages of sea trout between the two sites. Furthermore, fish from Lake Rovatnet had a larger back calculated mean smolt size and greater age at smoltification compared to fish tagged in the River Snilldalselva. This was probably caused by environmental differences between the watercourses. The parr in the Sjøa watercourse could reside in Lake Rovatnet, enabling them to

have better growth before smoltification. In contrast, the River Snilldalselva offers few deep pools and there is no access to lakes. Hence, variable environmental conditions, constraints in food supply or limited availability of appropriate shelter may cause the parr in this river to smoltify at younger age than in the Sjøa watercourse. This is consistent with previous studies on how the environment influences smoltification in partly migrating trout populations (Jonsson and Jonsson 1993, Wysujack et al. 2009). The group of fish tagged in the river mouth of River Sjøa in spring 2013 were smaller and younger at smoltification than the fish tagged in the Lake Rovatnet, possibly because some of these fish originated from the neighbouring watercourse.

MIGRATORY DISTANCES

Large inter-individual variation in the migration distance was observed. Some individuals remained in the innermost parts of the fjord, while others spent most of their marine residence outside the study area. The proportions of short and long distance migrants varied greatly among the groups of tagged fish. Fish captured at different locations and times of the year may have been at different stages in their life history, which may have influenced their subsequent migratory behaviour. Other causes for the variations observed in migratory strategies may have been due to behavioural and/or genetic differences. Previous studies have also shown large variation in migration distance among populations of anadromous sea trout (Jensen 1968, Svårdson and Fagerström 1982, Berg and Berg 1987), which these authors attributed to combinations of environmental and genetic factors (Klemetsen et al. 2003). del Villar-Guerra et al. (2013) suggested that variables such as morphological characteristics, ontogeny, genetics and life history might influence the sea trout's marine behaviour and the extent of its marine migration.

No difference was found in body length between short and long distance migrants, and individuals of all size classes performed long distance migrations. By contrast, Jensen et al. (2014) found that large individuals were more likely to conduct long distance marine migrations than smaller individuals. They suggested that this could be caused by a higher abundance of suitable fish prey for the larger individual's further out in the fjord at their study site. Similarly, Knutsen et al. (2001) found that small post-smolt sea trout fed inshore on shallow water prey communities while larger sea trout were feeding further offshore on pelagic fish.

Fast growing sea trout change to a more piscivorous diet at a smaller size and younger age than slower growing individuals (Klemetsen et al. 2003), which might explain why in this study some smaller individuals conducted long distance migrations. Alternatively, the small long distance migrants may have had similar feeding behaviour as the short distance migrants, but dispersed further out in the fjord by chance, or due to competition with conspecifics in inshore areas and the availability of suitable alternative habitat and conditions further away from the river mouth.

The long distance migrants had poorer body condition than short distance migrants at the time of tagging, suggesting that individuals with a poorer body condition experienced a greater need to maximize benefits from distant feeding opportunities. Wysujack et al. (2009) found that poor body condition promoted migratory behaviour in brown trout parr. Similarly, Davidsen et al. (2014) found that starved sea trout post-smolts migrated further out into a fjord compared to fully fed individuals. However, Boel et al. (2014) found a different pattern in their study of migration distances of brown trout in a freshwater system, where energy stores were positively correlated with migration distances. An alternative hypothesis to account for the pattern observed in this study may be that fish with poor body condition were outcompeted from the preferred shore habitats. Migratory strategies have previously been shown to be influenced by different needs for

food intake (Halttunen et al. 2013), and Damsgård et al. (1998) showed that starving fish may undertake more risky behaviour than well fed individuals.

MARINE RESIDENCE DURING SUMMER

Large intragroup variation in marine residence time during the summer months was observed. Individuals tagged in the Lake Rovatnet during spring 2012 had the largest intragroup variation, while individuals tagged in Lake Rovatnet in autumn 2012 had the smallest variation. Previous studies have revealed that marine residency varies both among and within populations, with a range of factors influencing the duration of the marine residence of an individual, such as age, maturity (Jonsson 1985) and environmental conditions in fresh water prior to the seawards migration (Jensen and Rikardsen 2008). In the present study, the duration of the seaward migration for 27 of the tagged fish was found to be positively correlated to the body length (L_N) and smolt age, but negatively correlated to the date of sea entry.

Our fish spent on average 68% of their marine residence time in the innermost parts of the fjords, near the mouth of the river where they were tagged. Since all fish in the present study were veteran migrants with one or more previous marine seasons, and since seawater tolerance in salmonids is known to increase with body size (Hoar 1988, Ugedal et al. 1998), most individuals in the present study probably had good osmoregulatory capabilities. Larsen et al. (2008) suggested that local adaptation may cause differences in seawater tolerance among sea trout populations. However, the innermost parts of both Snillfjord and Hemnfjord had levels of salinities similar to the outer parts of the fjord system during the present study, further suggesting that salinity likely did not affect the spatial distribution of the experimental fish in the fjords to any great extent.

Long distance migrants, who were found to be older than both short and medium distance migrants, surprisingly spent a shorter time at the sea than individuals moving shorter distances. Previous studies have shown that older sea trout individuals generally return earlier from the marine migration (Jonsson 1985), however, the reasons for this remain obscure.

LITTORAL VERSUS PELAGIC HABITAT UTILIZATION

The sea trout stayed more often in littoral than pelagic habitats, based on the observed higher proportions of registrations of tagged fish on acoustic receivers in near shore compared to pelagic areas. These results are consistent with findings by Jensen et al. (2014), who found that sea trout in the Alta Fjord only spent 33% of their time in the pelagic habitat. The near shore habitat utilization is also consistent with previous studies on sea trout feeding behaviour, which suggest that the main prey (crustaceans, polychaetes, insects and fish) are found in near shore, shallow areas (Pemberton 1976, Knutsen et al. 2001). However, the data also show that the pelagic zone may be an important habitat for especially the long distance migrants, and pelagic feeders are in other studies have been shown to feed almost exclusively on fish (Rikardsen and Amundsen 2005). The long distance migrants in this study spent a minimal portion of their total marine residence time in the innermost areas of the fjord, compared to short and medium distance migrants. Long distance migrants had greater proportions of pelagic registrations than medium distance migrants, and tended (nearly statistically significant) to show greater proportions of pelagic registrations compared to short distance migrants.

Overall, the data suggests that the long distance migrants had a higher degree of pelagic feeding behaviour, that they were in lower condition at the start of the migration and that they returned earlier than the medium and short distance migrants. It is likely that these fish found more energy rich prey in the outer part of the fjord and therefore potentially gained weight faster

and therefore also returned earlier to freshwater as they had utilized their compensatory growth potential. Energy rich pelagic fish species are often found to be a considerable part of the diet in larger sea trout, with herring (*Clupea harengus* L. 1758) as a key prey species (Pemberton 1976, Knutsen et al. 2001, Rikardsen and Amundsen 2005, Rikardsen et al. 2006).

In summary, this study showed that sea trout both within and between watercourses draining to the same fjord system may differ in morphology, life history, migration behaviour and marine habitat use. Such plasticity may reinforce population resilience in areas with dynamic environmental conditions or during periods of climatic changes. Altered patterns of fish migration have often documented as an effect of contemporary global climate change is (e.g. Cotton 2003, Parmesan 2007, Visser et al. 2009). A better understanding of the underlying causes of the different marine migratory strategies in sea trout is now needed in order to predict how changes in the marine habitat and different anthropogenic impacts may influence brown trout populations with anadromous individuals.

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Figure captions:

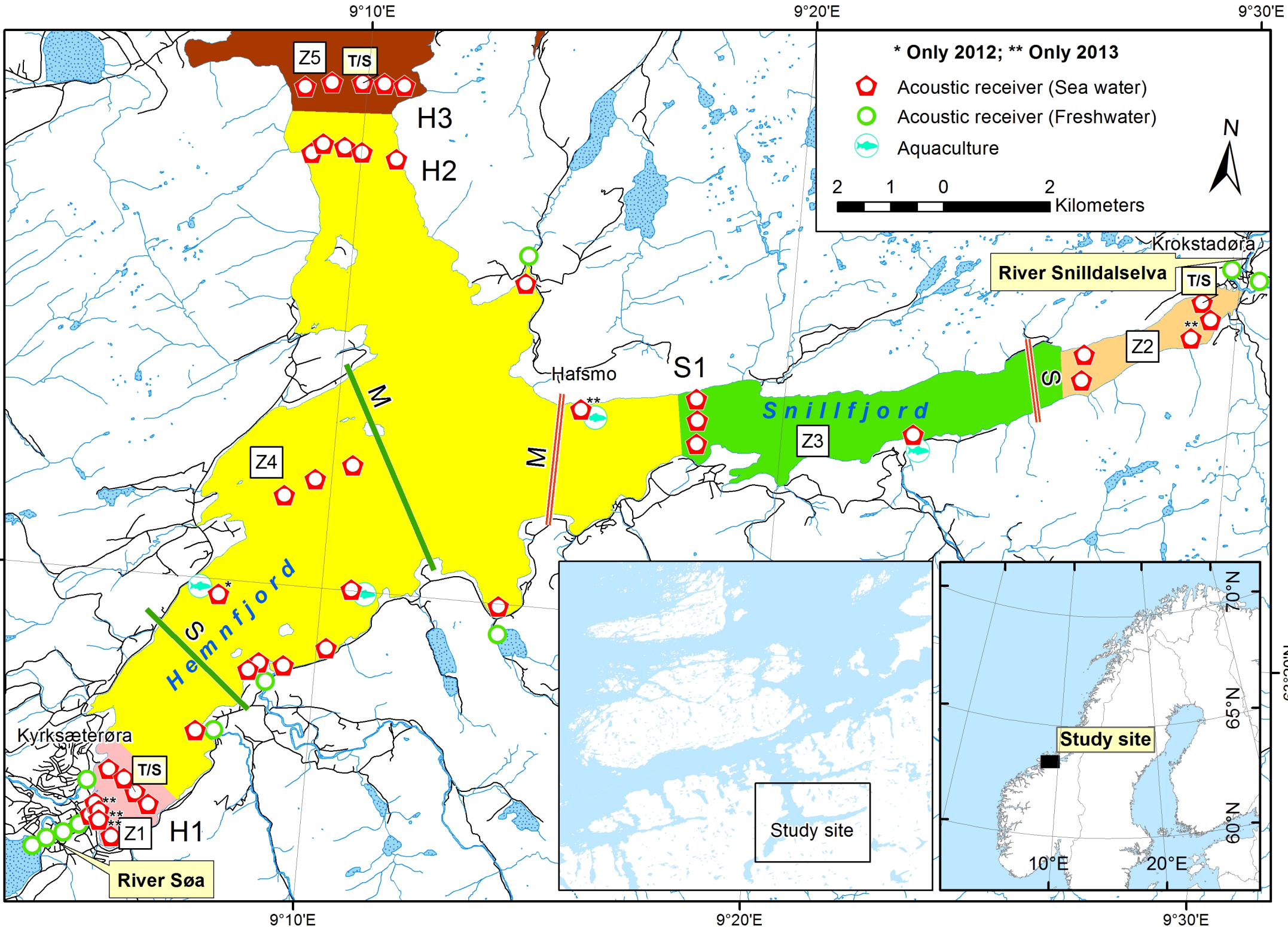
Figure 1: Locations of automatic receivers (red pentagon = marine, green circle = freshwater) and temperature and salinity data loggers (T/S) in the study area. Area zones (Z1-Z5) and outer boundaries for definition of short (S) and medium (M) migration distance (fish from the Sjøa watercourse = green lines, fish from the Snilldalselva River = red lines). Arrays across the fjord included both near shore and pelagic receivers (H1, H2, H3 and S1).

Figure 2: Total residence time (days) in the marine environment during 1 April – 1 October 2012 or 2013 for tagging groups HS12 (tagged in Lake Rovatnet in spring 2012), HA12 (tagged in Lake Rovatnet in autumn 2012), HS13 (tagged in river mouth of River Sjøa in spring 2013), SA12 (tagged in River Snilldalselva in autumn 2012), and SS13 (tagged in the river mouth of River Snilldalselva in spring 2013). The box-and-whisker plots show median values (black lines), the interquartile ranges (boxes) and the 5th and 95th percentiles (whiskers).

Figure 3: Residence time in the different fjord zones of short, medium and long distance migrants during 1 April-1 October. The different fjord zones are indicated in Fig. 1. The box-and-whisker plots show median values (black lines), the interquartile ranges (boxes) and the 5th and 95th percentiles (whiskers). Circles indicate outliers.

Figure 4: Proportions of individuals' registrations at near shore (white) and pelagic (grey) receivers at array H1, H2, H3 and S1 during 1 April-1 October. The box-and-whisker plots show median values (black lines), the interquartile ranges (boxes) and the 5th and 95th percentiles (whiskers). Circles indicate outliers.

Figure 5: Proportions of pelagic registrations at receiver arrays (H1, H2, H3 and S1) for short, medium and long distance migrants during 1 April-1 October. The box-and-whisker plots show median values (black lines), the interquartile ranges (boxes) and the 5th and 95th percentiles (whiskers). Circles indicate outliers.



63°20'N

9°10'E

9°20'E

9°30'E

63°20'N

70°N

65°N

60°N

Study site

10°E

20°E

Study site

Kyrksæterøra

River Sør

River Snildalselva

Krokstadøra

Hafsmo

Snillfjord

Hemnfjord

H3

H2

H1

S1

Z5

T/S

Z4

Z2

Z3

Z1

T/S

M

M

S

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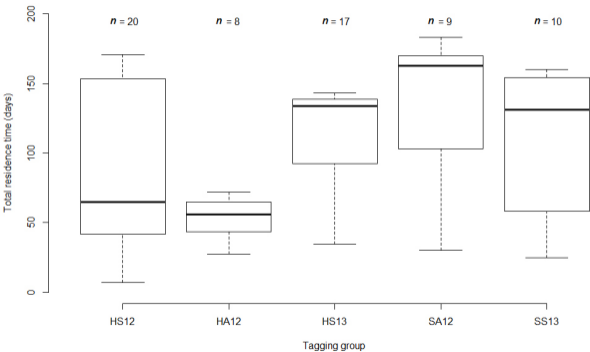
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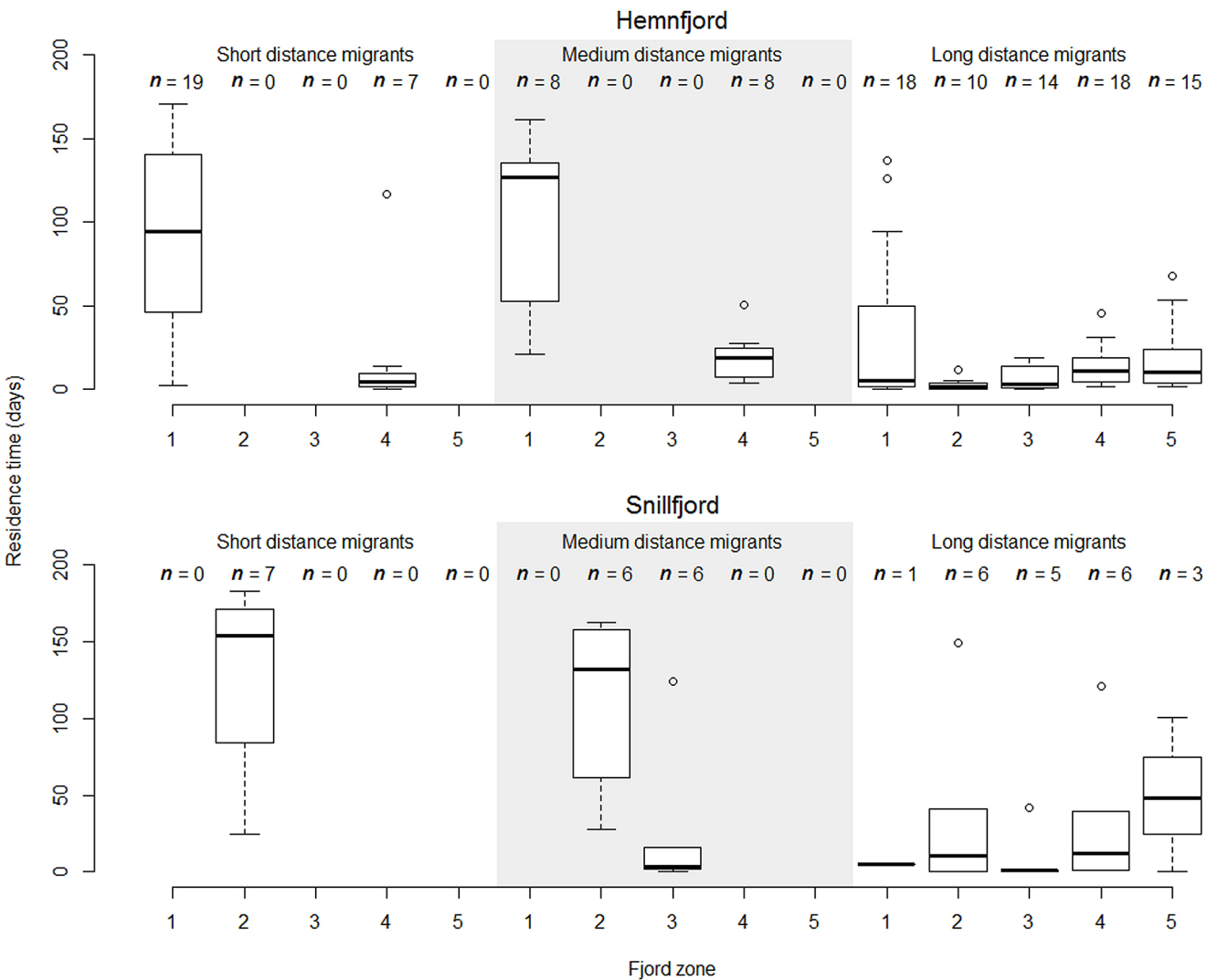
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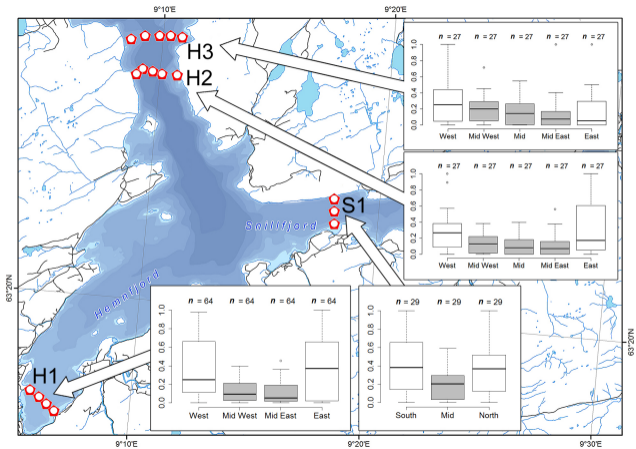
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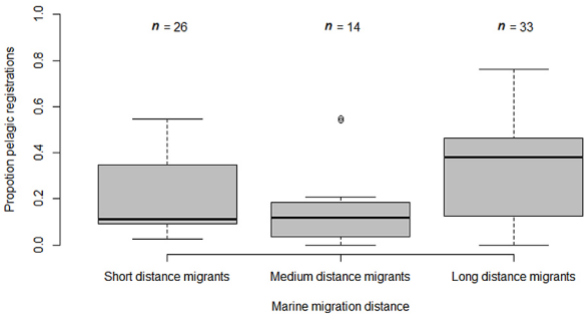
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Tables

Table 1: Tagging groups, tagging location, number of individuals, natural body length (L_N), body mass, body condition, age, back calculated smolt length, age at smoltification and number of previous marine seasons prior to tagging of fish in the different groups.

Tagging group		HS12	HA12	SA12	SS13	HS13	
Tagging date		12-14 April 2012	17-18 September 2012	19-20 September 2012	22-23 April 2013	3-12 May 2013	
Capture and tagging site		Søa (Lake Rovatnet)	Søa (Lake Rovatnet)	Snilldalselva (river and river mouth)	Snilldalselva (river mouth)	Søa (river mouth)	
<i>n</i>		30	21	20	15	29	
Natural length (mm)	Mean ± SD	396 ± 61	412 ± 121	392 ± 75	381 ± 53	417 ± 55	
	Range	335-600	270-700	310-650	275-460	330-580	
Body mass (g)	Mean ± SD	586 ± 287	866 ± 908	581 ± 419	620 ± 286	713 ± 337	
	Range	330-1600	210-3660	310-2180	220-1210	300-1970	
Fulton's K	Mean ± SD	0.90 ± 0.12	0.95 ± 0.12	0.89 ± 0.09	1.05 ± 0.10	0.89 ± 0.10	
	Range	0.74-1.22	0.77-1.30	0.73-1.07	0.87-1.33	0.75-1.07	
Scale reading estimates	Smolt length (mm)	Mean ± SD	166 ± 42	182 ± 52	132 ± 30	140 ± 34	137 ± 32
		Range	105-270	112-276	98-197	102-236	96-210
		<i>n</i> (cover)	22 (73%)	14 (67%)	18 (90%)	12 (80%)	22 (76%)
	Age at smoltification (years)	Mean ± SD	2.63 ± 0.72	3.00 ± 0.74	2.35 ± 0.61	2.27 ± 0.65	2.19 ± 0.40
		Range	2-4	2-4	2-4	2-4	2-3
		<i>n</i> (cover)	16 (53%)	12 (57%)	17 (85%)	11 (73%)	21 (72%)
	Previous marine seasons	Mean ± SD	3.39 ± 1.24	3.92 ± 2.36	3.43 ± 1.02	2.40 ± 0.52	3.06 ± 0.68
		Range	2-7	2-10	2-6	2-3	2-4
		<i>n</i> (cover)	18 (60%)	13 (62%)	14 (70%)	10 (67%)	16 (55%)
	Age (years)	Mean ± SD	5.69 ± 1.65	6.73 ± 2.37	5.85 ± 1.28	4.78 ± 0.83	5.20 ± 0.77
Range		4-10	4-13	5-9	4-6	4-7	
<i>n</i> (cover)		13 (43%)	15 (71%)	13 (65%)	9 (60%)	15 (52%)	

Table 2: Differences in morphology and life history among fish from watercourses and tagging groups (HS12; Lake Rovatnet in spring 2012, HA12; Lake Rovatnet in autumn 2012, SA12; River Snilldalselva in autumn 2012, SS13; Mouth of River Snilldalselva in spring 2013, HS13; Mouth of River Sjøa in spring 2013). Significant *P*-values are shown in bold, non-significant Tukey ANOVA values are excluded.

	Morphological and life history characteristic	Alternative hypothesis (H ₁)	Statistical test	<i>n</i>	<i>P</i>
Differences between fish tagged in Lake Rovatnet and fish tagged in River Snilldalselva	Body length	HS12 and HA12 \diamond SA12 and SS13	<i>t</i> -test	86	0.321
	Body condition	HS12 and HA12 \diamond SA12 and SS13	<i>t</i> -test	86	0.127
	Smolt length	HS12 and HA12 \leq SA12 and SS13	<i>t</i> -test	66	< 0.001
	Age at smoltification	HS12 and HA12 \leq SA12 and SS13	<i>t</i> -test	56	0.007
	Previous marine seasons	HS12 and HA12 \leq SA12 and SS13	<i>t</i> -test	55	0.055
	Age	HS12 and HA12 \leq SA12 and SS13	<i>t</i> -test	50	0.042
Differences between fish tagged in Lake Rovatnet and fish tagged in mouth of River Sjøa	Length	HS12 and HA12 \diamond HS13	<i>t</i> -test	80	0.422
	Body condition	HS12 and HA12 \diamond HS13	<i>t</i> -test	80	0.258
	Smolt length	HS12 and HA12 \leq HS13	<i>t</i> -test	58	< 0.001
	Age at smoltification	HS12 and HA12 \leq HS13	<i>t</i> -test	49	< 0.001
	Previous marine seasons	HS12 and HA12 \diamond HS13	<i>t</i> -test	47	0.136
	Age	HS12 and HA12 \leq HS13	<i>t</i> -test	43	0.012
Differences between fish tagged in River Snilldalselva fish tagged in mouth of River Sjøa	Body length	SA12 and SS13 \geq HS13	<i>t</i> -test	64	0.025
	Body condition	SA12 and SS13 \leq HS13	<i>t</i> -test	64	0.014
	Smolt length	SA12 and SS13 \diamond HS13	<i>t</i> -test	52	0.817
	Age at smoltification	SA12 and SS13 \diamond HS13	<i>t</i> -test	49	0.372
	Previous marine seasons	SA12 and SS13 \diamond HS13	<i>t</i> -test	40	0.813
	Age	SA12 and SS13 \diamond HS13	<i>t</i> -test	37	0.528
Differences between groups of tagging	Body length	HS12 \diamond HA12 \diamond SA12 \diamond SS13 \diamond HS13	ANOVA	115	0.78
	Body condition	SS13 \leq HS12	Tukey ANOVA	45	0.014
	Body condition	SS13 \leq HS13	Tukey ANOVA	43	0.009
	Smolt length	HS12 \leq SA12	Tukey ANOVA	40	0.05
	Smolt length	HA12 \leq SA12	Tukey ANOVA	32	0.004
	Smolt length	HA12 \leq HS13	Tukey ANOVA	36	0.008

Smolt length	HA12 ≤ SS13	Tukey ANOVA	26	0.044
Age at smoltification	HA12 ≤ HS13	Tukey ANOVA	33	0.004
Age at smoltification	HA12 ≤ SA12	Tukey ANOVA	29	0.049
Age at smoltification	HA12 ≤ SS13	Tukey ANOVA	23	0.044
Previous marine seasons	HS12 < HA12 < SA12 < SS13 < HS13	ANOVA	71	0.098
Age	HA12 ≤ SS13	Tukey ANOVA	24	0.032

Table 3: Model selection for estimating the determinants of the duration of the marine residence time. The models estimate the relative contributions to the duration of the marine residence time from the parameters age (A), body length (L), number of previous marine seasons (P), residual values (resvalbc) from the linear model $\log(\text{condition}) \sim \log(\text{length})$ (R), Julian day of sea entry (SE), smolt age (SA), smolt length (SL), and maximum distance migrated away from the home river (S). AIC is the score based on Akaike information criterion. AIC weights represent the relative likelihood of the model. The table displays the four best fitting of the total of 576 tested models.

Model	AIC	Δ AIC	AIC weights	df
[A, L, SE, SA, S]	220.8160284	0	0.111953643	8
[A, L, SE, SA, SL, S]	221.6453596	0.829331157	0.073952227	9
[A, L, P, SE, SA, S]	222.7925525	1.976524071	0.041671725	9
[A, L, R, SE, SA, S]	222.8040131	1.987984688	0.041433616	9

Table 4: Natural body length (L_N), Fulton's body condition, age, back calculated smolt length, age at smoltification, number of previous marine seasons and total marine residence time during summer of short, medium and long distance migrants.

	Migration distance	Short distance migrants	Medium distance migrants	Long distance migrants	Total	
	<i>N</i> (%)	35 (40%)	16 (18%)	37 (42%)	88 (100%)	
Natural body length (mm)	Mean	404	380	414	404	
	SD	± 55	± 38	± 84	± 67	
	Range	320-580	330-460	330-690	320-690	
Fulton's body condition	Mean	0.95	0.94	0.89	0.92	
	SD	± 0.13	± 0.12	± 0.11	± 0.12	
	Range	0.75-1.33	0.78-1.22	0.73-1.30	0.73-1.33	
Scale reading estimates	Smolt length (mm)	Mean	137	127	166	148
		SD	± 35	± 37	± 44	± 44
		<i>n</i>	26	12	31	69
	Age at smoltification (years)	Mean	2.24	2.18	2.68	2.41
		SD	± 0.52	± 0.60	± 0.80	± 0.69
		<i>n</i>	25	11	25	61
	Previous marine seasons	Mean	3.00	2.64	3.52	3.18
		SD	± 0.61	± 0.67	± 1.34	± 1.09
		<i>n</i>	17	11	27	55
	Age (years)	Mean	5.13	4.90	6.12	5.57
		SD	± 0.72	± 0.74	± 1.62	± 1.35
		<i>n</i>	16	10	25	51
	Total marine residence time (days)	mean	108	128	76	100
		SD	± 55	± 41	± 43	± 51
		<i>n</i>	26	14	24	64