Faculty of Biosciences, Fisheries and Economics
Department of Arctic and Marine Biology

Migration and habitat use of sea trout post-smolts *Salmo trutta* in a Norwegian fjord system

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Anne Cathrine Flaten
Bio-3950 Master thesis in Biology
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Supervisors

Jan G. Davidsen, NTNU University Museum, Trondheim

Eva B. Thorstad, NINA Trondheim

Audun H. Rikardsen, UIT The Arctic University of Norway

Front page photo by Anne Cathrine Flaten

Photo of a sea trout smolt *Salmo trutta*

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Tromsø, May 2015

Anne Cathrine Flaten

Summary

The migration and habitat use of sea trout post-smolts were investigated in a fjord system in Central Norway during the period from 30 April – 26 November 2014. The main aims were to investigate timing of sea entry and freshwater return, return rate, marine residence time, spatial use of the fjord system and migration distance. Fifty sea trout smolts were tagged with acoustic transmitters and tracked with 43 automatic listening receivers distributed throughout the study area. Median seaward migration date was 22 May and median return date to freshwater was 4 July. Of the 40 seaward migrating smolts, 26 returned to freshwater, resulting in a minimum return rate to freshwater of 65%. During transition from the river to the fjord, 80% of the tagged smolts migrated during the night, however, no diurnal pattern was observed during the upriver migration. Mean marine residence time was 38 days, but there was large individual variation ranging from 22-99 days. The innermost parts of the study area were more utilized than the outer part of the fjord system during the sea residency, and with more use of the near shore areas defined as littoral habitat than the open, pelagic areas. However, a widespread distribution was observed, and a large proportion of the post-smolts was observed to utilize the outer part of the fjord system. All of the tagged post-smolts utilized larger marine areas than the river mouth area during the summer, and 67% of the post-smolts had a minimum migration distance of 25 km, 27% had a minimum migration distance of 14 km while the last 6% had a minimum migration distance of 4 km. Eight of the 26 returning individuals (31%) performed a second marine migration during the same summer, after returning to Lake Rovatnet in early June. The spatial use of the fjord system between the first and second marine migration showed two distinctive patterns. The innermost part of the fjord was more often used during the first period, however, more time was spent in the outer part of the fjord during the second migration. Regardless of the high predation risk post-smolts may experience in the marine phase, a widespread distribution and habitat utilization were observed in this study, in addition to a high marine survival rate. Thus, the results indicate that the sea trout post-smolts displayed variable migration behaviour and habitat utilization during their first marine migration. Nevertheless, due to the fact that the bigger post-smolts, to a larger extent, returned to the home river and also utilized areas in the outer part of the fjord, body size seemed to be an important factor in determining the migration behaviour and survival in this study.

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1. Introduction

Brown trout (*Salmo trutta* L. 1758) is a salmonid species with a widespread distribution across Europe, Western Asia and Africa (MacCrimmon et al. 1970). The widespread distribution is mainly due its ecological variability and ability to disperse and adapt to new waters, and the fact that it has been introduced to new areas by human activities (MacCrimmon and Marshall 1968). Like all salmonids, brown trout spawn in freshwater, and populations that occur in lakes or rivers with free access to the sea are often partially migratory. Some individuals within a population may stay resident while others become migratory as anadromous brown trout (sea trout) (Jonsson and Jonsson 1993, 2011, Klemetsen et al. 2003). The sea trout usually migrate in search of better feeding grounds to improve its condition, which would lead to increased growth and eventually better fitness (Jonsson and Jonsson 1993, Klemetsen et al. 2003). An individual's propensity to migrate seems to be partly genetically determined and partly caused by phenotypic plasticity, including the trade-offs between benefits and costs (Jonsson 1989, Jonsson and Jonsson 1993). Before migrating to sea, the juveniles, also called parr, go through physiological and morphological changes that are adaptive for the saline environment in the sea (McCormick 2012). The transformation from parr to smolt is known as smoltification, during which the fish develop the ability to osmoregulate in seawater (Hoar 1976, McCormick 2012). After entering the fjord, they are termed post-smolts (Ritter 1977). The costs of migrating to sea may be high energy expenditure related to smoltification and swimming, adaptation to the saline environment, in addition to higher risk of predation and parasite infections (Gross 1987, Jonsson and Jonsson 1993).

Following the downwards migration to sea, the sea trout post-smolts may feed close to the estuary and in shallow waters close to shore, which may be due to better feeding opportunities than in the open pelagic waters masses (Davidsen et al. 2014a). Sea trout are usually not found far from their home river. Unlike Atlantic salmon (*Salmo salar* L. 1758), sea trout seldom migrate out of the fjord system and into the open sea (Jonsson and Jonsson 2011), and they have also been observed to be rather stationary during the marine phase (Berg and Berg 1987a). Additionally, there is a high predation pressure on salmonid post-smolts in the early marine phase, particularly in the open water masses (Hvidsten and Møkkelgjerd 1987). Lyse et al. (1998) studied the behaviour of sea trout post-smolts in the early marine migration phase, and found the distribution to be confined to the littoral zone with preference to shallow waters. Therefore, predation avoidance can be another factor determining the distribution and behaviour at this stage of the marine migration, and if so, the post-smolt should be confined to shallow waters where shelter can provide protection from predators (Werner and Hall 1988). Dieperink et al. (2002) observed that body size is an important factor in determining the vulnerability to predation, with smaller fish being more exposed to predation after transition to the marine environment. However, the sea trout is known for displaying a large plasticity in life-history strategies (Jonsson and Jonsson 2011), and sea trout have also been observed to be feeding in the open pelagic water masses, most likely as an opportunistic, conditional response to high prey availability (Rikardsen and Amundsen 2005).

Atlantic salmon and various species of Pacific salmonids have been subjects for several marine biotelemetry tracking studies (Drenner et al. 2012). The sea trout is among the salmonid species that have been least studied in the marine environment. In general, there is limited knowledge on the marine phase of sea trout, and especially on first time migrants and their behaviour in the marine environment (Drenner et al. 2012). In western-Norway and mid-Norway there has been a significant decline in the sea trout populations over the past two decades (Anon. 2010). The reasons for this decline are unclear, however, Anon. (2010) concluded that changes in environmental conditions in the sea are important factors, including increased salmon lice (*Lepeoptheirus salmonis* Krøyer, 1838) infestation, fish diseases and ecosystem changes in the sea. Therefore, increased understanding and knowledge of the marine migration phase and habitat use is critical in order to maintain sustainable sea trout populations. The studies of brown trout have mainly focused on the freshwater phase, with emphasis on biology and the behaviour in the riverine part of their migration (Alm 1950, Jensen 1968, Jonsson 1982, Berg and Berg 1987a). With new and more advanced telemetry equipment, the focus is being directed towards the marine stage of the migration of salmonids. Conducting a comprehensive biotelemetry study is both time consuming and complicated, however, in order to further conserve and manage the Norwegian sea trout stocks in a sustainable way in the future, knowledge of their migrations and habitat use is important.

In the current study, sea trout smolts were tagged with individually coded transmitters and tracked with deployed receivers in order to investigate the characteristics of the marine migration patterns during a summer season. The main focus of this thesis was to study migration and habitat use of sea trout post-smolts in Hemnfjord and Snillfjord in Central Norway. The main aims were to investigate:

1. Timing of sea entry and freshwater return, and return rate.
2. Total marine residence time and residence time in different fjord zones, as well as habitat use in littoral, cliff and pelagic areas.
3. Individual migration pattern in relation to migration distance, and daily area use throughout the study period.

2. Material and method

2.1 Study area

The study was conducted in the two fjords Hemnfjord and Snillfjord in Sør-Trøndelag county, central Norway (fig. 1). These fjords amount to a study area that ranges over 60 km^2 of sea surface and 65 km of shoreline. Various industries and infrastructure are located in the fjord system, including a silicone production plant with a wharf, three salmon farms and two land-based production facilities for salmon smolt. The silicone production plant is located close to the innermost part of Hemnfjord, where the community center of Hemne municipality is situated.

Hemnfjord and Snillfjord have several watercourses with both Atlantic salmon and sea trout. Søa watercourse in Hemne municipality is known among anglers as one of the best sea trout watercourses in this area. The watercourse has a drainage basin of 113 km^2, and Lake Rovatnet, from which River Søa drains, has a surface area of 7.65 km^2. The anadromous section of the watercourse includes Lake Rovatnet, and provides suitable overwintering grounds for sea trout. Two minor rivers drain into Lake Rovatnet, and these two, Eidselva and Leneselva, are considered as the main spawning grounds for the sea trout population in this watercourse. The river connecting Lake Rovatnet to Hemnfjord is River Søa, which is two kilometers long. The Søa watercourse is regulated and provides water to the power plant in Hemne municipality. The water that runs through the power plant has its outlet to the fjord two km from the estuary of River Søa.

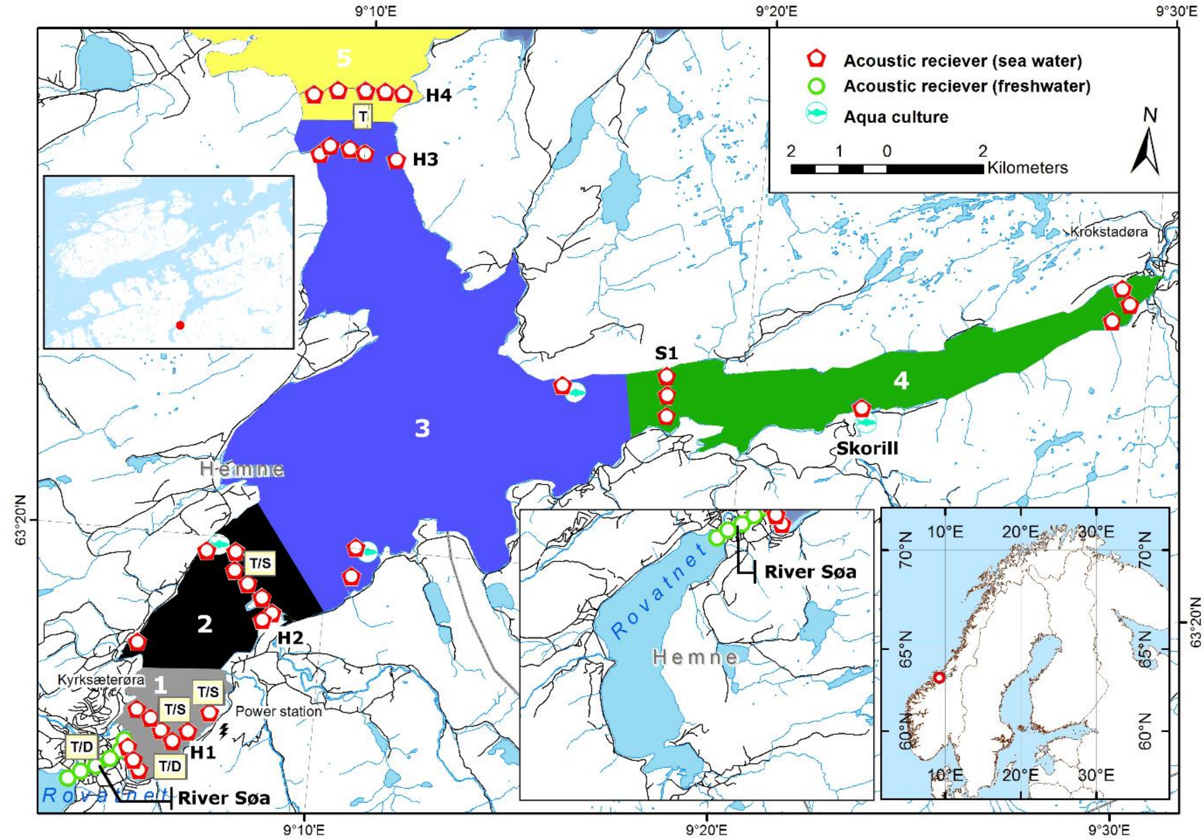


Figure 1: Map of the study area, Hemnfjord and Snillfjord in Central Norway, showing positions of deployed receivers in the fjord system (red polygons) and receivers deployed in River Søa (green circles). Temperature and salinity recorders are marked with T/S symbols and a temperature recorder is marked with T. Aquaculture locations are marked with fish symbols, including the land-based smolt production facility (Skorill). H1, H2, H3, H4 and S1 indicate positions of receiver arrays.

2.2 Recording of environmental variables

The environmental factors temperature and salinity were monitored in different parts of the fjord system by use of data storage tags. Four temperature and salinity recorders (DST-milli-CT, Star-Oddi, Iceland) were mounted below the buoys of automatic listening stations, at a depth of one meter. Three data storage tags recorded both temperature and salinity, and one DST recorded only temperature. The DSTs were in operation for a period of 10 months, from the beginning of February 2014 to the end of November 2014, however, only data from 1 April – 13 October is included in this paper. One temperature and salinity recorder was deployed in inner Hemnfjord (Array H1, fig. 1), one near the outlet of the power plant, two kilometers from the estuary of River Søa, and one further out in the fjord (Array H2 fig. 1). The temperature recorder was deployed in the outer part of the study area at the outermost array (Array H4, fig. 1). In addition to the environmental monitoring in the fjord, temperature and water discharge (www.nve.no) from Lake Rovatnet was registered during the period from 1 April – 10 September 2014.

2.3 Smolt capture and tagging

A total of 50 sea trout smolts were captured and tagged with acoustic transmitters. The first fish was tagged on 8 April 2014. The remaining 49 smolts were tagged during a one-month period from 30 April 2014 – 30 May 2014. The fish were captured and tagged 80 meters below the outlet of Lake Rovatnet (picture 1), where they were captured using a rotary screw trap located in the middle of River Søa. The trap was first placed in the river for a trial run on 7 April, which resulted in tagging of the first fish. However, Lake Rovatnet was still covered with ice during this period, and due to the spring melting, ice deteriorated rapidly and floating ice could cause damage to the screw trap. Therefore, the trap was pulled up on land until 22 April.

Picture 1: Location of the rotary screw trap in River Søa, 80 meters below the outlet of Lake Rovatnet. The red buoy indicates the position of the second receiver placed below the outlet of Lake Rovatnet.

The trap was in operation from 22 April – 7 of June, and during this period the trap was inspected and emptied at 08:00 every day. The captured smolts were relocated and kept in three holding tanks on land. A total of 199 sea trout were caught in the rotary screw strap (fig. 2a). The mean number of fish captured per day was 4.9 (median = 3, SD = ± 5.8) during a period of 41 days.

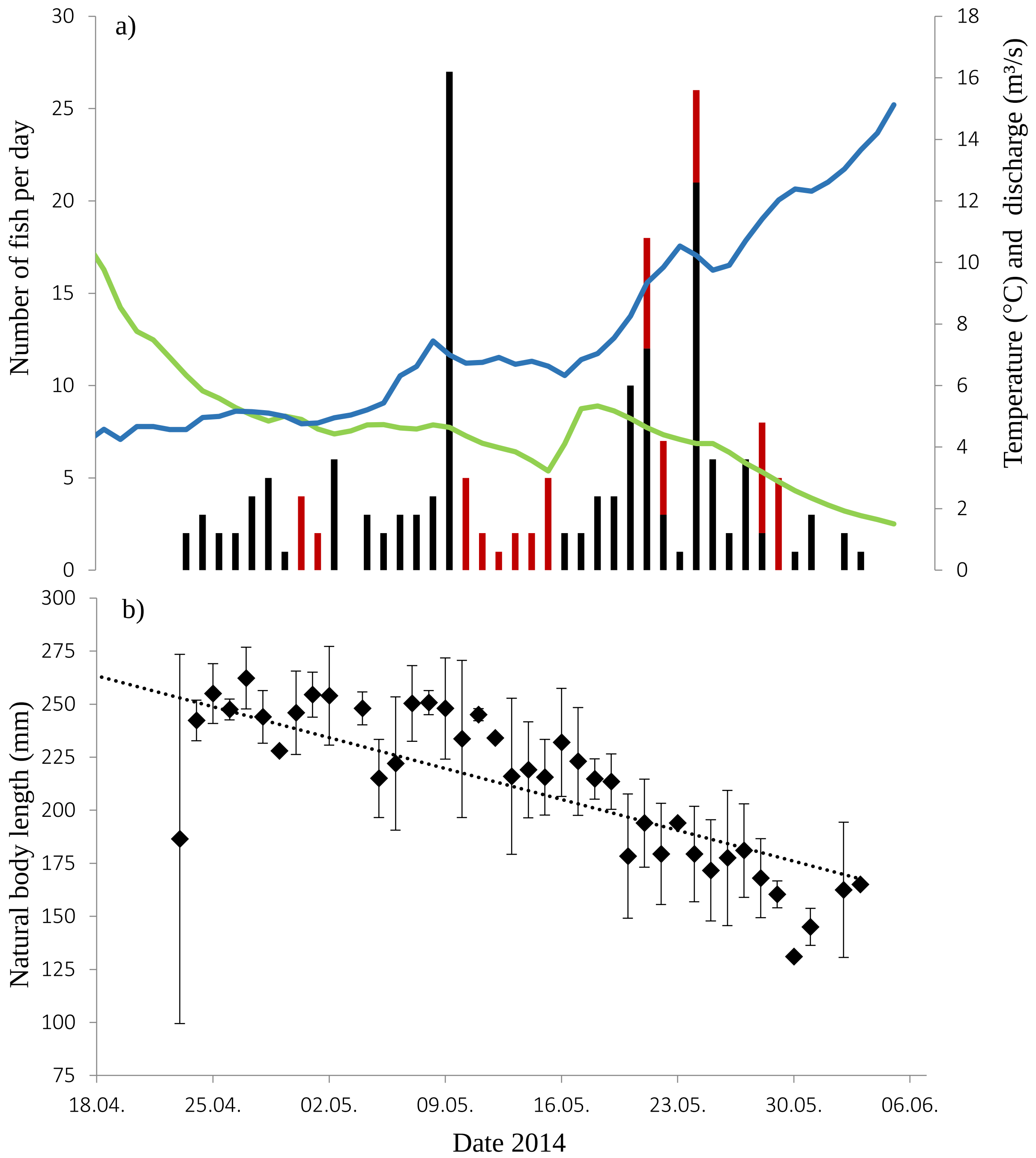


Figure 2: a) Number of smolts captured in the rotary screw trap per day, during the period 22 April – 7 June 2014. A total of 199 sea trout smolts were caught, and the red columns represent the 50 smolts tagged. One sea trout smolt was captured 8 April (not shown). The trap was not operational from 8 April – 22. April. Mean daily water temperature (°C, blue line) and mean daily water discharge (m³/s, green line) from Lake Rovatnet are also shown. **b)** Mean natural body length for all fish captured per day during the period 22 April – 7 June 2014, including standard deviation.

Natural body length and body mass were measured for all individuals tagged (Table 1). The sea trout smolts were implanted with individually coded acoustic transmitters (Thelmabiotel AS Trondheim, Norway, www.thelmabiotel.com, model LP-7.3, 7.3mm × 18.0mm, mass in water:air of 1.2:1.9 g, ping rate 90/30). These acoustic transmitters were specifically designed for use in smolt, when fish size is the limiting factor. Prior to the tagging procedure, the fish was anaesthetized with 2-phenoxyethanol (EC No 204-589-7; SIGMA-chemical CO., USA; www.sigmaaldrich.com) with a concentration of 0,5mL/L water. After 4.5 minutes, the fish reached full anaesthesia and was transferred to a surgery tube, where an incision of 1.0-1.5 cm was made in the body cavity on the ventral surface anterior to the pelvic girdle. The tag was cleaned and then inserted into the body cavity. During the surgical procedure, freshwater was supplied to the fish with a small tube through the mouth of the fish, providing continuously freshwater to the gills. For closing of the incision, two separate sutures (RESORBA Wundversorgung GmbH & Co. KG, Germany; www.resorba.com; 5/0 Resolon) were used. After surgery, each fish was kept in a container with freshwater for recovery. Both the anesthesia and recovery containers were covered to reduce exposure to light and therefore unnecessary stress. The surgery procedure lasted less than 5 minutes. The smolts were immediately released into the river at the capture site when they had recovered from the anesthesia (mean recovery time 12 minutes), and could swim normally.

Table 1: Tagging date, number of individuals, natural body length and body mass of tagged smolts captured in the River Søa in 2014

		Natural length (mm)		Body mass (g)	
Date	*n*	Mean + SD	Range	Mean + SD	Range
08.04.	1	225.0	225.0-225.0	85.0	85.0-85.0
30.04.	4	244.8 ± 18.4	219.0-262.0	111.5 ± 26.9	85.0-149.0
01.05.	2	254.5 ± 10.6	247.0-262.0	126.5 ± 19.1	113.0-140.0
14.05.	12	230.2 ± 27.8	177.0-267.0	93.7 ± 30.0	44.9-141.0
15.05.	5	215.6 ± 17.8	196.0-239.0	73.5 ± 16.8	58.6-99.1
21.05.	6	192.2 ± 10.3	176.0-205.0	54.7 ± 7.9	43.0-64.0
22.05.	4	168.3 ± 24.1	151.0-204.0	39.3 ± 18.6	27.0-67.0
24.05.	5	170.2 ± 19.5	154.0-202.0	40.8 ± 15.6	31.0-68.0
30.05.	11	168.7 ± 13.4	150.0-192.0	37.7 ± 8.8	26.0-56.0
Total	50				

2.4 Acoustic receivers and tracking of tagged sea trout smolts

A total of 43 receivers (Vemco Inc. model VR2W; www.vemco.com) were used to track the tagged fish, 37 receivers were deployed in the fjord system while the six remaining were placed in River Søa (fig. 1). A total of 21 receivers were deployed in arrays, and in that way enabled tracking of each individual smolt migrating between different areas in the fjord system. Five arrays were deployed in the fjord system (array H1, H2, H3, H4, S1, fig. 1). The first array was placed 1 kilometer from the outlet of River Søa (array H1, 4 receivers fig. 1), and one array was deployed 4 kilometers from the river mouth (array H2, 4 receivers, fig. 1). In the outermost part of the study area of Hemnfjord, two sets of arrays were deployed (array H3 and H4, 5 receivers each, fig. 1). In Snillfjord, one array was placed at the outer part of the fjord (array S1, 3 receivers, fig. 1). In addition to these five arrays, receivers were attached to three fish farms, one was attached near the water outlet from the land based production facility for salmon smolt in Snillfjord, two were attached to both sides of the silicone production wharf and one close to the outlet from the Søa hydropower plant (fig. 1). The remaining six receivers in the fjord were deployed along the shoreline and close to the harbour in the inner part of Hemnfjord (fig. 1). The last six receivers were placed in six different locations in River Søa (green circles, fig. 1). All receivers deployed in this particular study were part of the Ocean Tracking Network (www.oceantrackingnetwork.org).

The six receivers in River Søa were mounted on 50 mm iron pipes that were hammered into the riverbed. When deploying the receivers in the fjord system, they were attached to 14 mm polyester ropes 5 meters below buoys at the sea surface. To avoid drifting of the buoys when deployed in the fjord, a 100 kg anchor was attached to each of them to keep them in place. The receivers attached to the fish farms, the smolt production facility, the silicone production wharf and the harbor were mounted on 14 mm ropes attached to fixed structures at these sites (fig. 1).

2.5 Receiver performance

A range test was performed at the receiver of array H1 (fig. 1) 10 April 2014 under optimal conditions (calm, clear weather) by deploying a transmitter (Thelmabiotel AS, model LP-7.3.) at 4 meters depth, increasing distance to the receiver in steps of 50 meters the first 300 meters, and in steps of 25 meters from 300-450 meters. The maximum receiver range was found to be 300 meters. The transmitter used for the range test was similar to the acoustic transmitters used to tag the fish in the present study.

All of the tagged individuals were registered at one or both receivers in the estuary when migrating to the fjord. Array H1 and H2 also successfully registered the individuals when passing. Array H3, H4 and S1 did not cover the entire distance across the fjord, so the number of fish recorded at these sites is a minimum estimate.

2.6 Age determination by scale analysis

Fish scales were sampled from all tagged fish. The fish scales were analysed to determine the age of each fish, and to investigate whether or not these fish were first-time sea migrants. A selection of the most informative scales from each fish was done using a light stereoscope. Replacement scales are scales missing annual rings, so these were not included in the analysis. The selected scales were placed on a 1 mm Lexan plate and then printed on the plate using an iron press. The prints were photographed with a computer-controlled stereoscope, making it possible to age-determine the smolts by patterns of annual rings. Annual growth and age at smoltification were estimated based on length of the scale and the relative length between each winter growth zone (Závorka et al. 2014).

2.7 Data Analysis

2.7.1 Data filtering prior to analysis

The initial number of registrations from the 43 receivers was 180 935. Prior to the statistical analysis, Microsoft Access 2013 (www.microsoft.com) was used to prepare the receiver data. A total of seven receivers (the two receivers in the outlet from River Søa, the two receivers at Søa power plant outlet and the three innermost receivers in Hemnfjord, fig. 1) were considered to contain more erroneous registrations than the rest of the receivers in the study area, due to a high number of simultaneously visiting fish, and hence, code collision among signals from different transmitters creating registrations of false codes. Microsoft Access was therefore used to apply a visual basic coded filter to the data from these receivers. The filter was constructed to require a minimum of two registrations from a tagged individual within a time span of 10 minutes for the filter to accept the registrations as true (Pincock 2012). The seven receivers had an initial number of registrations of 109 504 before filtering. When applying the filter, a total of 3293 registrations were considered false (3.0 %) and excluded from further statistical analysis. The total number of registrations used for the statistical analysis was 177 642.

2.7.2 Statistical analysis

After filtering and extracting relevant data using Microsoft Excel and Microsoft Access 2013, statistical analysis was conducted using RStudio version 0.98.1091 (www.r-project.org). When conducting one and two-way analysis of difference between groups, Welch's t-test was applied, assuming unequal variances between groups. For non-normally distributed data, log-transformation was conducted, or the non-parametric Mann-Whitney U-test was applied, for analysis of difference between two groups. Kruskal-Wallis' non-parametric test was applied due to unequal variances between groups and non-normally distributed data, for the analysis of difference between three or more groups. The Tukey ANOVA was applied when the data met the assumption of normally distributed data and equal variance between the groups. For the pairwise multiple comparison of mean ranks, the Tukey and Kramer (Nemenyi) test with Tukey-Dist approximation for independent samples was applied (Pohlert 2014).

2.7.3 Investigation and calculation of marine residence time

In order to investigate the residence time in different area zones, the receivers were assigned to these zones based on their geographical location (fig. 1). Zone 1, located in inner Hemnfjord included the two receivers at the outlet of River Søa, the three innermost receivers, all receives at array H1 and the two receivers stationed at the power plant outlet. Zone 2 include array H2 and the two receivers at the silicone production wharf, one at the fish farm and one stationed further south (fig. 1). Zone 3 was assigned to central Hemnfjord, including array H3, two receivers at two fish farms and one control receiver close to one of the fish farms. Zone 4 was assigned to Snillfjord, which included array S2, the three innermost receivers and the receiver at the smolt production facility. Zone 5 included only array H4. Zone 6 included the four remaining receivers located in River Søa, and were used to distinguish between marine and freshwater residency in later analysis.

In order to calculate the marine residence time in different fjord zones, certain criteria were followed:

- When determining transition from freshwater to saltwater, the fjord residence started at the first registration at a marine receiver.
- When determining transition from saltwater to freshwater, the freshwater residence started at the last registration at a marine receiver.
- Transition to a new zone occurred when the fish was registered at a station within the next zone.
- If 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.
- If transition to a zone further into the fjord, the residence time started in the next zone at the time of the first registration at a receiver in the next zone.

When calculating the marine residence time in the fjord zones, the two receivers in the estuary of River Søa were included as part of the fjord. Total marine residence time and total residence time in the different fjord zones were calculated using Microsoft Excel and Microsoft Access. Marine residence time was calculated as the total time spent in the marine environment during the summer. Only fish that completed the marine migration and returned to River Søa, were included in the analysis (n = 26), and individuals lost during the study period were excluded (n = 24).

2.7.4 Littoral vs. pelagic and cliff habitat use

To investigate the habitat use of the tagged sea trout smolts, the arrays containing both pelagic and littoral receivers (H1, H2, H3, H4 and S1, fig. 1) were used. The two receivers, in each array, deployed near shore, or in areas with shallow water (< 10 meters depth) where the sea trout was likely to feed at or near the bottom, were defined as littoral habitat. Receivers deployed close to steep cliff walls along the shoreline, were defined as cliff habitat. Receivers deployed over deep water, without coastline or shallow areas (< 25 meters depth) within the receiver range were defined as pelagic receivers. At each array, the proportional number of registrations across the receivers was calculated for each fish, which gave a rough estimate of habitat utilization of pelagic, littoral and cliff areas during the study period from 30 April – 26 November. All individuals that performed a marine migration (n = 40) were included in this analysis.

2.7.5 Short and long distance migrants

For investigation of marine migration distance, the tagged individuals were categorized into short and long distance migrants, according to which arrays they were registered at during the study period 30 April – 26 November 2014. Short distance migrants were defined as individuals only registered in inner Hemnfjord with no registrations further out than array H2 (fig. 1). Long distance migrants were divided into two groups. One group of individuals was categorized as long distance migrants to Snillfjord, which were fish registered by array S1 (fig. 1), but without any registrations at array H3 and H4 (fig. 1) in the outer part of the study area. The second group was categorized as long distance migrants to the outer part of the study area, with registrations at array H3 or H4 (fig. 1). Minimum migration distance of each group was based on individuals registered at array H2, S1 and H3 or H4. All individuals that migrated to the outer parts of the study area (array H3 or H4), except two, were also registered at array S1 in

Snillfjord. The minimum migration distance from the river mouth was 4 km for short distance migrants, 14 km for long distance migrants to Snillfjord and 25 km for long distance migrants to the outer part (15 km for the two individuals never registered in Snillfjord). Individuals that were lost and not registered at array H3, H4 or S1 were excluded.

2.7.6 Daily distribution and individual migration pattern

For investigation of daily distribution of tagged individuals in the study area, zone 1, 2, 3, and 4 (fig. 1) were combined and regarded as the fjord zone. Zone 5, including array H3 and H4, was defined as the outer part of the study area. This investigation shows the daily distribution of the tagged individuals in freshwater, the inner fjord area and the outer part of the fjord during the study period from 30 April – 26 November 2014. Individual migration pattern (Appendix 1, 2 and 3) was investigated for the individuals that migrated to the fjord post tagging. The same fjord zones used in the calculation of residence time were also used in the investigation of individual migration patterns (fig. 1). However, array H3 were in this case combined with array H4 and included to zone 5.

3. Results

3.1 Environmental variables

3.1.1 Water temperature

The mean water temperature for the outer part of the study area (Array H4, mean = 12.3 °C, SD ± 3.6) during the period 1 april – 13 October, was slightly lower than in the inner part of Hemnfjord (Array H1, mean = 13.4 °C, SD ± 4.0), the middle part of Hemnfjord (Array H2, mean = 13.2 °C, SD ± 3.9) and at the Søa power plant outlet (mean = 13.3 °C, SD ± 4.1).

Table 2: Location of the temperature loggers, mean water temperature (T °C) and standard deviation, minimum and maximum temperature during the period 01.04.2014 – 13.10.2014.

Temperature logger site	Mean T ± SD (°C)	Minimum T (°C)	Maximum T (°C)
Power plant outlet	13.3 ± 4.1	5.1	20.5
Array H1	13.4 ± 4.0	5.9	20.5
Array H2	13.2 ± 3.9	5.6	20.0
Array H4	12.3 ± 3.6	5.7	17.9

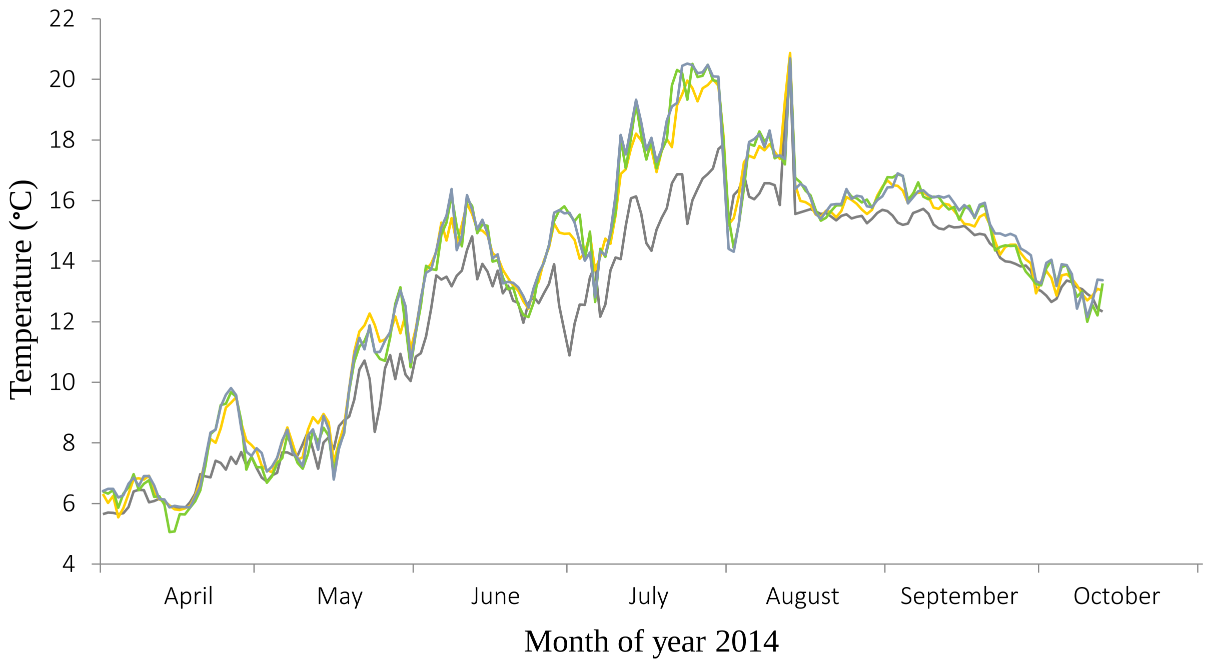


Figure 3: Mean daily water temperature (°C) at 1 meters depth in the inner part of Hemnfjord (blue), in the middle of Hemnfjord (Array H2, yellow), at the Søa power plant outlet (green) and in the outer part of the study area (Array H4, grey) during the period 1 April – 13 October 2014.

3.1.2 Salinity

Three of the four data loggers deployed in the fjord system also recorded salinity throughout the study period (table 3), which showed that the salinity close to Søa power plant outlet (mean = 10.7 ‰, SD ± 9.6) was much lower than the inner part of Hemnfjord (mean = 26.8 ‰, SD ± 4.5) and the middle part of Hemnfjord (mean = 22.1 ‰, SD ± 8.9).

Table 3: Location of the salinity loggers, mean salinity (‰) and standard deviation, minimum and maximum salinity during the period 01.04.2014 – 13.10.2014.

Salinity logger site	Mean ± SD (‰)	Minimum (‰)	Maximum (‰)
Array H1	26.8 ± 4.5	14.0	34.6
Array H2	22.1 ± 8.9	7.4	33.3
Power plant outlet	10.7 ± 9.6	0.5	32.7

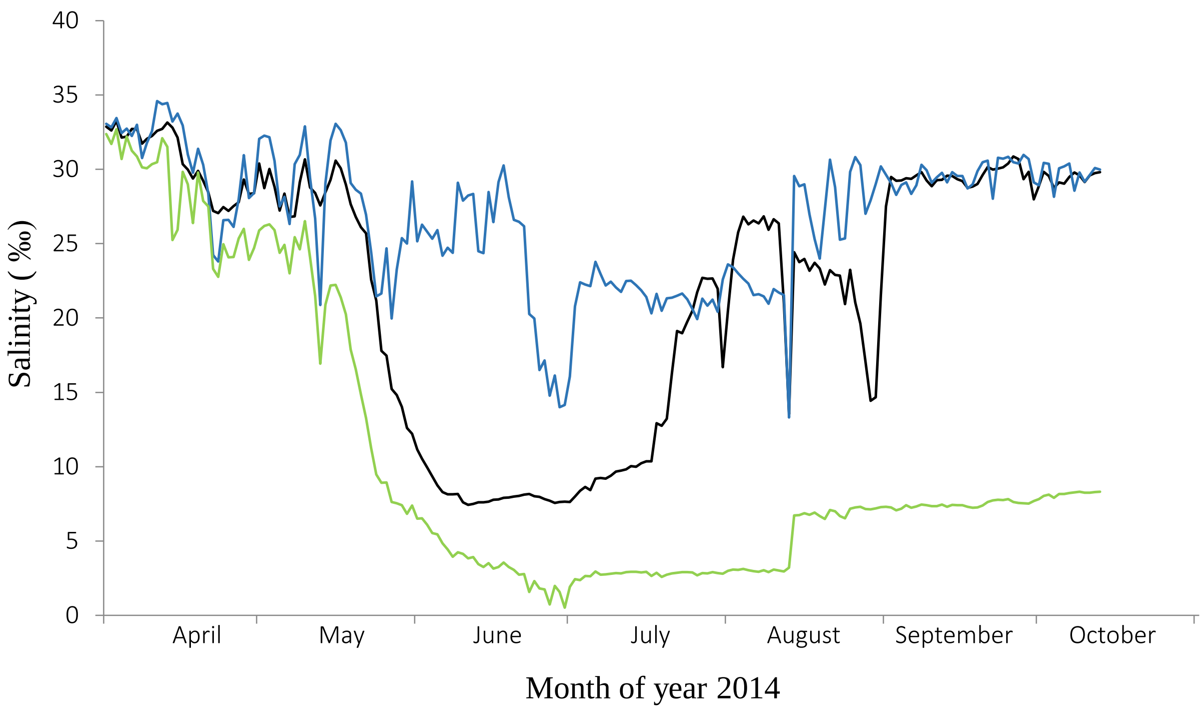


Figure 4: Mean daily salinity at 1 meters depth in the inner part of Hemnfjord (blue), in the middle part of Hemnfjord (Array H2, black) and at Søa power plant outlet (green) during the period 1 April – 13 October 2014.

3.2 Biological characteristics and fate of tagged fish

According to scale analysis, all 50 tagged individuals were first time migrants at capture. Eight individuals were found to have increased growth the year before tagging, nevertheless, these were most likely first time migrants, and included as smolts in the analyses. Mean age was estimated to be 3.0 years (range 2 – 4 years, SD = ± 0.7). Mean natural body length was 202 mm (range 150 – 267 mm, SD = ± 36). There was a significant positive correlation between natural body length and age at capture (Pearson Correlation = 0.57, $p < 0.001$) (fig. 5).

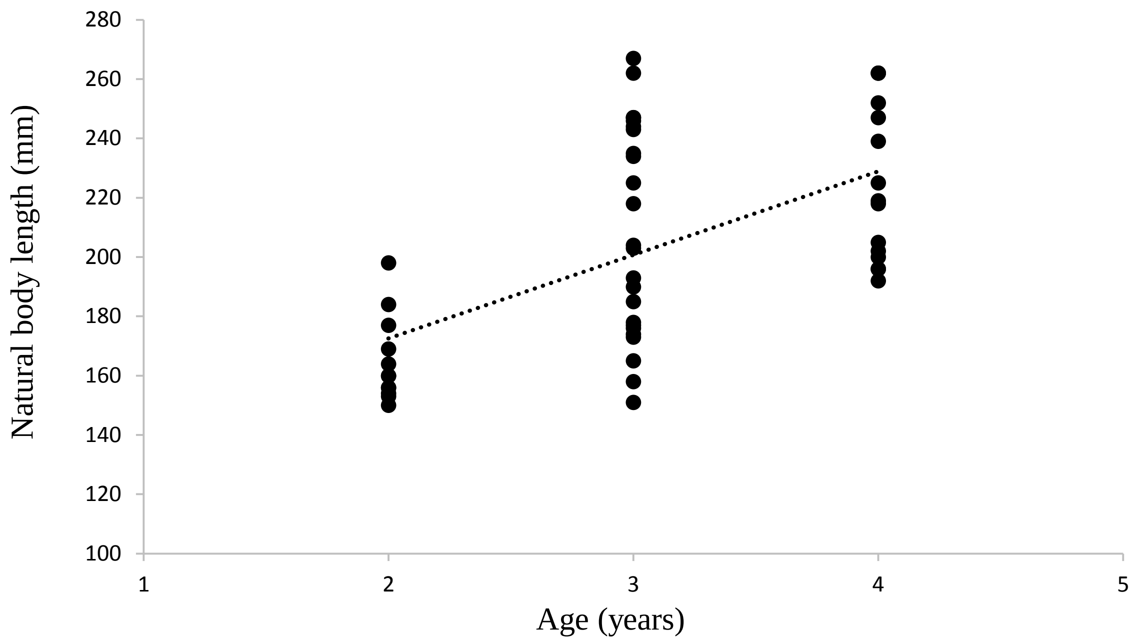


Figure 5: Correlation between natural body length (mm) and age (year) at capture for the 50 tagged smolts (black dots).

During the study period, 10 of the 50 tagged sea trout individuals were last recorded at the two receivers close to Lake Rovatnet (fig. 1), and were never recorded to leave the watercourse post tagging. Of these 10 individuals, seven were last recorded at the receiver located at the outlet of Lake Rovatnet, which indicated that these individuals moved upstream and stayed in the lake. The last three individuals were last recorded at the receiver deployed 150 m below the outlet of Lake Rovatnet.

Of the 40 seaward migrating individuals, 26 individuals (Appendix 1) returned to Søa River, while 14 individuals (Appendix 2) were lost during the marine residence period. The reason for losing these individuals is not known. All 14 individuals were last registered at a marine receiver, of which seven were last registered in the inner parts of Hemnfjord, three in mid-Hemnfjord, one in Snillfjord and three in the outermost part of the fjord system. The remaining 26 seaward migrating individuals returned to River Søa, which gives a minimum return rate to freshwater of 65%. Four individuals were lost during the upwards migration in River Søa, and the remaining 22 individuals migrated all the way back to Lake Rovatnet (44%). The 40 seaward migrating individuals (fig. 6a) had a longer natural body length than the 10 individuals (fig. 6a) that were not recorded to leave Søa watercourse (*t*-test, $n = 50$, $p = 0.027$). Of the 40 migrating individuals, those 26 returning to Søa watercourse (fig. 6b), had a longer natural body length than the 14 individuals (fig. 6b) that were last registered at a marine receiver (*t*-test, $n = 40$, $p = 0.029$).

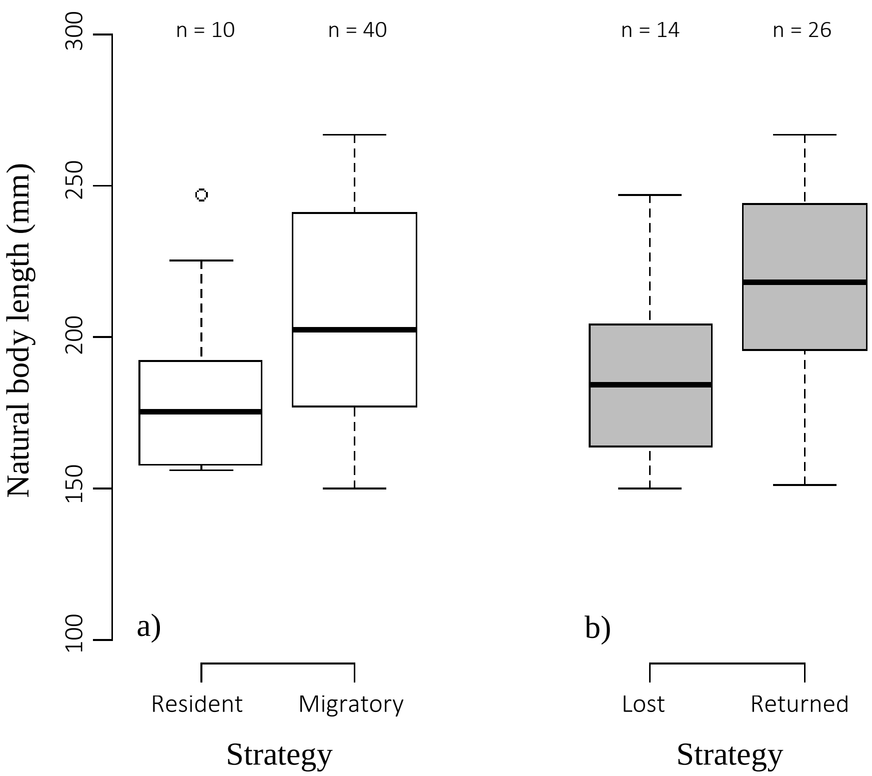


Figure 6: Natural body length (mm) of tagged fish in relation to their behavioural strategy. **a)** Resident group: individuals that stayed in Lake Rovatnet. Migratory group: individuals that migrated to the fjord. **b)** Individuals that were lost during the marine residence period and individuals that returned to River Søa. The box – and whisker plots show median values (black lines), the interquartile ranges (boxes) and the 5th and 95th percentiles (whiskers). The circle indicates an outlier.

3.3 Timing of smolt migration and freshwater return

Median seaward migration date for all 40 tagged migrating individuals was 22 May (range 30 April – 8 June, fig. 7). The median return date for the 26 individuals that migrated back to freshwater was 4 July (range 8 June – 6 September, fig. 8). Eight of the 26 individuals (31 %) that returned from the sea migration performed a second sea migration during the same summer (see section 3.6).

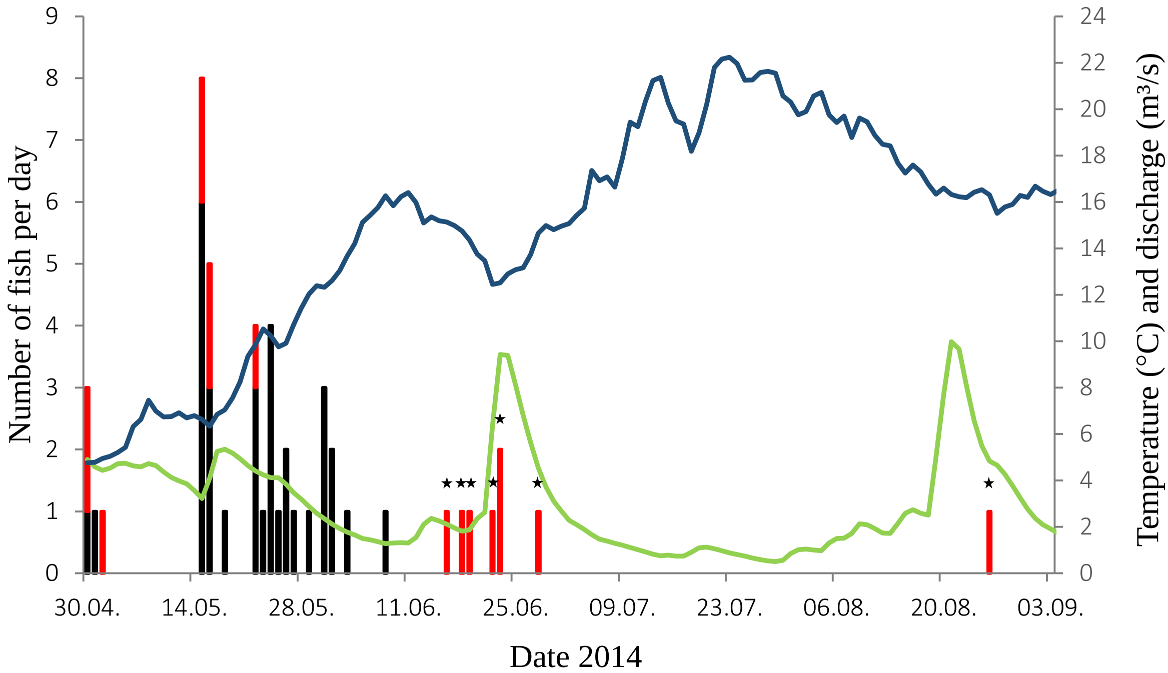


Figure 7: Water temperature (blue line) and water discharge (green line) during the outward migration period, from River Søa to Hemnfjord, of the 40 acoustic tagged sea trout. The bars represent number of outward migrating individuals per day. The black bars represent the individuals that only had one marine migration during the summer period, while the red bars represent the individuals that migrated twice. The red bars with stars represent the individuals' second seaward migration.

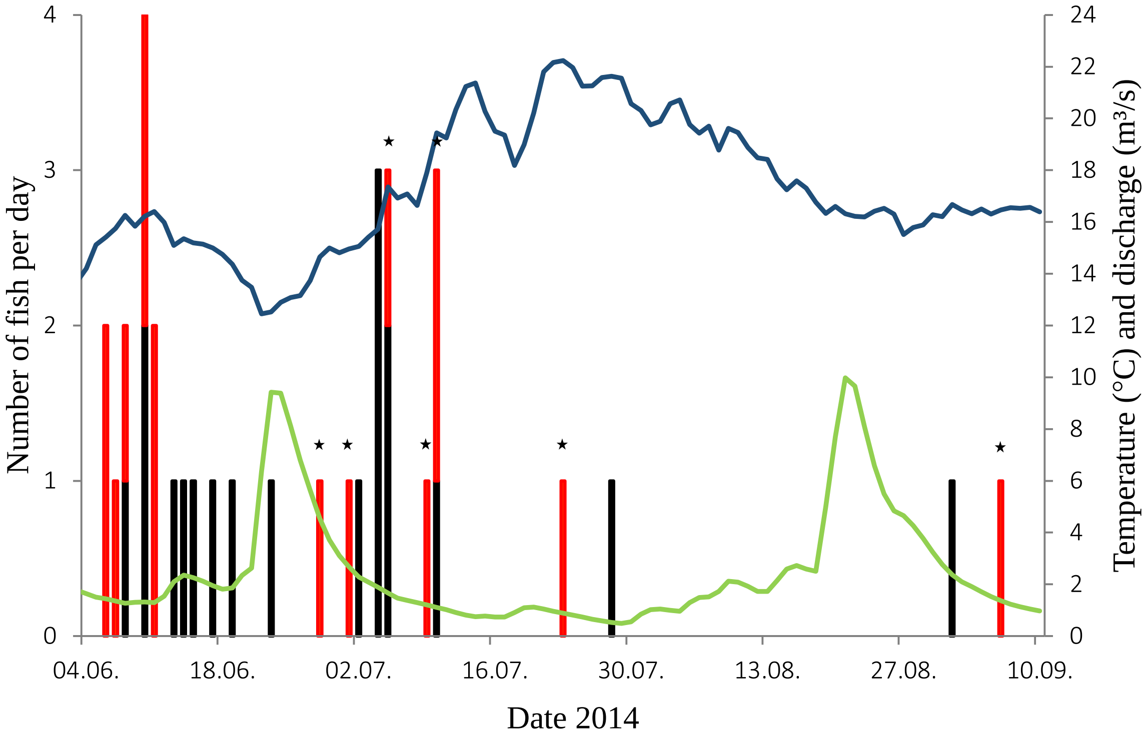


Figure 8: Water temperature (blue line) and water discharge (green line) during the return to freshwater, from Hemnfjord to River Søa, of the 26 returning sea trout individuals. The bars represent number of individuals per day entering freshwater. The black bars represent the number of individuals that only had one marine migration during the summer period, while the red bars represent the number of individuals that migrated twice. The red bars with stars represent the individuals' second freshwater return.

Number of tagged post-smolts in the main fjord system was highest during 22 May – 4 July (fig. 9). From 20 May – 9 July, there were continuous registrations of tagged post-smolts in the outer part of the fjord (fig. 9). From 9 June, there was an increase in number of fish registered in freshwater (fig. 9), however, from 22 June there was a higher number of post-smolts registered in the fjord again (fig. 9), due to a return migration to sea for eight individuals (see section 3.6). By the end of July, most tagged post-smolts had returned to freshwater (fig. 8 and 9).

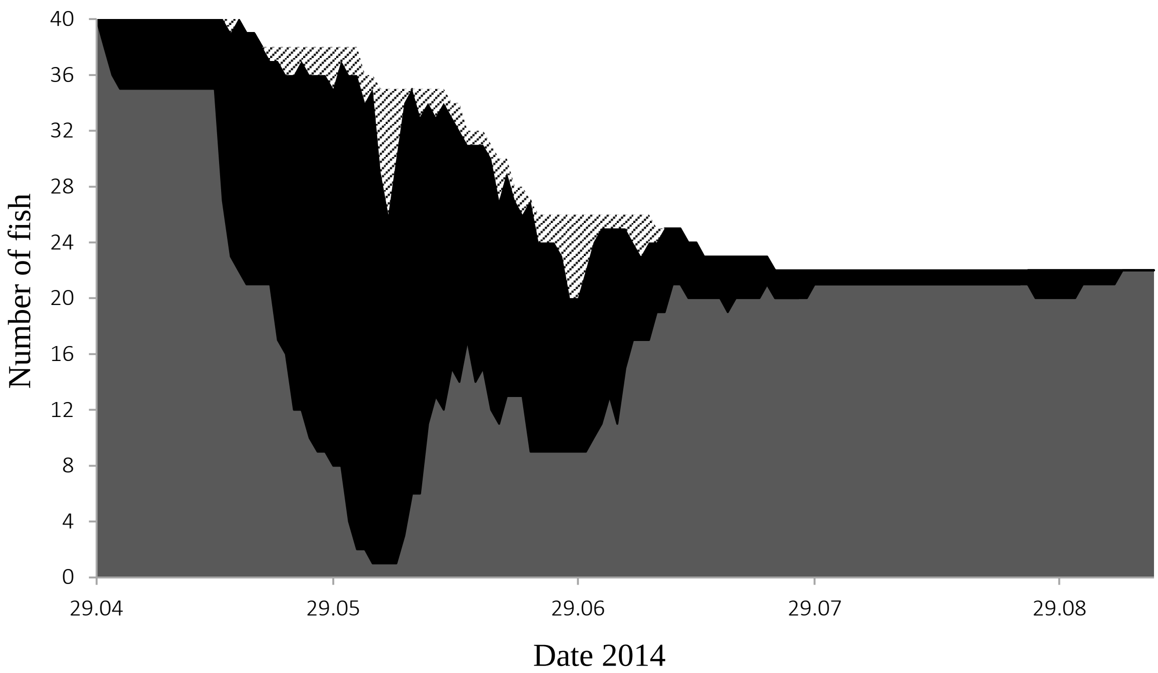


Figure 9: The number of individuals registered simultaneously in freshwater (■), in the fjord system (■) and in the outermost part of the study area (▨) during the marine residence period summer 2014.

A higher proportion of the tagged sea trout was observed to migrate out from River Søa to the fjord during the evening and nigh (32 out of 40, 80%) than during the day (8 out of 40, 20%) (Chi-square, n = 40, p < 0.001, fig. 10). However, no difference in proportion of individuals migrating during day and night was found for the 26 returning individuals during the return to freshwater (Chi-square, n = 26, p = 1, fig. 11).

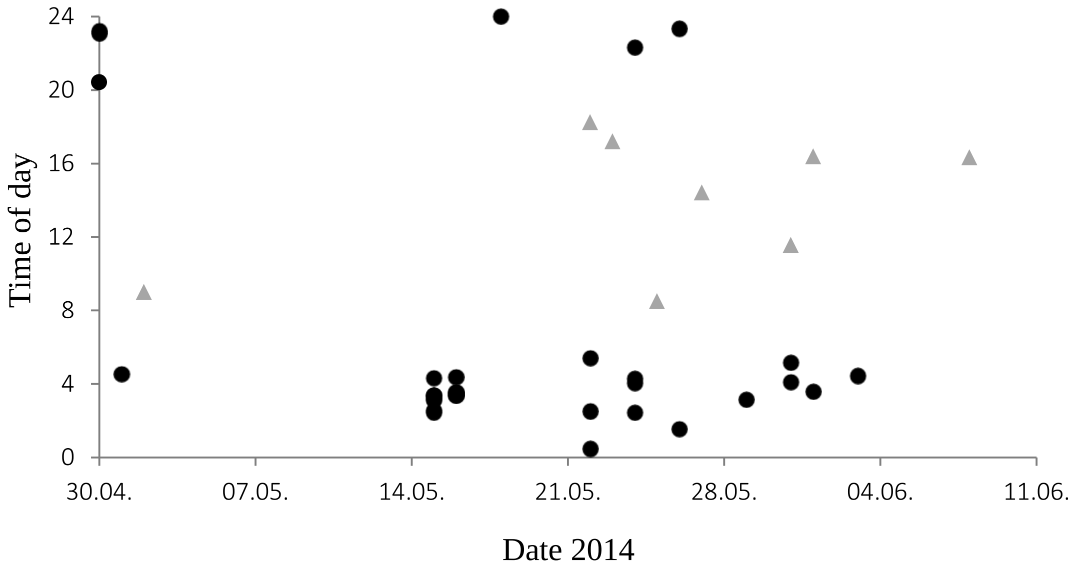


Figure 10: Date and time of day for the 40 outward migrating individuals from River Søa to the fjord system. Grey symbols represent individuals migrating during daytime (08:00-20:00), while black symbols represent individuals migrating during the night.

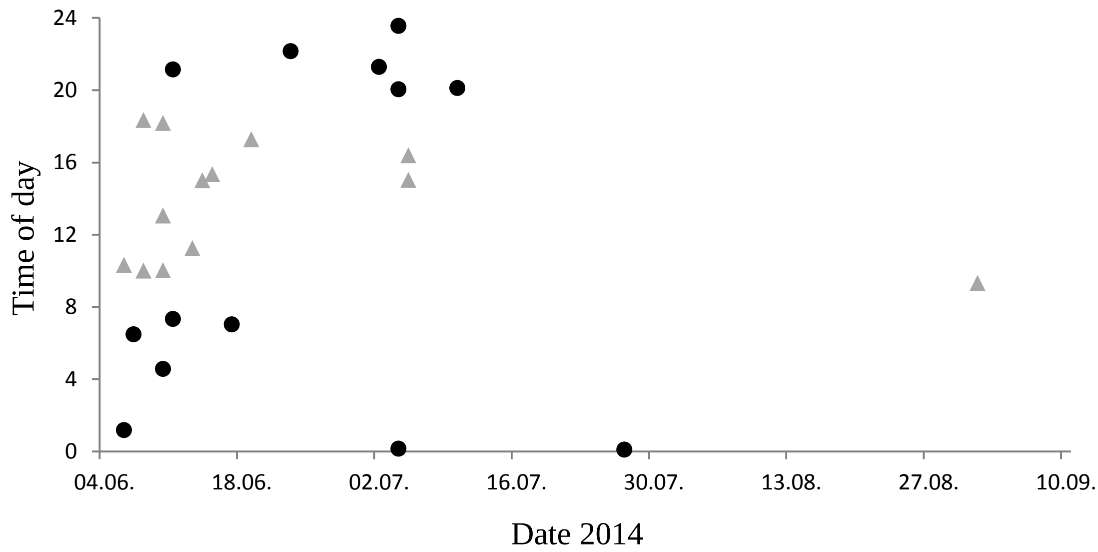


Figure 11: Date and time of day for the 26 returning individuals from the fjord to freshwater. Grey symbols represent individuals migrating during daytime (08:00-20:00), while black symbols represent individuals migrating during the night.

3.4 Marine residence time and spatial use of the fjord system

3.4.1 Total marine residence time and residence time in fjord zones

The tagged sea trout displayed large individual variation in total residence time in the marine environment. Median marine residence time was 37.9 days (range 22.4 – 98.9 days, SD = ± 17.2). Large individual variation in residence time in the different fjord zones were observed for the 26 individuals that returned to freshwater, before the end of the study period 26 November 2014 (fig. 12). There was a difference in time spent in the different zones (Kruskal-Wallis test, $p < 0.001$). The tagged individuals spent longer time in zone 1 (median = 9.0 days, fig. 11) than in zone 5 (median = 4.1 days, post-hoc, Nemenyi test, $p = 0.021$). Longer time was also spent in zone 2 (median = 10.5 days) than in zone 3 (median = 5.5 days) and 5 ($p = 0.028$, $p < 0.001$).

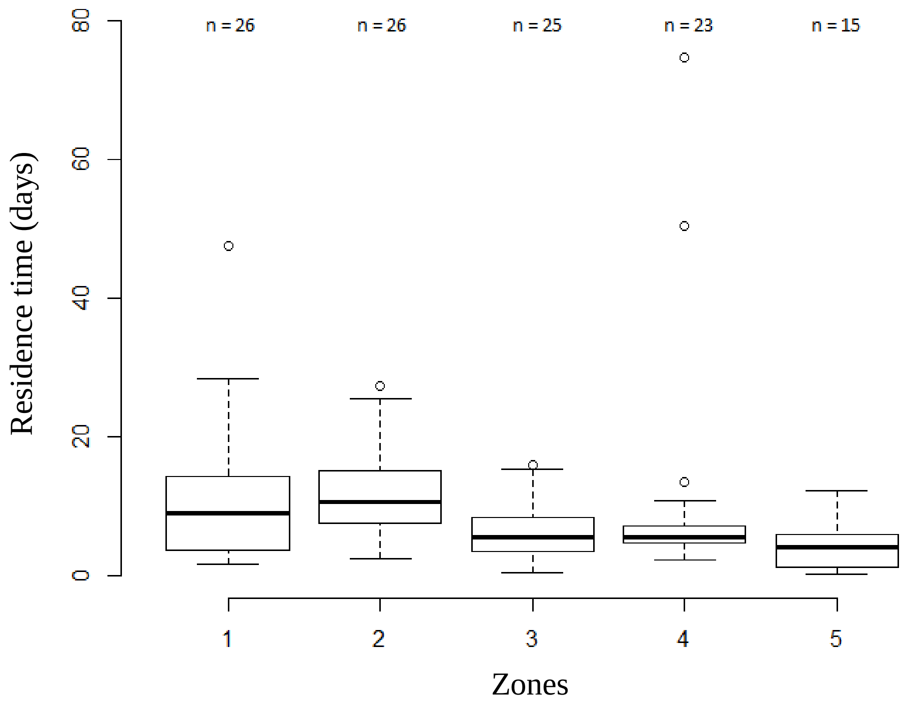


Figure 12: Residence time in fjord zones 1-5 during the study period 30 April – 26 November 2014. The box – and whisker plots show median values (black lines), the interquartile ranges (boxes) and the 5^{th} and 95^{th} percentiles (whiskers). The circles indicate outliers.

3.4.2 Littoral vs. pelagic habitat use

There was large individual variation in use of the pelagic and littoral areas in the fjord system. At array H1 (fig. 13), the tagged individuals had higher proportions of their registrations at the receivers close to shore (littoral habitat) compared to receivers in the pelagic habitat (two sided *t*-test, $n = 126$, $p < 0.001$). Also for array H2 (fig. 13), the tagged fish had higher proportions of their registrations at the recivers close to shore (two sided *t*-test, $n = 121$, p = 0.007).

At array S1 (fig. 13) there was also higher proportions of registrations in the littoral and cliff habitat than in the pelagic habitat (two sided *t*-test, $n = 75$, $p = 0.012$). At this array, there was a higher proportion of registrations in the littoral habitat than at the pelagic habitat (two sided *t*-test, $n = 51$, $p < 0.001$). When comparing the receiver in the cliff habitat and the receiver in the pelagic habitat, there was no difference in proportions of registrations (two sided *t*-test, $n = 47$, $p = 0.65$).

In the outer part of the study area at array H3 (fig. 13), there was no difference in proportions of registrations in the littoral or cliff habitat compared to the three receivers in the pelagic habitat (two sided *t*-test, $n = 69$, $p = 0.086$). There was no difference in proportions of registrations when comparing the receiver in the cliff habitat (West, array H3, fig. 13) and the three receivers in the pelagic water masses (two sided *t*-test, $n = 53$, $p = 0.53$). Similarly, there was no difference in proportions of registrations when comparing the receiver in the littoral habitat (East, array H3, fig. 13) and the three pelagic receivers (two sided *t*-test, $n = 56$, $p = 0.074$).

At array H4 (fig. 13), there was no difference in proportions of registrations in the littoral or cliff habitat compared to the three receivers in the pelagic habitat (two sided *t*-test, $n = 64$, $p = 0.26$). No difference was found between the cliff habitat (West, fig. 13) and the three receivers in the pelagic water masses (two sided *t*-test, $n = 53$, $p = 0.12$). There was also no difference between the littoral habitat (East, fig. 13) and the pelagic habitat (two sided *t*-test, $n = 52$, $p = 0.65$).

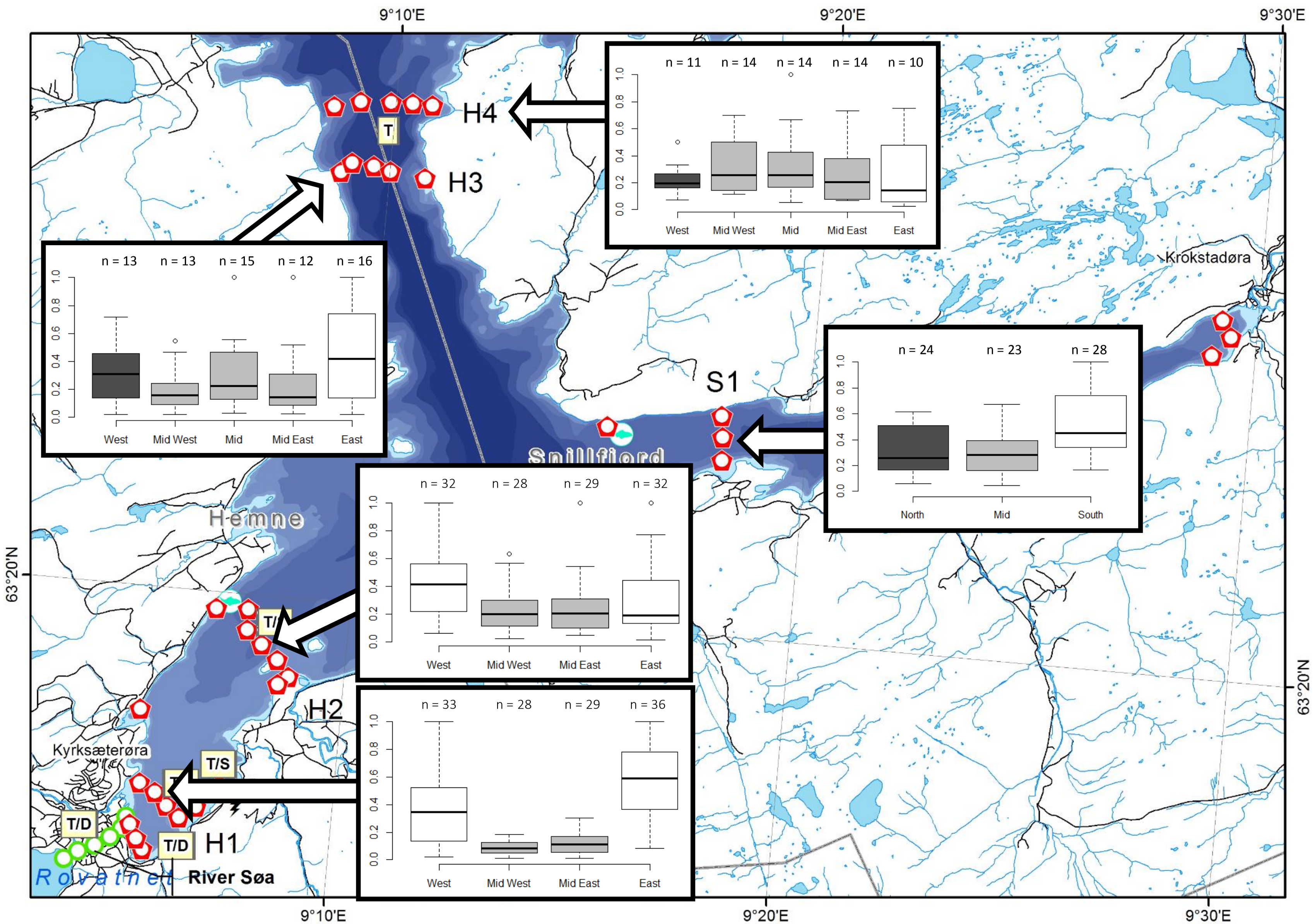


Figure 13: Proportions of individual registrations near shore (white), in pelagic habitat (light grey) and cliff areas (dark grey) at the receiver arrays H1, H2, H3, H4 and S1. The box-and-whisker plots show median values (black lines), the interquartile ranges (boxes) and the 5th and 95th percentiles (whiskers). Circles indicate outliers.

3.5 Short and long distance migrants and migration patterns

3.5.1 Biological characteristics of short and long distance migrants

A total of 33 tagged individuals were categorized as either short or long distance migrants. Only two individuals (6%) were never registered further out than array H2 (fig. 1), and these were categorized as short distance migrants. Nine individuals (27%) migrated to Snillfjord (minimum distance 15 km), past array S1 (fig. 1) and further into the fjord, and were never recorded in the outer part of the fjord. A total of 22 individuals (67%) migrated further out to the outer part of the study area, past array H3 or H4 (fig. 1, minimum distance 25 km). Only two individuals were never registered at array S1 and further into Snillfjord, while the other 20 post-smolts were also registered in Snillfjord and in the outer part of the fjord. All of these 31 post-smolts were defined as long distance migrants. The short distance migrants had a median natural body length of 207 mm (range 151 – 262 mm, SD ± 78). The long distance migrants to Snillfjord (LDM to Snillfjord) had median natural body length of 176 mm (range 153 – 262 mm, SD ± 36). The long distance migrants to the outer part of the study area (LDM to the outer fjord) had a median natural body length of 212 mm (range 178 – 267 mm, SD ± 27). When comparing the two long distance groups, the LDM to the outer part had a longer natural body length than the LDM to Snillfjord (Mann-Whitney *U*-test, $n = 31$, $p = 0.028$, fig. 14).

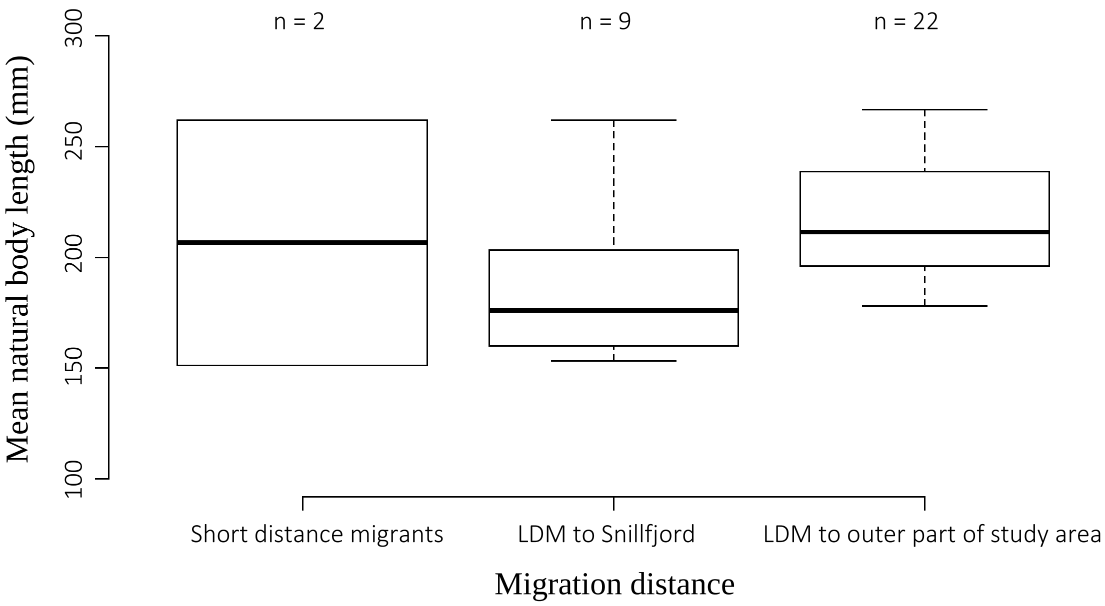


Figure 14: Natural body length (mm) of tagged individuals categorized as short distance migrants or long distance migrants to Snillfjord (LDM to Snillfjord) or long distance migrants to the outer part of the study area (LDM to outer part of study area). The box-and-whisker plots show median values (black lines), the interquartile ranges (boxes) and the 5th and 95th percentiles (whiskers).

3.5.2 Marine residence time for short and long distance migrants

There was large individual variation in total marine residence time within the groups (fig. 15). The short distance migrants consisted of only two individuals, with a median residence time of 53 days (range 40 - 65 days). The LDM to Snillfjord had a median residence time of 36 days (range 24 – 66 days) and the LDM to outer fjord had a median residence time of 40 days (range 22 – 99 days). There was no difference in marine residence time between the two long distance migrant groups (Mann-Whitney *U*-test, $n = 24$, $p = 0.49$).

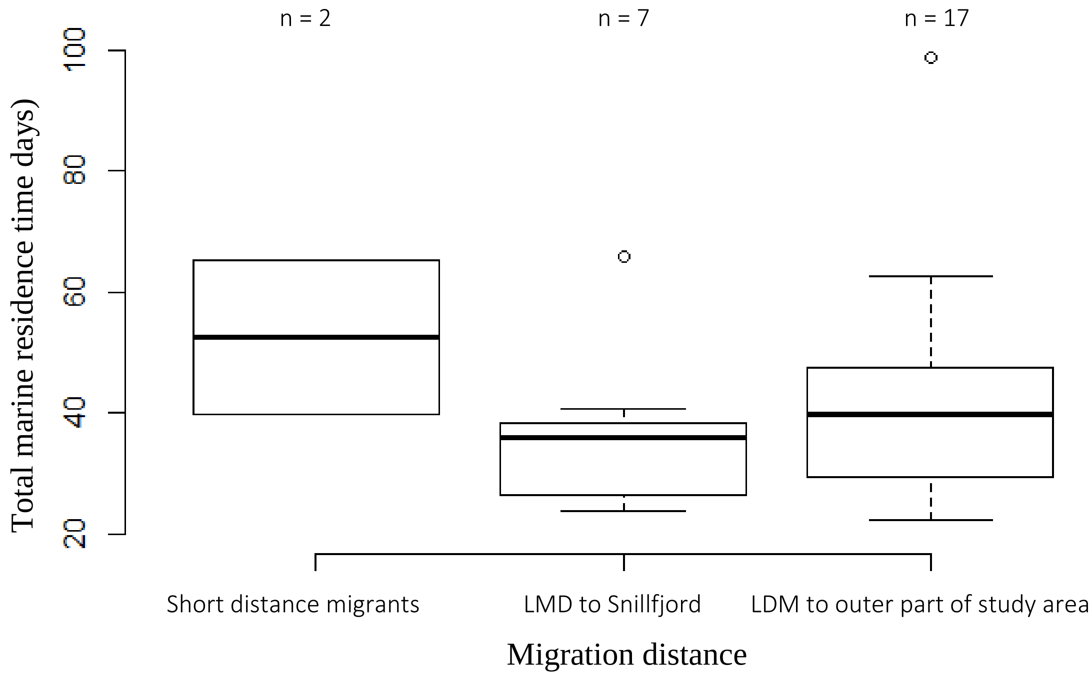


Figure 15: Total marine residence time for the tagged individuals categorized as short distance migrants or long distance migrants to Snillfjord (LDM to Snillfjord) or long distance migrants to the outer part of the study area (LDM to outer part of study area) in the study period 30 April – 26 November 2014. The box-and-whisker plots show median values (black lines), the interquartile ranges (boxes) and the 5^{th} and 95^{th} percentiles (whiskers). Circles indicate outliers.

3.6 Individuals performing a second marine migration

3.6.1 Timing of smolt migration and freshwater return

Eight of the 26 returning sea trout individuals (31%) performed a second marine migration during the same summer (Appendix 3). There was no difference in natural body length between the individuals migrating once, and those migrating twice (Mann-Whitney *U*-test, $n = 26$, $p = 0.15$). The median seaward migration date the first period, was 15 May (range 30 April – 22 May, fig. 7), median return date was 9 June (range 6 June – 11 June, fig. 8). Median seawards migration day the second time was 22 June (range 16 June – 26 August, fig. 7), and median return date was 9 July (range 28 June – 6 September, fig. 8).

3.6.2 Total marine residence time and residence time in fjord zones

During the first marine migration, the eight individuals had a median total residence time of 26.0 days at sea (range 19.0 – 40.0 days, SD = ± 8.2). All individuals migrated back to Lake Rovatnet during their freshwater residency before they returned to the fjord the second time. The median residence time in freshwater before migrating to sea again, was 14.0 days (range 5.0 – 79.0 days, SD = ± 23.8). For the second marine migration, the median total residence time at sea was 14.5 days (range 11.0 – 25.0 days, SD = ± 4.9). These eight individuals spent longer time at sea during the first marine residence period than during the second (Mann-Whitney *U*-test, $n = 16$, $p = 0.002$).

When comparing residence time in the different fjord zones during the first and second migration, the eight individuals spent longer time in zone 2 during the first migration period (fig. 16a, median = 9.1 days) than during the second period (fig. 16b, median = 2.0 days, two sided *t*-test, n = 16, $p < 0.001$). However, longer residence time in zone 5 was observed during the second migration period (fig. 16b, median = 5.9 days) than during the first migration period (fig. 16a, median = 1.2 days, two sided *t*-test, n = 10, $p = 0.019$). In zone 1, 3 and 4, no difference in residence time was observed between the first and second migration period (two sided *t*-test, zone 1; n = 16, $p = 0.19$, zone 3; n = 15, $p = 0.11$, zone 4; n = 13, $p = 0.67$).

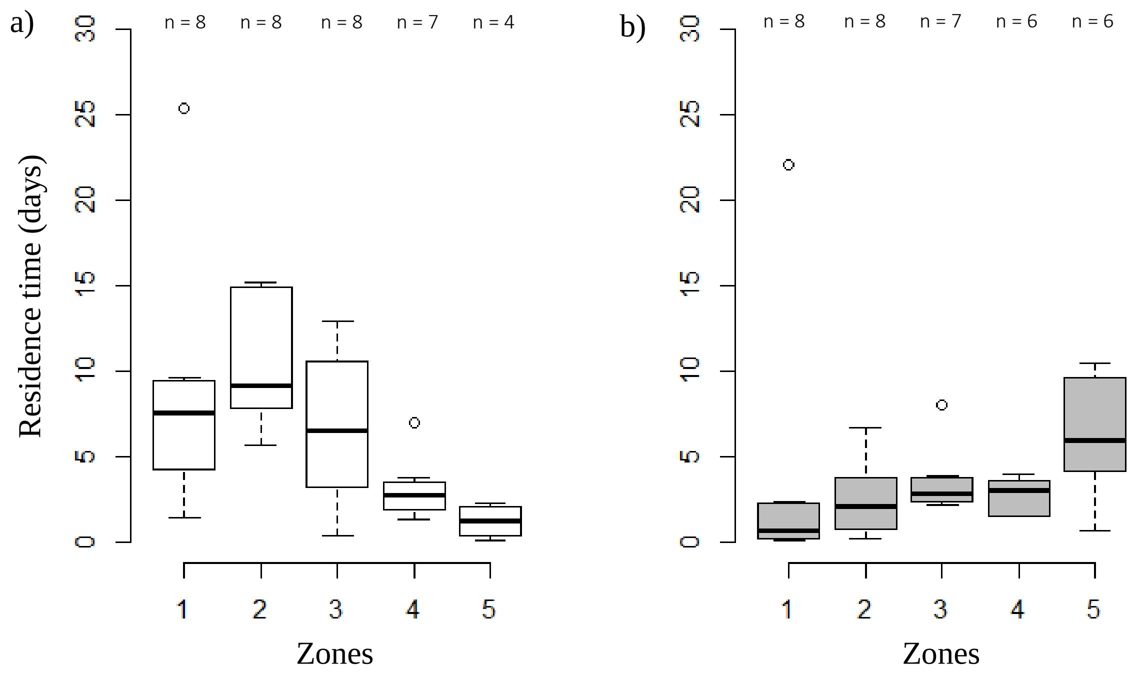


Figure 16: a) Residence time in fjord zones 1-5 during the first marine migration. **b)** Residence time in fjord zones 1-5 during the second marine migration. The box – and whisker plots show median values (black lines), the interquartile ranges (boxes) and the 5th and 95th percentiles (whiskers). Circles indicate outliers.

3.6.3 Littoral vs. pelagic habitat use during the first and second marine migration

At array H1 and H2 (fig. 17), the eight individuals had higher proportions of their registrations at the receivers in the littoral habitat compared to receivers in the pelagic habitat (two sided *t*-test, $p < 0.001$ and $p = 0.037$) during their first marine residence period. At array S1, H3 and H4, there was no difference in proportions of registrations when comparing the receivers in the littoral or cliff areas and the pelagic areas (two sided *t*-test, $p = 0.74$, $p = 0.097$ and $p = 0.52$). During the second marine migration period, no differences in proportions of registrations between the littoral or cliff and pelagic areas at array H1, H2, S1, H3 and H4 were observed (two sided t-test, $p = 0.22$, $p = 0.74$, $p = 0.76$, $p = 0.29$, $p = 0.64$).

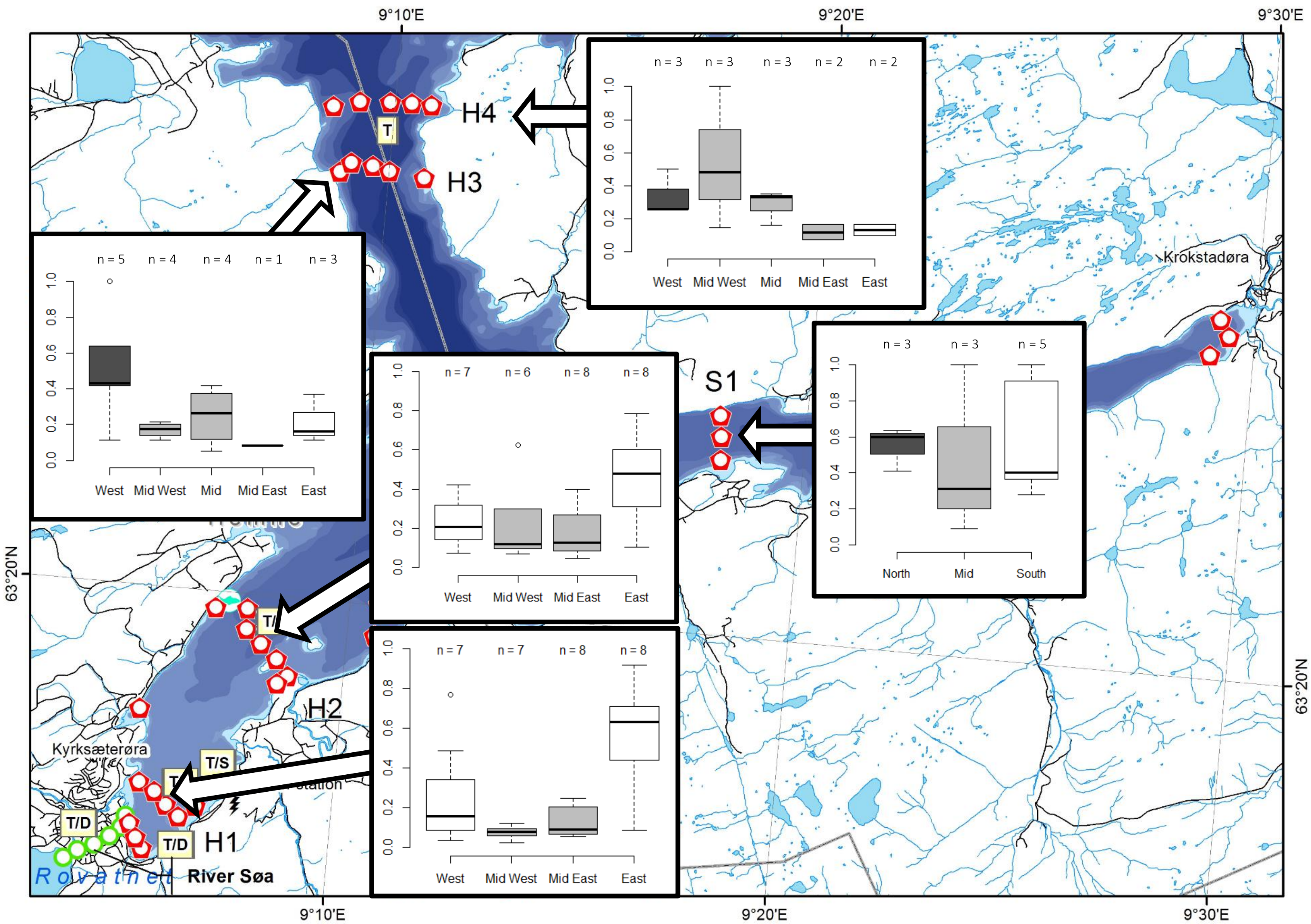


Figure 17: Proportions of individual registrations at near shore (white), in pelagic (light grey) and cliff areas (dark grey) across the receiver arrays H1, H2, H3, H4 and S1 during the first marine residence period. The box-and-whisker plots show median values (black lines), the interquartile ranges (boxes) and the 5th and 95th percentiles (whiskers). Circles indicate outliers.

4. Discussion

Large individual variation in time spent in the marine environment was found for the tagged post-smolts, and similar results were also found for the use of different fjord areas. The post-smolts distributed themselves over large areas of the fjord system, and even the smallest individuals utilized larger marine areas than the inner part of the fjord. The number of returning individuals was high, with a return rate of 65%. Body length seemed to be an important factor in determining the marine survival and the distribution of the tagged post-smolts in the fjord system, with the largest individuals utilizing areas in the outer area of the fjord. The migration to outer fjord areas and widespread habitat use contradicted my expectation that the post-smolts' distribution would be limited to the inner areas of the fjord, as Lyse et al. (1998) found in their study on wild sea trout post-smolts.

4.1 Biological characteristics and fate of tagged fish

4.1.1 First time migrants.

All 50 tagged individuals were according to the scale analysis first time migrants at capture. Eight individuals had a slightly increased growth the year before tagging, which could imply that this increased growth was due to the good feeding conditions in Lake Rovatnet, or that these individuals might have been feeding close to the estuary. Landergren (2001) observed that parr may utilize brackish water when accessible, and that smolting appears not to be essential for adapting to the slightly increased saline waters. Thus, an estuarine feeding behaviour could be beneficial in terms of better feeding opportunities and increased growth before performing a marine migration. In this case, all tagged individuals had the morphological characteristics of a smolt, in terms of reduced parr marks and extensive silvering and darkened fin margins, and the increased growth for these eight individuals were not sufficient to be explained by feeding in an estuarine environment. Good feeding conditions in Lake Rovatnet had most likely resulted in increased growth for these smolts. The mean smolt age was estimated to be 3.0 years for the individuals captured and tagged, which corresponds with the findings of Davidsen et al. (2014b), in their study on adult sea trout from the same watercourse.

4.1.2 Body length as a factor for migration and freshwater return

The individuals that performed a marine migration were larger than the individuals that remained resident in Lake Rovatnet after tagging. A size-dependent migratory behaviour could be related to physiological problems when entering seawater, higher risk of predation and the overall physiological state of the fish before and after the smoltification. The ability to osmoregulate is generally better for bigger smolts (Parry 1960, Hoar 1976, Urke et al. 2013), however, there is limited knowledge about the physiological variation in wild smolts during the outward migration from Norwegian watercourses (Ugedal et al. 2014). All fish were categorized as smolts at tagging, assuming that they were physiologically adapted for a marine residency, therefore, other reasons than physiology are more likely to explain the observed size-dependent migration. The fact that the smallest smolts did not leave the watercourse, could also be related to the possible negative effects of the handling and tagging process, since smaller smolts may be more vulnerable to the surgical implantation (Jepsen et al. 2002, Lacroix et al. 2004). The disadvantage with surgical implantation is that it requires more practice and skills than other methods. There is a possibility that the wound may not heal and that the sutures may open, in addition to the negative effects the fish may experience related to swimming performance, feeding and growth (Thorstad et al. 2013). In this study, the surgical procedure was done with skilled personnel and with minimum handling as possible, with the release of the fish immediately after recovery from the anaesthetisation. In addition, the tag size was determined by the specific study objects, which in this case were smolts (≥ 150 mm). Tag effect studies indicate that there is no general rule for how big the tag can be related to the fish body size without having negative impacts on the fish (Jepsen et al. 2005), nevertheless, it cannot be excluded that the smallest individuals were negatively impacted from the tagging procedure, which caused them to remain in freshwater. Three out of ten individuals were last registered downstream Lake Rovatnet, which could indicate that the tag was malfunctioning or expelled through the incision site. It could also be that the fish were preyed upon post-tagging, died shortly after in the river out of range from the receiver, or that they simply were moving about in the river out of range the whole summer.

The number of tagged individuals that returned to River Søa was high, with a return rate of 65%. This should be regarded as a minimum number, due to the unknown fate of the individuals that did not return from the marine residency before the study was ended. Studies conducted by Jensen and Rikardsen (2008) and Davidsen et al. (2014b) have shown that adult sea trout are able to overwinter in the marine environment in central and northern Norway, therefore, it cannot be excluded that the post-smolts in this study remained in the sea during winter. Alternative reasons for the loss of returning individuals from the fjord might have been malfunctioning tags that ceased to transmit signals. The post-smolts last registered at the outer receiver arrays, might have migrated out of the fjord and into a neighboring fjord system, and then returned after the study was ended. The return rate in this study was high compared to previous studies. Davidsen et al. (2014a) observed that 16% of tagged hatchery-reared sea trout post-smolts returned to the river after the first summer at sea, while a long-term study conducted by Jonsson and Jonsson (2009) in River Imsa in the period from 1976-2005, found that on average 15% of wild sea trout post-smolts survived the marine migration.

Body size seemed to be an important factor determining the marine survival in this study. The post-smolts that returned to River Søa had a longer natural body length than the post-smolts lost during the marine residency. This observation could indicate that the smallest and weakest individuals were more exposed to predation or other mortality factors. The risk of predation is higher if the post-smolt is compromised in terms of poorer osmoregulatory ability, which could lead to decreased swimming ability and antipredatory behaviour. Thorstad et al. (2007) suggested that the weakest individuals were also those with the lowest migration speed, thus, the chance of being predated was more likely. On the other hand, the high return rate could be due to a high abundant smolt cohort this present year, as observed in River Imsa (Jonsson and Jonsson 2009), where the proportion of returning sea trout post-smolts increased linearly with the abundance. However, only 199 smolts were caught in the rotary screw trap during the period it was operational, which does not imply a highly abundant smolt cohort this year. Schooling behaviour of post-smolts has been observed to reduce the predation risk, which together with a decreased predation pressure due to a functional response to other suitable prey items (Wood and Hand 1985), could be a plausible explanation for such a high return rate.

4.2 Timing of smolt migration and freshwater return

All tagged seaward migrating individuals migrated from Søa River to the sea within a period of 5-6 weeks, from the beginning of May till early June. A higher proportion (80%) of smolts migrated from freshwater to sea during nighttime than during the day. This is consistent with previous findings of sea trout smolts and Atlantic salmon smolts (Moore and Potter 1994, Moore et al. 1998, Davidsen et al. 2009). Nocturnal migration could be a strategy for minimizing or preventing predation by visual predators (Solomon 1982, Jepsen et al. 2006). The smolt mortality is usually high in the transition between freshwater and saltwater (Dieperink et al. 2002), and previous studies have observed that the mortality during the downstream migration is size dependent (Dieperink et al. 2001, Kallio-Nyberg et al. 2007). Thus, a nocturnal migration strategy would be beneficial for smaller individuals that may be more vulnerable for predation in the early marine migration phase. Davidsen et al. (2009) also found that a larger proportion of the Atlantic salmon post-smolts entered sea during night than during day. It would seem that there is a complex system, where multiple factors such as temperature, daylight and tidal cycles influence the timing of the transition between freshwater and saltwater. A nocturnal migration strategy has also been observed for adult sea trout during the outward migration (Davidsen et al. 2014b). It can be speculated that such behaviour as adults is a strategy residing from the smolt migration. Adult sea trout are less exposed to predation, and a nocturnal migration strategy might not be as necessary in terms of survival as it might be for first time migrants.

4.3 Marine residence time and spatial use of the fjord system

There was a large individual variation in total marine residence time, ranging from 22-99 days. Similarly, large individual variation in time spent in the different areas of the fjord was found, however, most of the tagged post-smolts migrated throughout the entire fjord system. This study showed that even the smallest individuals utilized larger marine areas than the innermost part of the fjord. Nevertheless, the areas in Hemnfjord were more used than the outermost part of the study area. No difference in residence time was found between the inner parts of Hemnfjord and Snillfjord, which indicates that Snillfjord is an equally important area for the sea trout as Hemnfjord. One reason for keeping close to the home river could be the access of freshwater or brackish water, due to variable seawater tolerance in sea trout. River Snilldalselva has its outlet in inner Snillfjord, which provides freshwater, and could be a reason for why the tagged individuals also migrated to this area. However, from mid-May, the power plant created an upper surface layer of freshwater all the way out to middle Hemnfjord. Therefore, osmoregulatory problems do not seem to explain the prolonged stay in inner Hemnfjord. On the contrary, the decreased salinity may have influenced the post-smolts to utilize larger areas of Hemnfjord, and not just the areas close to the estuary. Hemnfjord and Snillfjord are narrow fjords with vast areas of kelp forests and brown algae where post-smolts may be able to find sufficient food resources, in addition to suitable places to hide from both avian and larger marine predators. If both Snillfjord and Hemnfjord provide similar resources and environments, it could be beneficial for the post-smolt to utilize larger areas of the fjord system migrating along the shoreline.

4.4 Littoral vs. pelagic habitat use

The tagged fish utilized the shallow and near shore areas more frequently than the open water masses in the inner Hemnfjord. Also in the outer part of Snillfjord, the littoral area was more frequently used that the pelagic areas. However, no difference was found between the cliff and pelagic areas. The more frequent use of near shore areas is consistent with findings of Lyse et al. (1998), Jensen et al. (2014) and Davidsen et al. (2014b), who all observed the same habitat utilization of littoral areas for post-smolts and adult sea trout. Feeding opportunities in shallow areas could be favorable in terms of prey choice, as shown in previous studies (Lyse et al. 1998, Knutsen et al. 2001). Smaller individuals usually prefer shallow water prey, such as crustaceans, surface insects and polychaetes, while larger individuals also prey on fish (Klemetsen et al. 2003). The advantages of utilizing near shore areas could also be that predation is less likely to occur, due to more hiding places among rocks and bottom vegetation.

The results in this study gave a rough estimate of the utilization of littoral and pelagic habitat, as it is calculated based on the relative numbers of registrations across the receiver arrays. By using the proportional number of registrations across the receiver arrays to investigate the use of littoral and pelagic areas, it was assumed that the receiver range for each receiver within each array was homogenous when conducting the statistical analysis. However, due to the fact that the range of each receiver is known to vary, and that the number of registrations was used as a measure of time spent in the different areas, could in this case be a source for biased results. A variety of factors, such as the chemical and physical properties of the water, the underwater topography and turbulence in the water could limit the range at different locations. Therefore, there is a probability of heterogeneous receiver range throughout the fjord system (Kessel et al. 2014), and tagged fish close to shore and in shallow areas could have been less likely to be detected due to signal shielding and transmission absorption of the signal.

4.5 Short and long distance migrants and migration patterns

The proportion of long distance migrants was high, and based on their geographical distribution these individuals were divided into two groups. One group of long distance migrants only migrated to Snillfjord and were never observed in the outer area of the fjord system. A larger group of post-smolts was observed migrating to the outer part of the study area, in addition to being registered in Snillfjord. The post-smolts migrating to the outer part of the study area had a longer body length than those only migrating between inner Hemnfjord and Snillfjord.

However, no difference in total marine residence time was found for the two long distance migrant groups. Food availability or requirements for certain food prey, could be a possible explanation for why the longest individuals utilized the areas towards the open sea. Fast growing individuals change to a more piscivorous diet at a smaller size and younger age (Klemetsen et al. 2003), than conspecifics of smaller sizes, which could cause the longest individuals to exploit other habitats than the others. Also, Davidsen et al. (2014a) found that starved hatchery reared sea trout post-smolt migrated further out in the fjord compared to fully fed individuals. These findings could indicate that individuals with higher metabolism and growth rate are more willing to migrate and perform longer migrations searching for suitable food items.

4.6 Individuals performing a second marine migration

Eight individuals had two separate marine migrations during the same summer. After returning to Lake Rovatnet from the first marine residency, these post-smolts migrated a second time to the fjord. The marine residency was longer the first than the second time. The return to freshwater in early June could be a behavioural response in order to avoid or reduce salmon lice infestation (Birkeland and Jakobsen 1997). These findings correspond to a study conducted in Etnefjord, in south-western Norway (Gjelland et al. 2014). They found that salmon lice infestation influenced the migration patterns, as most of the infested tagged fish stayed in proximity of a less saline environment. The eight individuals in the present study migrated back to freshwater after the first marine residency within a short period of six days in early June (week 23-24). The reasons for the premature freshwater return seem to have affected these eight post-smolts simultaneously, considering that all returned to freshwater in less than a week. Data from the fish farming localities in the study area showed that there was an increase in the number of salmon lice at one of the farms in the fjord during week 22, with a treatment against salmon lice during week 24 (data provided by Aqua Gen). These data may explain why a freshwater return took place during a one week period after an observed peak in number of salmon lice in the farms. On the other hand, there were only eight individuals that were observed to display such a migration behavior, and it cannot be concluded whether or not there was a connection between the premature freshwater return and salmon lice infestation.

Limited food resources could also be an explanation for the observed behaviour. Variable food prey availability could have caused these eight post-smolts to return to their home lake, following a return to the fjord to explore if the conditions had improved later on in the season.

However, this does not explain why only these individuals displayed such a behaviour, unless food resources were patchily distributed throughout the season, leading food deprived fish to choose a freshwater return if the costs were higher than the benefits of staying sea resident. Another reason could be that these individuals were utilizing areas, in which schools of cod (*Gadus morhua* L. 1758) or saithe (*Pollachius virens* L. 1758) or bigger predators like porpoises (*Phocoenidae* Gray, 1825) were approaching, leading the post-smolts to move back into freshwater. Results from previous studies have shown high predation rates in estuaries, with an estimated cod predation rate of 20% in River Orkla (Hvidsten and Lund 1988), and 25% in the estuary of River Surna (Hvidsten and Møkkelgjerd 1987), which suggests that staying close to the river mouth, may increase the risk of being predated.

The spatial use of the fjord system between the first and second marine migration showed two distinctive patterns. Use of the innermost areas close to the tagging watercourse was highest during the first migration, whereas during the second migration, a higher residence time in the outer area of the fjord was observed. After having performed the first marine residency, the eight individuals may have displayed an experienced migration behaviour the second time, and the observed migration pattern and distribution may be due to a response of learning (Dodson 1988). Prey availability could also be a plausible explanation. Due to a premature return to freshwater, the need for food may have been increased, leading the post-smolts to perform longer migrations searching for profitable food items in order to compensate for the lack of resources during the period in freshwater. Water temperature may also have influenced the use of inner and outer areas in the fjord system. Studies conducted by Rikardsen et al. (2007) and Jensen et al. (2014) observed that the sea trout were actively seeking areas of higher water temperatures, which in this case, corresponds to the findings of higher residence time in the outer area during the second migration. There was an increase in water temperature in the fjord system throughout the summer, which could favor a prolonged stay in the outer area during the second migration compared to the first. Both the optimal and preferred temperatures may vary among populations and with size of each individual (Elliott and Elliott 2010). Nevertheless, the water temperature in the inner parts of Hemnfjord were slightly higher compared to the outer fjord area throughout the entire summer, therefore, it should have been preferable for the sea trout smolts to stay in the inner most areas during the summer. Additionally, if temperature were of such importance, it would most likely have influenced all tagged post-smolts in similar ways, which in this case was not observed.

4.7 Present results and further conservation of Norwegian sea trout stocks

The results in this study indicated that body size was an important factor affecting both the marine survival and the observed migration behaviour. Thus, factors such as ontogeny, morphology and life-history characteristics seem to be important determinants affecting the sea trout smolt behaviour during the transition from freshwater to saltwater and the migration behaviour during the marine residency. Large individual variation was observed in both the total marine residency and for the spatial use of the fjord system, nevertheless, a surprisingly widespread distribution was observed. Results from this study contradicts previous findings, in that a large proportion of the tagged individuals were seen to migrate to the outer parts of the study area, towards the open sea. Previous studies have observed that sea trout post-smolts usually do not migrate far from their home river, in addition to being rather stationary during the marine residency (Berg and Berg 1987b, Davidsen et al. 2014a). In this study, the post-smolts seemed to utilize the entire fjord system during the summer season, regardless of the high predation risk post-smolts may experience in the marine phase. The results may reflect the highly variable life-history strategies these sea trout post-smolts may inhabit.

Marine migration and habitat utilization of sea trout are important areas of research. There is sparse information concerning the marine phase, and with the recent decline of sea trout populations over the last two decades along western-Norway and mid-Norway, detailed information about the marine phase of the migration is necessary in order to map the different factors influencing the sea trout post-smolts during the marine phase. Few studies have been conducted aiming to increase the general knowledge of the smolts' ecology and survival in populations unaffected or little affected by anthropogenic activities. Increased knowledge of the natural variation in the smolts' physiology, behaviour and migration is necessary in order to recognize and identify possible threats during the marine phase in populations affected by anthropogenic activities. Factors such as increased salmon lice infestation, pathogens and diseases from farming activities, harbour development and other environmental changes could influence the survival and behaviour of sea trout during the sea residency. Therefore, it is important and strongly advocated that long-term surveillance of sea trout populations, including environmental factors, and research on the underlying causes for variation in migration behavior and marine survival is carried out. Considering that the sea trout is heavily dependent on the marine areas it utilizes for growth, knowledge about the sea trout's whereabouts in the sea is essential in terms of modelling and assessing the distribution, utilization and behaviour.

5. References:

Alm, G. 1950. The sea trout population in the Åva stream. Report Institute of Freshwater Research, Drottningholm 31:26–56.

Anon. 2010. Status for norske laksebestander i 2010. Rapport fra Vitenskapelig råd for lakseforvaltning 2:1–213.

Berg, O. K., and M. Berg. 1987a. Migrations of sea trout, *Salmo trutta* L., from the Vardnes river in northern Norway. Journal of Fish Biology 31:113–121.

Berg, O. K., and M. Berg. 1987b. The seasonal pattern of growth of the sea trout (*Salmo trutta* L.) from the Vardnes river in northern Norway. Aquaculture 62:143–152.

Birkeland, K., and P. J. Jakobsen. 1997. Salmon lice, *Lepeophtheirus salmonis*, infestation as a causal agent of premature return to rivers and estuaries by sea trout, *Salmo trutta*, juveniles. Environmental Biology of Fishes 49:129–137.

Davidsen, J. G., M. Daverdin, J. V Arnekleiv, L. Rønning, A. D. Sjursen, and J. I. Koksvik. 2014a. Riverine and near coastal migration performance of hatchery brown trout *Salmo trutta*. Journal of Fish Biology 85:586–96.

Davidsen, J. G., S. H. Eldøy, A. D. Sjursen, L. Rønning, E. B. Thorstad, T. F. Næsje, K. Aarestrup, F. Whoriskey, A. H. Rikardsen, M. Daverdin, and J. V Arnekleiv. 2014b. Habitatbruk og vandringer til sjøørret i Hemnfjorden og Snillfjorden. NTNU Vitenskapsmuseet naturhistorisk rapport 2014-6:1–51.

Davidsen, J. G., A. H. Rikardsen, E. Halttunen, E. B. Thorstad, F. Økland, B. H. Letcher, J. Skarhamar, and T. F. Næsje. 2009. Migratory behaviour and survival rates of wild northern Atlantic salmon *Salmo salar* post-smolts: Effects of environmental factors. Journal of Fish Biology 75:1700–1718.

Dieperink, C., B. D. Bak, L.-F. Pedersen, M. I. Pedersen, and S. Pedersen. 2002. Predation on Atlantic salmon and sea trout during their first days as postsmolts. Journal of Fish Biology 61:848–852.

Dieperink, C., S. Pedersen, and M. I. Pedersen. 2001. Estuarine predation on radiotagged wild and domesticated sea trout (*Salmo trutta* L.) smolts. Ecology of Freshwater Fish 10:177–183.

Dodson, J. 1988. The nature and role of learning in the orientation and migratory behavior of fishes. Environmental Biology of Fishes 23:161–182.

Drenner, S. M., T. D. Clark, C. K. Whitney, E. G. Martins, S. J. Cooke, and S. G. Hinch. 2012. A synthesis of tagging studies examining the behaviour and survival of anadromous salmonids in marine environments. Plos One 7:e31311.

Elliott, J. M., and J. A. Elliott. 2010. Temperature requirements of Atlantic salmon *Salmo salar*, brown trout *Salmo trutta* and Arctic charr *Salvelinus alpinus*: Predicting the effects of climate change. Journal of Fish Biology 77:1793–1817.

Gjelland, K. Ø., R. M. Serra-Llinares, R. D. Hedger, P. Arechavala-Lopez, R. Nilsen, B. Finstad, I. Uglem, O. Skilbrei, and P. A. Bjørn. 2014. Effects of salmon lice infection on the behaviour of sea trout in the marine phase. Aquaculture Environment Interactions 5:221–233.

Gross, M. R. 1987. Evolution of diadromy in fishes. American Fisheries Society Symposium 1:14–25.

Hoar, W. S. 1976. Smolt transformation: Evolution, behavior, and physiology. Journal of the Fisheries Research Board of Canada 33:1233–1252.

Hvidsten, N. A., and R. A. Lund. 1988. Predation on hatchery-reared and wild smolts of Atlantic salmon, *Salmo salar* L., in the estuary of River Orkla, Norway. Journal of Fish Biology 33:121–126.

Hvidsten, N. A., and P. I. Møkkelgjerd. 1987. Predation on salmon smolts, *Salmo salar* L., in the estuary of the River Surna, Norway. Journal of Fish Biology 30:273–280.

Jensen, J. L. A., and A. H. Rikardsen. 2008. Do northern riverine anadromous Arctic charr *Salvelinus alpinus* and sea trout *Salmo trutta* overwinter in estuarine and marine waters? Journal of Fish Biology 73:1810–1818.

Jensen, J. L. A., A. H. Rikardsen, E. B. Thorstad, A. H. Suhr, J. G. Davidsen, and R. Primicerio. 2014. Water temperatures influence the marine area use of *Salvelinus alpinus* and *Salmo trutta*. Journal of Fish Biology 84:1640–1653.

Jensen, K. W. 1968. Sea trout (*Salmo trutta* L.) of the river Istra, Western Norway. Report Institute of Freshwater Research, Drottningholm 48:185–213.

Jepsen, N., E. Holthe, and F. Økland. 2006. Observations of predation on salmon and trout smolts in a river mouth. Fisheries Management and Ecology 13:341–343.

Jepsen, N., A. Koed, E. B. Thorstad, and E. Baras. 2002. Surgical implantation of telemetry transmitters in fish: How much have we learned? Hydrobiologia 483:239–248.

Jepsen, N., C. Schreck, S. Clements, and E. B. Thorstad. 2005. A brief discussion on the 2 % tag/bodymass rule of thumb. In: Aquatic telemetry: advances and applications, Proceedings of the Fifth Conference on Fish Telemetry held in Europe, Ustica, Italy, 9-13 June 2003 (editors Spedicato, M. T., Lembo, G. and Marmulla, G.). FAO/COISPA, Rome, pp. 255-259.

Jonsson, B. 1982. Diadromous and resident trout *Salmo trutta*: is their difference due to genetics? Oikos 38:297–300.

Jonsson, B. 1989. Life history and habitat use of Norwegian brown trout (*Salmo trutta*). Freshwater Biology 21:71–86.

Jonsson, B., and N. Jonsson. 1993. Partial migration: niche shift versus sexual maturation in fishes. Reviews in Fish Biology and Fisheries 3:348–365.

Jonsson, B., and N. Jonsson. 2009. Migratory timing, marine survival and growth of anadromous brown trout *Salmo trutta* in the River Imsa, Norway. Journal of fish biology 74:621–38.

Jonsson, B., and N. Jonsson. 2011. Ecology of Atlantic salmon and brown trout: Habitat as a template for life histories. London: Springer Buisness Media B.V.

Kallio-Nyberg, I., I. Saloniemi, and M. L. Koljonen. 2007. Effects of parental and smolt traits on the marine survival of released Atlantic salmon (*Salmo salar*). Aquaculture 272:254–266.

Kessel, S. T., S. J. Cooke, M. R. Heupel, N. E. Hussey, C. A. Simpfendorfer, S. Vagle, and A. T. Fisk. 2014. A review of detection range testing in aquatic passive acoustic telemetry studies. Reviews in Fish Biology and Fisheries 24:199–218.

Klemetsen, A., P.-A. Amundsen, J. B. Dempson, B. Jonsson, N. Jonsson, M. F. O'Connell, and E. Mortensen. 2003. Atlantic salmon *Salmo salar* L., brown trout *Salmo trutta* L. and Arctic charr *Salvelinus alpinus* (L.): a review of aspects of their life histories. Ecology of Freshwater Fish 12:1–59.

Knutsen, J., H. Knutsen, J. Gjøsæter, and B. Jonsson. 2001. Food of anadromous brown trout at sea. Journal of Fish Biology 59:533–543.

Lacroix, G. L., D. Knox, and P. McCurdy. 2004. Effects of implanted dummy acoustic transmitters on juvenile Atlantic salmon. Transactions of the American Fisheries Society 133:211–220.

Landergren, P. 2001. Survival and growth of sea trout parr in fresh and brackish water. Journal of Fish Biology 58:591–593.

Lyse, A. A., S. O. Stefansson, and A. Fernö. 1998. Behaviour and diet of sea trout post-smolts in a Norwegian fjord system. Journal of Fish Biology 52:923–936.

MacCrimmon, H. R., and T. L. Marshall. 1968. World distribution of brown trout, *Salmo trutta*. Journal of the Fisheries Board of Canada 25:2527–2548.

MacCrimmon, H. R., T. L. Marshall, and B. L. Gots. 1970. World distribution of brown trout, *Salmo trutta*: further observations. Journal of the Fisheries Board of Canada 27:811–818.

McCormick, S. D. 2012. Smolt physiology and endocrinology. Fish Physiology 32:191–251.

Moore, A., M. Ives, M. Scott, and S. Bamber. 1998. The migratory behaviour of wild sea trout (*Salmo trutta* L.) smolts in the estuary of the River Conwy, North Wales. Aquaculture 168:57–68.

Moore, A., and E. C. E. Potter. 1994. The movement of wild sea trout, *Salmo trutta* L., smolts through a river estuary. Fisheries Management and Ecology 1:1–14.

Parry, G. 1960. The development of salinity tolerance in the salmon, *Salmo salar* (L.) and some related species. Journal of Experimental Biology 37:425–434.

Pincock, D. G. 2012. False detections: What they are and how to remove them from detection data. Vemco Application Note:1–11.

Pohlert, T. 2014. The pairwise multiple comparison of mean ranks package (PMCMR). R. Package.

Rikardsen, A. H., and P. A. Amundsen. 2005. Pelagic marine feeding of Arctic charr and sea trout. Journal of Fish Biology 66:1163–1166.

Rikardsen, A. H., O. H. Diserud, J. M. Elliott, J. B. Dempson, J. Sturlaugsson, and A. J. Jensen. 2007. The marine temperature and depth preferences of Arctic charr (*Salvelinus alpinus*) and sea trout (*Salmo trutta*), as recorded by data storage tags. Fisheries Oceanography 16:436–447.

Ritter, A. 1977. Salmonid terminology. ICES Journal of Marine Science 37:293–299.

Solomon, D. J. 1982. Smolt migration in Atlantic salmon (*Salmo salar* L.) and sea trout (*Salmo trutta* L.). In: Salmon and trout migratory behavior symposium. Seattle: University of Washington (editors Brannon, E. L. and Salo, E.O.), pp. 196-203.

Thorstad, E. B., A. H. Rikardsen, A. Alp, and F. Økland. 2013. The use of electronic tags in fish research - An overview of fish telemetry methods. Turkish Journal of Fisheries and Aquatic Sciences 13:881–896.

Thorstad, E. B., F. Økland, B. Finstad, R. Sivertsgård, N. Plantalech, P. A. Bjørn, and R. S. McKinley. 2007. Fjord migration and survival of wild and hatchery-reared Atlantic salmon and wild brown trout post-smolts. Hydrobiologia 582:99–107.

Ugedal, O., F. Kroglund, B. T. Barlaup, and A. Lamberg. 2014. Smolt – en kunnskapsoppsummering. Miljødirektoratet M-136:1–128.

Urke, H. A., T. Kristensen, J. V. Arnekleiv, T. O. Haugen, G. Kjærstad, S. O. Stefansson, L. O. E. Ebbesson, and T. O. Nilsen. 2013. Seawater tolerance and post-smolt migration of wild Atlantic salmon *Salmo salar* × brown trout *S. trutta* hybrid smolts. Journal of Fish Biology 82:206–227.

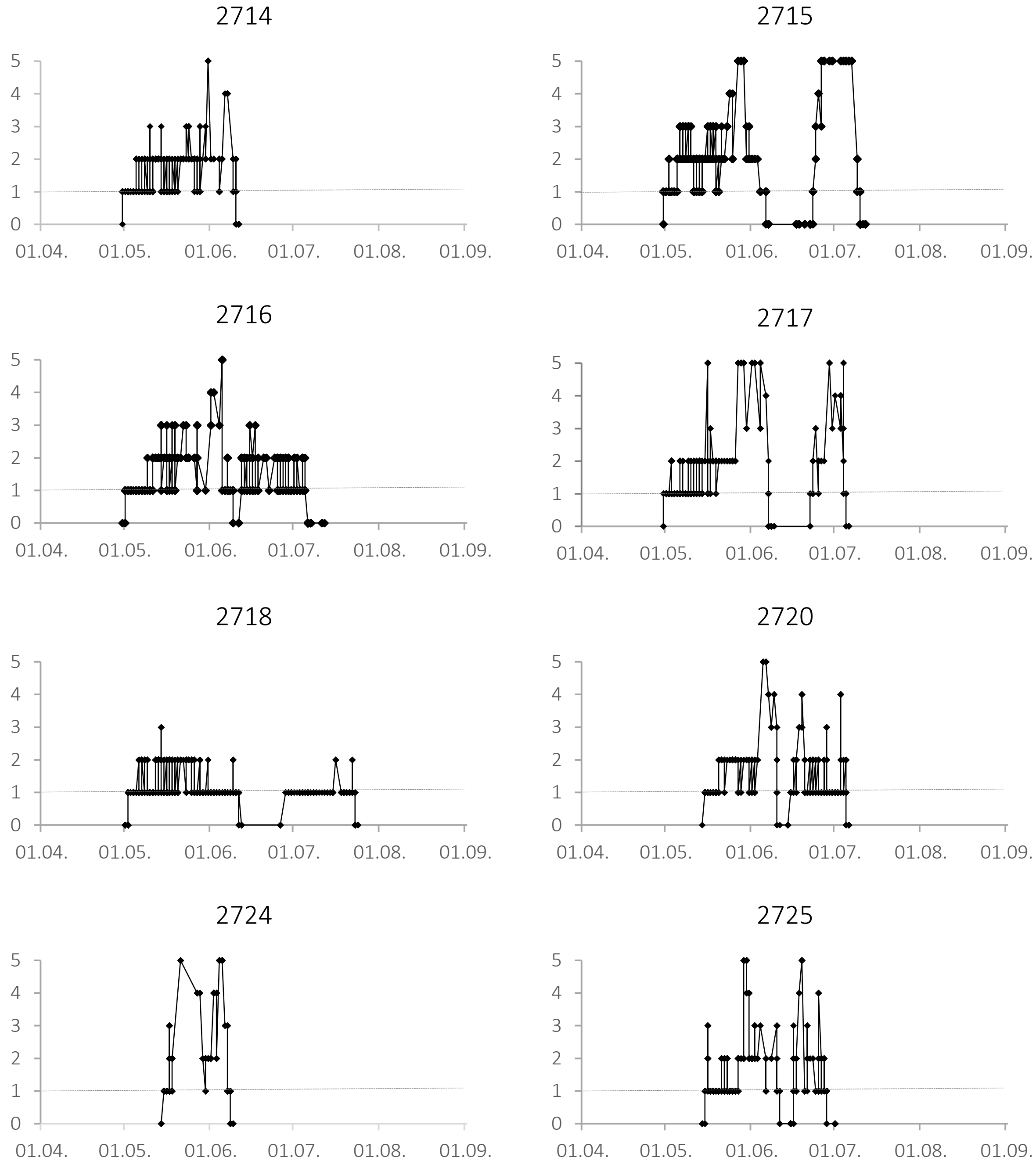
Werner, E. E., and D. J. Hall. 1988. Ontogenetic habitat shifts in bluegill: the foraging rate-predation risk trade-off. Ecology 69:1352–1366.

Wood, C. C., and C. M. Hand. 1985. Food-searching behaviour of the common merganser (*Mergus merganser*) I: functional responses to prey and predator density. Canadian Journal of Zoology 63:1260–1270.

Závorka, L., O. Slavík, and P. Horký. 2014. Validation of scale-reading estimates of age and growth in a brown trout *Salmo trutta* population. Biologia 69:691–695.

Appendix

Appendix 1: Migration pattern of each of the 26 returning individuals from sea entry to freshwater return. The numbers on the y-axis represent each zone, and x-axis date of year 2014. Zone 0 represents registrations in freshwater, zone 1 and 2 represent registrations in the inner parts of Hemnfjord, while zone 3 represents registrations in the Snillfjord area, and zone 4 the outermost part of the study area towards the open sea.



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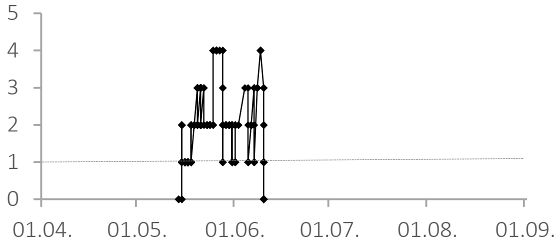

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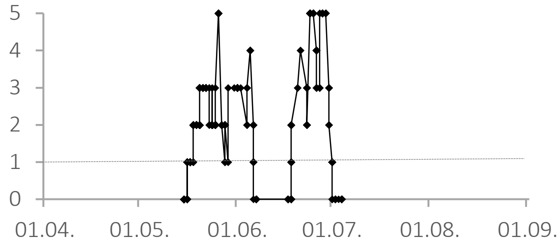

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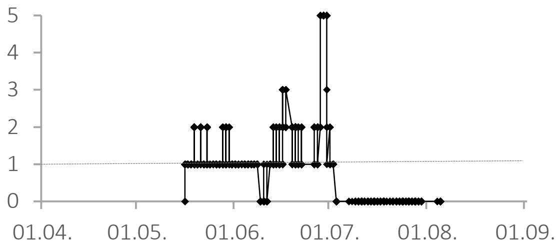

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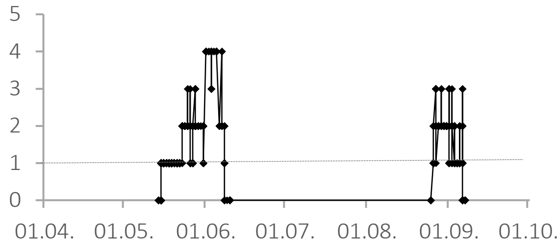

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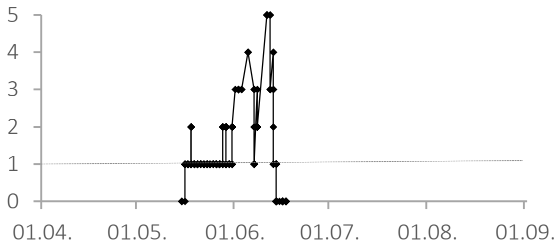

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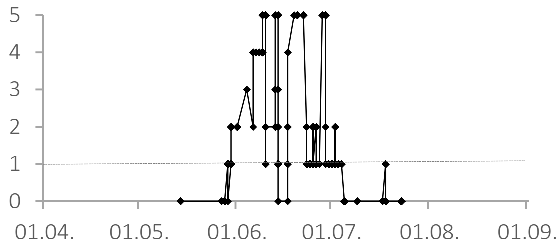

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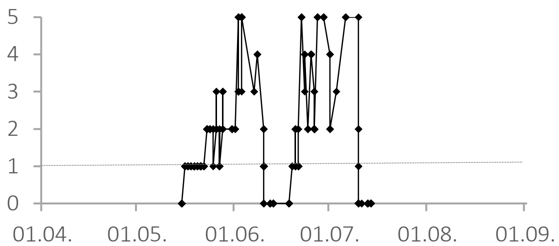

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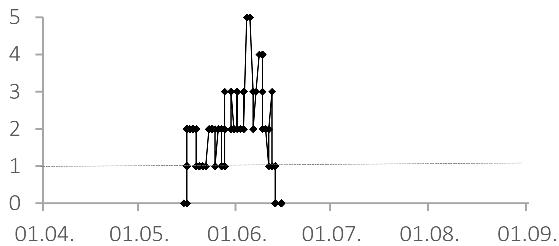

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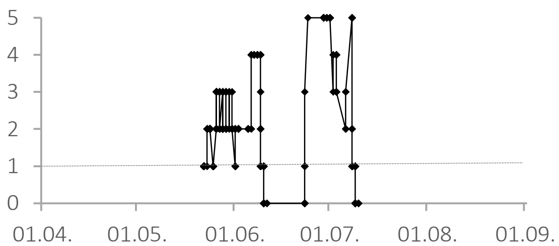

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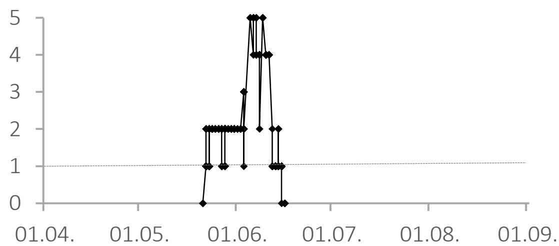

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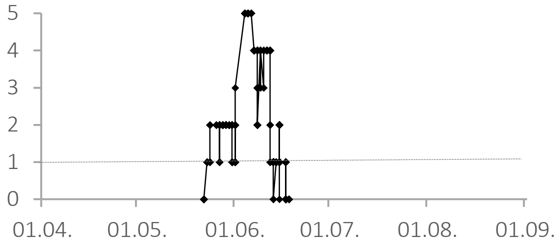

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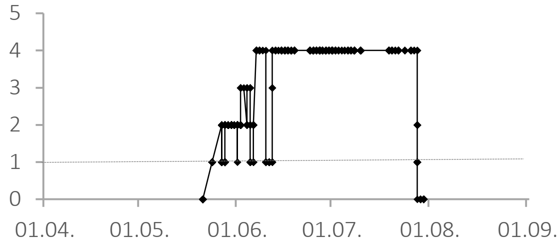

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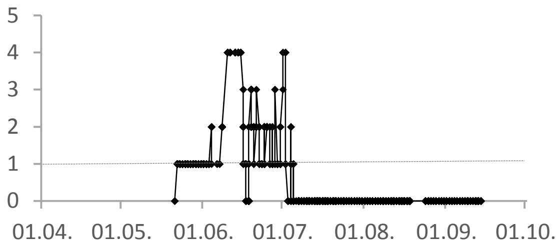

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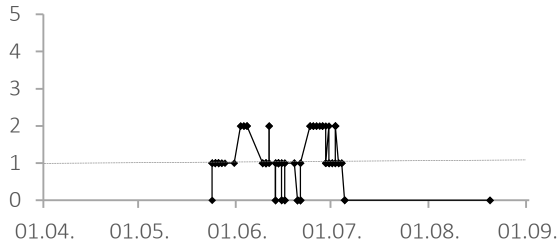

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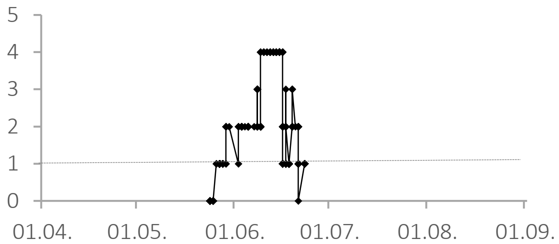

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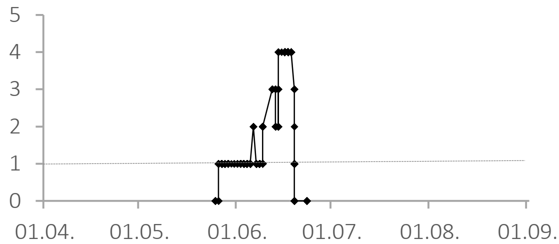

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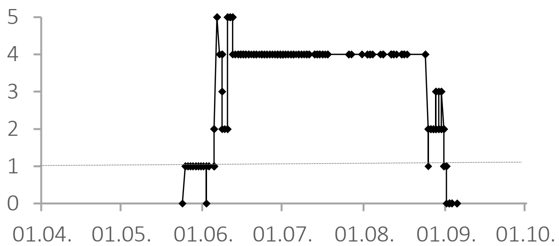

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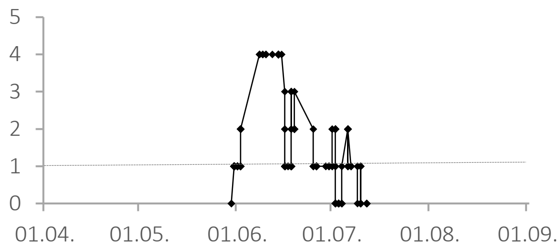
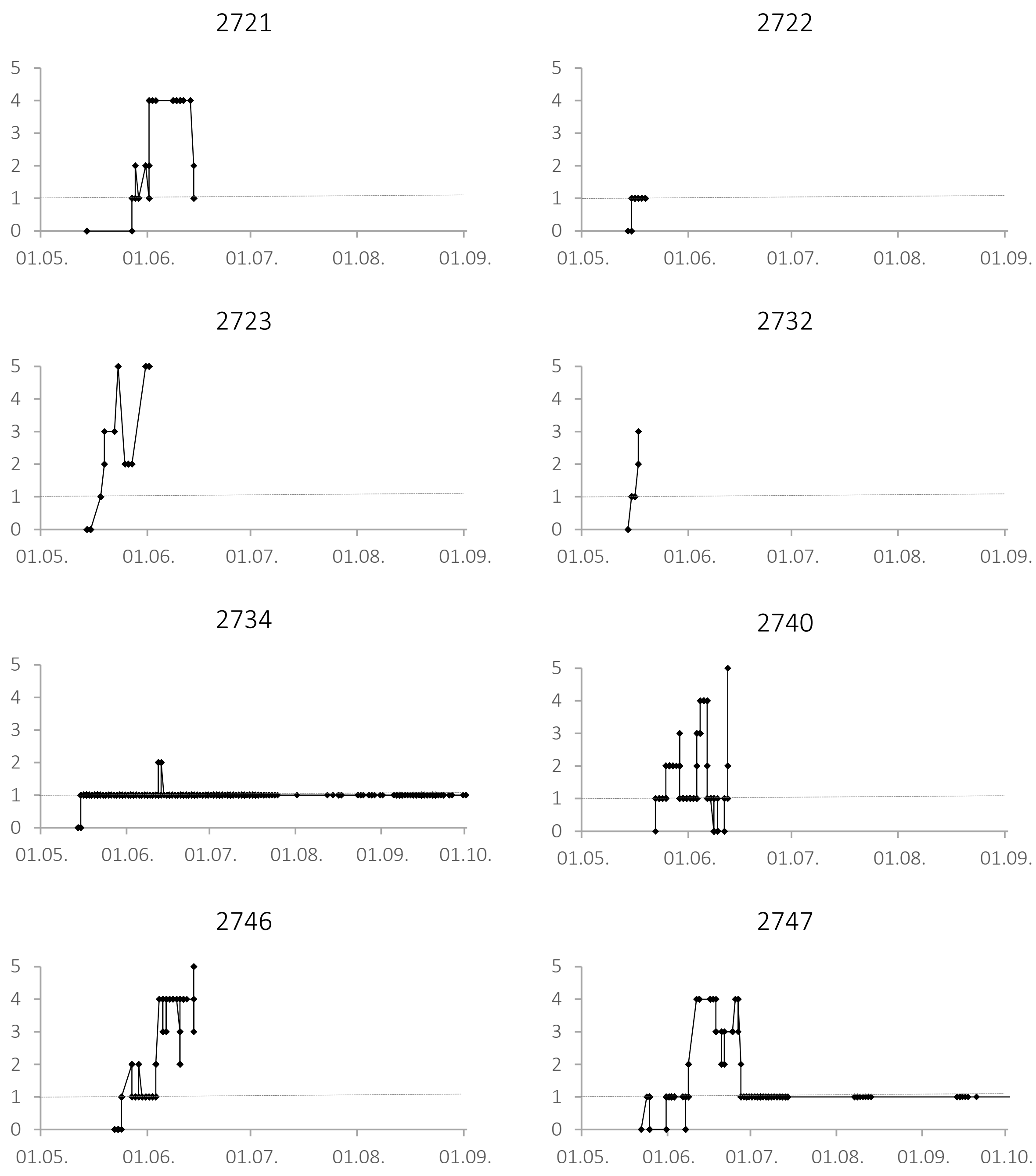
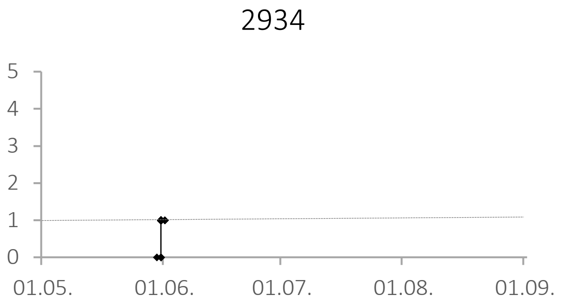
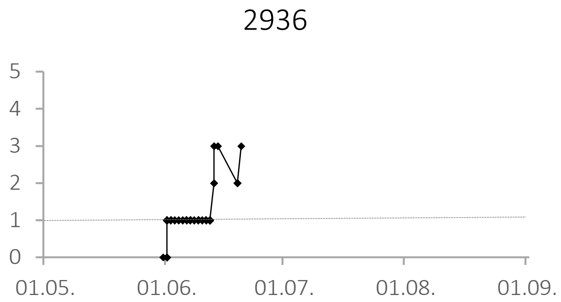


Appendix 2: Migration pattern for each of the 14 individuals lost during the study period. The numbers on the y-axis represent each zone, and x-axis date of year 2014. Zone 0 represents registrations in freshwater, zone 1 and 2 represent registrations in the inner parts of Hemnfjord, while zone 3 represents registrations in the Snillfjord area, and zone 4 the outermost part of the study area towards the open sea.




2934
5
4
3
2
1
0
01.05.
01.06.
01.07.
01.08.
01.09.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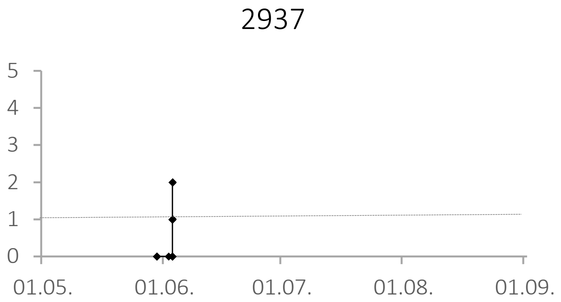
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3
2
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0
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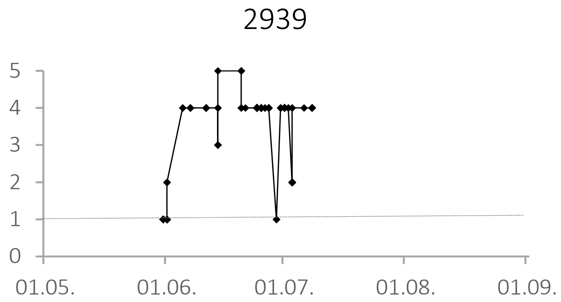
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3
2
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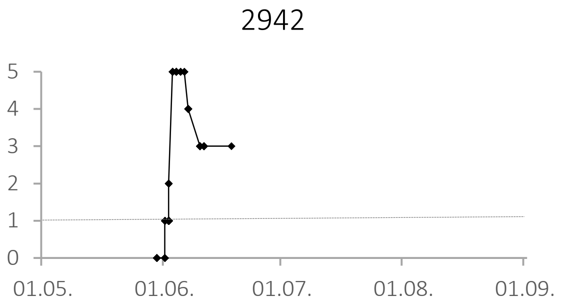
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2
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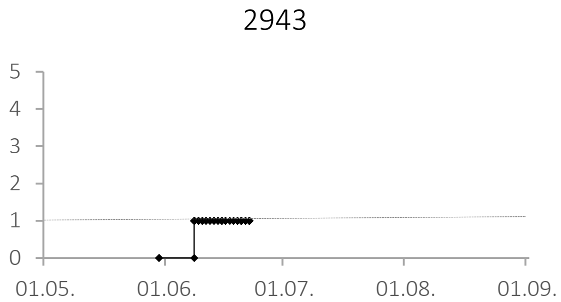
2943
5
4
3
2
1
0
01.05.
01.06.
01.07.
01.08.
01.09.

Appendix 3: Migration pattern from sea entry to freshwater return. These eight individuals performed two separately sea migrations from the study period 1 April – 1 September. The numbers on the y-axis represent each zone, and x-axis date of year 2014. Zone 0 represents registrations in freshwater, zone 1 and 2 represent registrations in the inner parts of Hemnfjord, while zone 3 represents registrations in the Snillfjord area, and zone 4 the outermost part of the study area towards the open sea.