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Spatial and temporal distribution and habitat use of sea trout *Salmo trutta* in a fjord system in Central Norway

- influence of morphology and life history on
marine behaviour

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Sammendrag:

Marin atferd og habitatbruk hos sjøørret *Salmo trutta* fra Søa-vassdraget og Snilldalselva i Sør-Trøndelag ble studert i 2012 og 2013. Fiskene ble merket med akustiske sendere, og ble fulgt ved hjelp av automatiske lyttestasjoner i fjordsystemet og tilknyttede vassdrag. Det ble funnet stor individuell variasjon i lengden av fjordoppholdet, hvor det korteste registrerte oppholdet var 7,1 dager, mens det lengste var 183 dager i månedene fra april til september. Det ble også observert stor variasjon i hvilke deler av fjorden som ble benyttet, hvor de innerste delene av både Snillfjord og Hemnfjord viste seg å være spesielt viktige oppholdssteder. Både fisk fra Søa og Snilldalselva hadde nemlig signifikant lenger oppholdstider i disse områdene sammenliknet med ytre områder. Gjennomsnittlig svømmedybde i perioden april – september (1,87 m) hadde signifikant variasjon mellom ulike habitattyper. Sjøørreten hadde dypere svømmedybde i litoralt og (2,11 m) og klippevegg-habitat (2,53 m) sammenliknet med pelagiske vannmasser (1,26 m). Sjøørreten hadde videre signifikant dypere gjennomsnittlig svømmeatferd om dagen (1,98 m) enn om natten (1,28 m). Svømmedybden ble også dypere utover sommeren, og økte linjert med stigende vanntemperatur. Det kan derfor tyde på at sjøørreten regulerer kroppstemperaturen sin ved å plassere seg i ulike vannlag. Mens noen individer holdt seg nær elven de ble merket i (< 4 km), gikk andre langt ut i fjordsystemet (> 16 km). Store individer (> 450 mm) så ut til å ha større sjanse for å gjennomføre lange vandringer. Fisk som gikk langt ut i fjordsystemet hadde lavere kondisjonsfaktor, og en tendens til å være større som smolt, være eldre og ha flere tidligere sjøvandringer. Fisk som vandret langt så videre ut til å benytte pelagiske områder i større grad enn fisk som holdt seg i indre deler av fjordsystemet. Dette tyder på at forskjellen som ble observert i vandringsdistanse kan være knyttet til ulike preferanser innen byttedyr, eller ulik atferd for å unngå predatorer. Forskjellene som ble observert i morfologiske trekk og livshistorie, tyder på at den marine atferden kan være en respons på dens tidligere miljø og dens tilstand når den går ut i sjøen. Dette har blitt foreslått i tidligere studier, hvor en har spekulert i om dette styres av variabler tilsvarende dem som avgjør om ung ørret smoltifiserer og vandrer ut i sjøen, eller blir værende i ferskvann. I praksis betyr dette at atferden til ørreten kan endres om miljøbetingelsene i sjøen forandres. Dette kan potensielt ha stor påvirkning for både de enkelte individene, men også for populasjonene som helhet. Det anbefales derfor å overvåke viktige miljøparametere over lang tid, og utføre flere studier på sammenhengen mellom morfologiske og livshistoriske trekk hos sjøørret, og hvordan slike trekk kan påvirke sjøørretens atferd i det marine miljø.

Summary:

Marine migration and habitat use of sea trout *Salmo trutta* from the watercourse Søa and the river Snilldalselva in Sør-Trøndelag in Central Norway was studied during summer in 2012 and 2013. Fishes were tagged with acoustic transmitters and their movements and behaviour recorded by automatic listening stations. Significant individual variation in the time spent in the marine environment was found, ranging from 7 days to 183 days during the months from April to September. The spatial distribution in the fjord system varied greatly between the tagged fishes. The innermost parts of the fjords near the tagging watercourses were particularly important areas for the tagged fishes. Both fish from Søa and Snilldalselva had significantly longer residence time in the inner areas compared other parts of the fjord system. Average swimming depth in the period from April to September (1.87 m) turned out to vary significantly between habitats. In littoral (2.11 m) and cliff habitats (2.53 m) the average swimming depth was significantly deeper than in pelagic areas (1.26 m), suggesting differences in prey selection or anti-predator behaviour between the various habitats. The average swimming depth was furthermore significantly deeper during day (1.98 m) than night (1.28 m). The sea trout had a progressively deeper swimming pattern from April towards late summer, positively correlating with water temperature, suggesting that the sea trout actively regulated its internal body temperature. While some individuals remained close to tagging watercourse (< 4 km) throughout the summer, other individuals migrated far out (> 16 km) in the fjord system. Large individuals (> 450 mm) seemed to be more likely to conduct long distance migrations than remaining in inner areas. Long distance migrants furthermore had poorer body condition in spring prior to migration, and tended to have greater length at smoltification and be older and more experienced migrants. Long distance migrants seemed to use pelagic areas more than short distance migrants, and tended to maintain pelagic swimming behaviour even when recorded in littoral habitat, suggesting that the migration distance might be linked to feeding behaviour. Furthermore, the observed differences in morphological characteristics and life history indicate, as suggested by previous studies, that the marine behaviour might be a continuum of a conditional strategy in partial migrating sea trout populations, affecting whether the sea trout remain in the innermost parts of the fjord, or migrate far out in the marine system. This implies that the marine behaviour of sea trout might be altered if the conditions in the marine environment change. Furthermore, variation in the marine environment might thus have great impact on an individual's growth and survival, and potentially alter the recruitment and population structure of sea trout stocks. In terms of conservation, the present study illustrates the importance of mapping the marine behaviour of sea trout, as the threats depends heavily on the marine areas it utilises. Gathering of long term data sets on marine environmental conditions, as well as more research on the underlying causes determining the wide range of the sea trout's marine behaviour is advocated, as it might prove to be essential for evaluating and modelling sea trout distribution, behaviour and main threats, and for identifying necessary conservation measures for Norwegian sea trout stocks.

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1 Introduction:

Brown trout (*Salmo trutta* L. 1758) is a salmonid species with indigenous populations in Europe, North Africa, and western Asia (MacCrimmon et al. 1970). However, because it's remarkable ability to disperse and colonize new areas, as well as its high reputation as a game fish and fine food (Klemetsen et al. 2003), brown trout is now introduced by man to all continents except Antarctica (MacCrimmon and Marshall 1968). With its wide ecological variability, brown trout is an opportunistic carnivore which has adapted to and found suitable niches in a variety of habitat types (Klemetsen et al. 2003). While some brown trout populations are top predators in huge lakes, reaching up to 18 kg of body mass by feeding on fish (Arnekleiv et al. 2007), other trout populations feed mainly on zooplankton, insects and benthic invertebrates (Klemetsen 1967). Brown trout is furthermore known for adapting temporary specialized feeding behaviour, and also undergoing niche shifts during its ontogeny (Klemetsen et al. 2003).

Brown trout often migrate to optimize its living conditions, either by migrating within its freshwater system, into brackish water or to the sea, seeking better feeding grounds and ultimately higher fitness (Jonsson and Jonsson 1993). Both migrants and resident individuals spawn together in fresh water during autumn (Campbell 1977, Jonsson 1985), and Hindar et al. (1991) found no genetic difference between resident and sea migratory individuals from the same spawning area. The reproductive gain of migration is more evident for females than males (Jonsson and Jonsson 1993), due to strong correlation between body size and egg production (Fleming and Gross 1990). The larger body size results in both higher number and better quality of eggs (Einum and Fleming 1999, Jonsson and Jonsson 1999), and furthermore gives the large females improved competitive ability for the best spots on the spawning grounds (Van Den Berghe and Gross 1989). For males, bigger body size implies competitive advantages in accessing females at the spawning grounds (Jonsson and Jonsson 1993). On the other hand, there is often high proportions of resident precocious mature males in migratory brown trout populations (Dellefors and Faremo 1988, Jonsson et al. 2001, Wysujack et al. 2009). With their small body size the resident males are often called satellites or sneakers, witch spawns with the migratory trout by sneaking into the spawning grounds between large territorial males and females, and represent a second reproductive strategy for males (Jonsson and Jonsson 1993). The

larger potential for increased fitness for females than males regarding sea migration, in addition to the satellite strategy amongst males, is probably why there is a higher proportion of females among migratory trout (Jensen 1968, Svärdson and Fagerström 1982, Jonsson 1985).

Anadromous individuals of brown trout (hereafter referred to as sea trout) usually migrate to sea during summer to feed, and return to fresh water for spawning and overwintering (Klemetsen et al. 2003). However, in watercourses with limited suitable overwintering grounds, populations are also known to utilize marine habitats during winter (Jensen and Rikardsen 2008, 2012). Disadvantages by sea migration is high energy cost related to smoltification, swimming and osmoregulation, as well as elevated risk of predation, illness and parasites (Jonsson and Jonsson 1993, Tully et al. 1993, Dieperink et al. 2001).

Sea trout populations in coastal rivers are often partially migratory, with some individuals remaining resident in fresh water while other become migratory (Jonnson 1989, Jonsson and Jonsson 1993). The appearance of a conditional strategy have been observed in rearing experiments, where parents have produced both resident and migratory offspring (Wysujack et al. 2009, Davidsen et al. in press), and furthermore in an experiment by Olsson et al. (2006), where changing the habitat of brown trout fry altered their tendency to migrate. Physiological characteristics as metabolic rate, growth rate, body size, energy surplus, sex and genetics are thought to influence the whether an individual adapt migratory or resident behaviour (Økland et al. 1993, Forseth et al. 1999, Garant et al. 2003, Wysujack et al. 2009). Wysujack et al. (2009) found that low feed availability increased the tendency of adapting morphological characteristics associated with migratory behaviour, and suggested that the environment, in combination with physiological and genetic factors, influenced the individual's probability of becoming migratory. This was furthermore strengthen by a rearing experiment conducted by Davidsen et al (in review), who found that starved individuals tended to be more migratory than fully fed individuals. The mechanisms controlling whether an individual becomes resident or migratory are yet to be fully understood (Acolas et al. 2012). However, it seems that an individual's tendency to migrate is partly genetically determined and partly caused by phenotypic plasticity (Jonsson and Jonsson 1993).

Previous studies on sea trout in the marine environment have revealed a wide variation in the behaviour, both in terms of migration timing and residence time (Jensen 1968, Jonsson 1985), migration distance (Berg and Berg 1987, Jensen et al. 2014) and prey choice (Knutsen et al. 2001, Rikardsen and Amundsen 2005). It has previously been suggested that behaviour and spatial distribution can vary within populations. Chernitsky et al. (1995) suggested that some trout resided in the river estuary of the River Varsina, while others migrate to the open Barents sea. Intra-population variation in marine migration distance were furthermore seen in a population studied by Villar-Guerra et al. (2013), where 47 % of the tagged sea trout post-smolts remained in the fjord, while 53 % migrated to the open Skagerrak sea. Here, the author suggested that the observed variation of migration distance might be caused by a continuum of partial migration, where there could be a decision-making point at sea entry, whether to stay in the fjord or migrate to the open sea (Villar-Guerra et al. 2013).

Most published marine biotelemetric tracking studies on sea trout, except studies conducted by Jensen and Rikardsen (2008, 2012) and Jensen et al. (2014) in fjords of northern Norway, have focused on post-smolt migration behaviour (e.g. Lyse et al. 1998, Moore et al. 1998, Thorstad et al. 2004). Hence, the aim of present study was to provide noble knowledge on the marine habitat utilization during the summer season of grown sea trout, which had conducted one or more previous marine migrations. Both spatial and temporary distribution were recorded throughout the summer using acoustic telemetry and individually coded transmitters, and the behavioural differences between short and long distance migrants in the marine fjord system were investigated. The observed marine migration patterns were compared to water temperature and salinity as well as the individuals morphological and life history characteristics, in order to address the hypothesis that such factors can influence the marine behaviour of the sea trout. The final aim of the study was to evaluate the implications of observed marine migration patterns for the population dynamics, as well as assessing the implications for future conservation of the Norwegian sea trout stocks.

2 Materials and Methods

2.1 Study area:

The study was performed in the two fjords of Hemnefjord and Snillfjord in Sør-Trøndelag county, central Norway, making the study area ranging over 60 km^2 of sea surface and 65 km of shoreline (fig. 1). This fjord system has several watercourses housing Atlantic Salmon (*Salmo salar* L. 1758) and sea trout. Hemnfjord and Snillfjord contain various infrastructure and industry. There are three aquaculture locations breeding salmon for the aquaculture industry, and two facilities for salmon smolt production. A silicon production plant, with an attached wharf is located next to Hemnfjord. The innermost part of Hemnfjord houses the community center of Hemne municipality, and the innermost part of Snillfjord houses the community center of Snillfjord municipality.

The sea trout used in this study were tagged in the Søa watercourse in Hemne municipality, and the river Snilldalselva in Snillfjord municipality (fig. 1). Søa watercourse has a drainage basin of 113 km^2. The anadromous section of Søa watercourse includes the lake Rovatnet, which with its surface area of 7.65 km^2 offers suitable overwintering grounds for its sea trout population. The stream Eidselva and the stream Leneselva are the largest streams draining to the lake Rovatnet, and these are considered major spawning grounds for the sea trout in the Søa watercourse. The river Søa, witch drains from Rovatnet to Hemnfjord, is 2 km long and is also known to contain sea trout spawning grounds. The Søa watercourse is regulated, supplying water to Søa power plant in Hemne municipality. The water going through this power plant has its outlet next to Hemnfjord, about 2 km from the estuary of the river Søa.

The river Snilldalselva has a drainage basin of 42.7 km^2 and an average yearly flow rate of 1.4 m^3 per second. The anadromous section is 4.8 km long, due to a physical migration barrier. Snilldalselva shares a common river estuary with the river Bergselva. Bergselva has a drainage basin of 69.3 km^2, an average flow rate of 2.1 m^3 per second, and an anadromous stretch of 1.1 km. Both Snilldalselva and Bergselva is highly influenced by floods, and with few deep pools these rivers is considered as poor overwintering grounds for its trout populations.

2.2 Environmental variables

Three temperature and salinity recorders (DST milli-CT, www.star-oddi.com) were deployed in the fjord system, one approximately 1 km out from the river estuary of Søa in the inner area of Hemnfjord (Array H1, fig. 1), one about 600 meters from the river estuary of Snilldalselva in the inner area of Snillfjord (Array S1, fig. 1), and one at the center ALS of the outermost ALS in the outer parts of the study area array (Array H4, fig 1). The temperature and salinity recorders placed in the fjord system were mounted below the buoys of automatic listening stations, at approximately one meter depth, in order to continuously monitor the temperature and salinity in the inner and outer parts of the study area.

2.3 Fish tagging and acoustic transmitters

Five groups of sea trout were captured and tagged with acoustic transmitters during the period from 12 April 2012 – 12 May 2013, see table 1. The first group (HS12) consisted of 30 sea trout that were caught and tagged in the outlet of the lake Rovatnet (fig.1) in the period from 12 – 14 April 2012. The second group (HA12) included 21 sea trout which were caught and tagged near the outlets of the stream Eidselva and the stream Leneselva in the lake Rovatnet (fig. 1), during 17 - 18 September 2012. Third group (SA12) consisted of 20 sea trout which were caught and tagged in the river and estuary of Snilldalselva (fig. 1) in the period from 19 – 20 September 2012. Forth group (SS13) included 15 sea trout which were caught and tagged in the estuary of Snilldalselva (fig. 1) in the period from 22– 23 April 2013. Fifth group of 30 individuals (HS13) were caught and tagged in the estuary of the river Søa (fig. 1) in the period from 3 – 12 May 2013. See table 1 for natural length and body mass of the tagged sea trout at the time of tagging.

Table 1: Tagging groups, tagging position, number of individuals, natural length (L_N) and body mass of tagged fish.

Tagging group	Date	Tagging position	n	Natural length (mm)		Body mass (g)	
				Mean ± SD	Range	Mean ± SD	Range
HS12	12-14 April 2012	Søa (lake Rovatnet)	30	396 ± 61	335 - 600	586 ± 287	330 – 1600
HA12	17-18 September 2012	Søa (lake Rovatnet)	21	412 ± 121	270 - 700	866 ± 908	210 – 3660
SA12	19-20 September 2012	Snilldalselva (river and estuary)	20	392 ± 75	310 - 650	581 ± 419	310 – 2180
SS13	22-23 April 2013	Snilldalselva (estuary)	15	381 ± 53	275 - 460	620 ± 286	220 – 1210
HS13	3-12 May 2013	Søa (estuary)	30	415 ± 56	330 - 580	699 ± 339	300 – 1970

All groups were caught using gillnets of 35-42 mm mesh width, which were checked continuously to reduce hang time in the net, and related stress and chance of injuries to the fish. The fishes were released from the nets using scissors, to prevent damage on gills, skin and scales. Prior to tagging the captured fishes were kept in a net cage in a relatively calm part of the river or shoreline.

The sea trout caught in 2012 were implanted with individually coded acoustic transmitters (HS12; n = 15 Thelmabiotel AS (www.thelmabiotel.com) model MP-9-long, L_N range 335 - 440 mm, n = 15 Thelmabiotel AS model MP-13, L_N range 350 - 600 mm. HA12; n = 10 Vemco Inc. (www.vemco.com) model V9-2x, L_N range 270 - 380 mm, n = 11 Vemco model V13-1x, L_N range 370 - 700 mm, SA12; n = 5 Thelmabiotel AS model MP-9-long, L_N range 310 - 400 mm, n = 6 Thelmabiotel model MP-13, L_N range 340 - 650 mm, n = 9 Vemco Inc. model V13-1x, L_N range 340 - 440 mm), where tag size was chosen depending on length and body condition of the fish. The fish caught in 2013 were tagged with individual coded acoustic transmitters, which in addition to presence, transmitted swimming depth (HS13; n = 29 Thelmabiotel AS model ADT-9-long, L_N range 330 - 580 mm, SS13; n = 15 Thelmabiotel AS model ADT-9-long, L_N range 320 - 460 mm).

Prior to insertion of the acoustic transmitter, the fish were sedated with 2-phenoxy-ethanol (EC No 204-589-7; SIGMAChemical Co., USA; www.sigmaaldrich.com) of a concentration of 0.5 ml l^{-1}. When reaching full anaesthesia, it was transferred to an operation tube, where a 1.5 - 2 cm cut was made in the body cavity on the ventral surface anterior to the pelvic girdle and the sterilized tag were inserted. The incision was closed using two independent monofilament sutures (RESORBA Wundversorgung GmbH & Co. KG, Germany; www.resorba.com; 5/0 Resolon). During the operation fresh water were pored over the gills. After sewing the cut, the tagged fishes were placed in a tub with fresh water for recovering. When recovered, fishes were released in a relatively calm part of the river or shoreline. The tagging operation where done in 3 – 5 minutes. The sedation and recovering tub were covered to reduce the stress by reducing light exposure.

2.4 Tracking of tagged fish

The tagged fishes were tracked using a total of 51 automatic listening stations (ALS, Vemco Inc. model VR2W and VR2). A total of 40 of the ALSs were deployed in the fjord system, while the remaining 11 ALSs were placed in attached watercourses, as shown in figure 1.

A portion of the ALSs were deployed as arrays, in order to detect all individuals migrating between different parts of the study area (Array H1, H2, H3, H4, S1, S2, S3, fig 1). An ALS array was deployed about 1 km from the river mouth of the river Søa (Array H1, 4 ALSs, fig. 1). Two arrays were deployed the outer part of the fjord system (H3 and H4, 5 ALSs each, fig. 1), and three arrays were deployed in Snillfjord (S1, S2 and S3, 2-3 ALSs, fig 1). In addition to the ALS arrays, automatic listening stations were deployed at three salmon farms, and near the water outlet from the production facility for salmon smolt in Snillfjord (fig. 1). Two ALSs were deployed at the silicon factory wharf in Hemnfjord, and one ALS was deployed near the water outlet of Søa power plant (fig. 1). The remaining stations were deployed along the shoreline and in estuaries of various watercourses (11 ALSs), and in a pelagic part of Hemnfjord (3 ALSs), see figure 1.

The ALSs deployed in the fjord system were mounted on 14 mm polyester ropes 5 meters below buoys at the sea surface. Anchors with weights ranging from 50 to 100 kg were used to avoid drifting and keep buoys in position. The ALSs at the salmon farming locations (fig. 1) and a boat harbor in the innermost part of Hemnfjord (fig. 1) were mounted on 14mm ropes attached to floating stages, while the ALS on the wharf of silicon production plant and at the smolt production facility in Snillfjord were mounted on 14 mm ropes attached to the quay structures. As the ALSs mounted on buoys, these ALSs were deployed 5 meters below the sea surface. The ALSs deployed in rivers were mounted on 50 mm iron pipes witch were hammered into the riverbed. The automatic listening stations deployed in the study area were part of the Ocean Tracking Network www.oceantrackingnetwork.org.
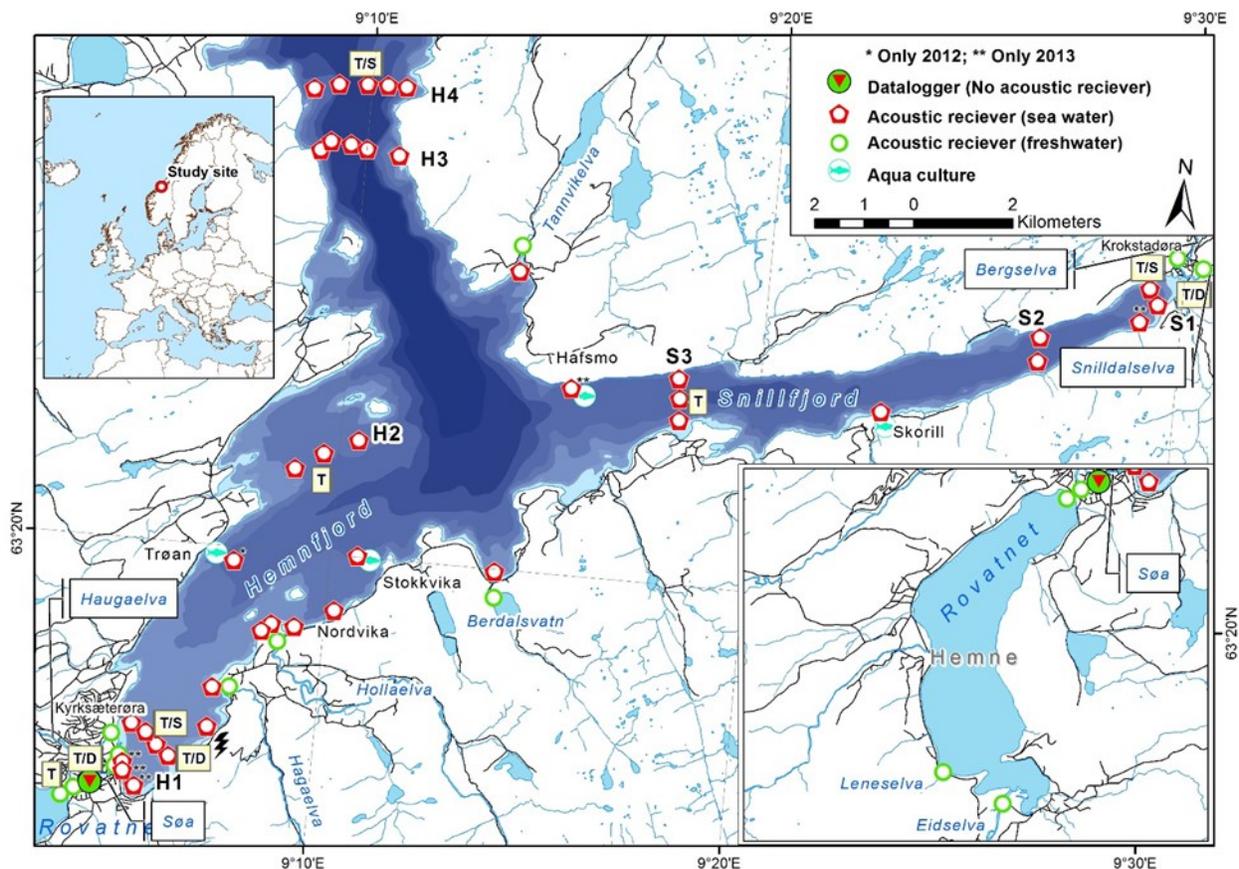
Figure 1: Map of study area, showing position of deployed ALS in freshwater (green circles), ALS in the fjord (Red polygon) and temperature and salinity recorders (T/S symbols). Fish symbol indicate position of aquaculture locations and smolt production facility (Skorill). H1, H2, H3, H4, S1, S2 and S3 indicate position of ALS arrays.

2.5 Receiver performance:

Receiver range was measured at the central ALS of array H1 (fig. 1) at 22.08.2013 (calm, clear weather, high tide) by deploying (Thelmabiotel AS, model ADT-9-long, 146 dB re 1uPa @1m) at 3 and 5 meters depth, increasing distance to the ALS in steps of 50 meters. Here, the ALS range was found to be approximately 300 - 350 meters. The acoustic transmitter type used in the range test was considered to have the shortest range of the various transmitters used in the present study.

The detectability at ALS arrays H1, S2, S3 and H3 (fig. 1) were further investigated by controlling if any fish had passed the array without being registered. Here, all the individuals were registered at the investigated arrays prior to first registration outside the arrays, indicating that the arrays successfully detected passing fish, and were consequently considered a reasonable assumption in later data analysis.

2.6 Scale sample analysis

In addition to measuring body mass and length, DNA and fish scales were sampled during the tagging procedure, for later analysis. In the present study, the scales were analysed to investigate the previous life history of the tagged individuals.

The most informative scales from each individual were selected using a light stereoscope. Replacement scales with annual rings missing were excluded. The selected scales were placed on a 1 mm Lexan plate, making a print in the Lexan of the scales using a pressing iron. The Lexan prints were pictured using a computer-controlled stereoscope. Using these pictures the age, age at smoltification and number of previous times at sea were determined by the patterns of annual rings. Using the length of the scale and relative length between each winter growth zone, the annual growth and body length at smoltification were estimated. Scale growth was assumed to be proportionally linked with length growth, as described in Lea-Dahls method (Dahl 1907, Lea 1910). Uncertain values of age, length of smoltification or annual growth, were excluded from relevant statistical analyses.

Due to variable scale quality, there were some uncertainties in readings of a portion of the scale samples. This concerned mainly age of smoltification, previous times at sea, and to some extent

the true age of the fish. In these cases, two or three alternate values were noted during the scale reading. In order to maximizing sample size, results with minor uncertainty were included in analysis. For further proofing of the scale results, a subset of scale pictures were sent to project partners at the Norwegian Institute for Nature Research (NINA) and the Technical University of Denmark (DTU). Here, they analysed the sub sample, only given the fish length and tagging date. These results were compared with the estimates in present study. Both estimates in present study, and subsample analysis from NINA and DTU were compared to parr sampling results collected in Søa watercourse by Koksvik et al (2003), and unpublished parr sampling done by the NTNU University Museum in the Søa watercourse and the river Snilldalselva, in order to draw conclusions about the most probable scale sample estimates.

2.7 Data Analysis

2.7.1 Data filtering prior to analysis

The initial number of registrations in the present study was 5 147 075, prior to filtration of false registrations. The filtering started by removing all registrations containing false fish ID's. Here, a total of 1360 (0.03 %) registrations were considered as false and excluded from further data analysis. Microsoft Access 2013 (www.microsoft.com) where further used to prepare the ALS data prior to statistical analyses. Data from the two ALS in the outlet from the river Søa, Søa power plant and the three innermost stations in Snillfjord were considered to contain high frequencies of false data, due to high number of simultaneously visiting tagged fishes. A visual basic coded filter was therefore constructed in Microsoft Access and applied to the data from these ALSs. The filter required at least two registrations from a tagged individual within a time span of 10 minutes to accept the registrations as true. The filter considered 46 223 (0.90 %) of the registrations as false, and these were excluded from relevant analyses. After filtering, Microsoft Access was further used to sort and extract relevant data prior to statistical analysis.

2.7.2 Statistical analysis:

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

2.7.3 Assigning area zones to ALSs

The ALSs were assigned different area zones codes based on their geographic location (fig. 2), in order to investigate residence in different parts of the fjord in later analysis. The Inner Hemnfjord area included ALSs deployed in array H1 and the innermost marine ALSs in Hemnfjord (zone 1, pink area fig. 2). The Inner Snillfjord area consisted of the three innermost marine ALSs in the Snillfjord, and ALSs at array S2 (zone 2, orange area fig. 2). Central Snillfjord included the ALSs deployed at Skorill and array S3 (zone 3, green area fig. 2). Central Hemnfjord included all marine ALSs further out than area zone 1 – 3, with an outer boundary at array H3 (zone 4, yellow area fig. 2). Outer areas consisted of ALS array H4 (zone 5, blue area fig. 2). All ALSs in freshwater were defined as area zone 6 in order to distinguish between marine and freshwater residency in later analyses.
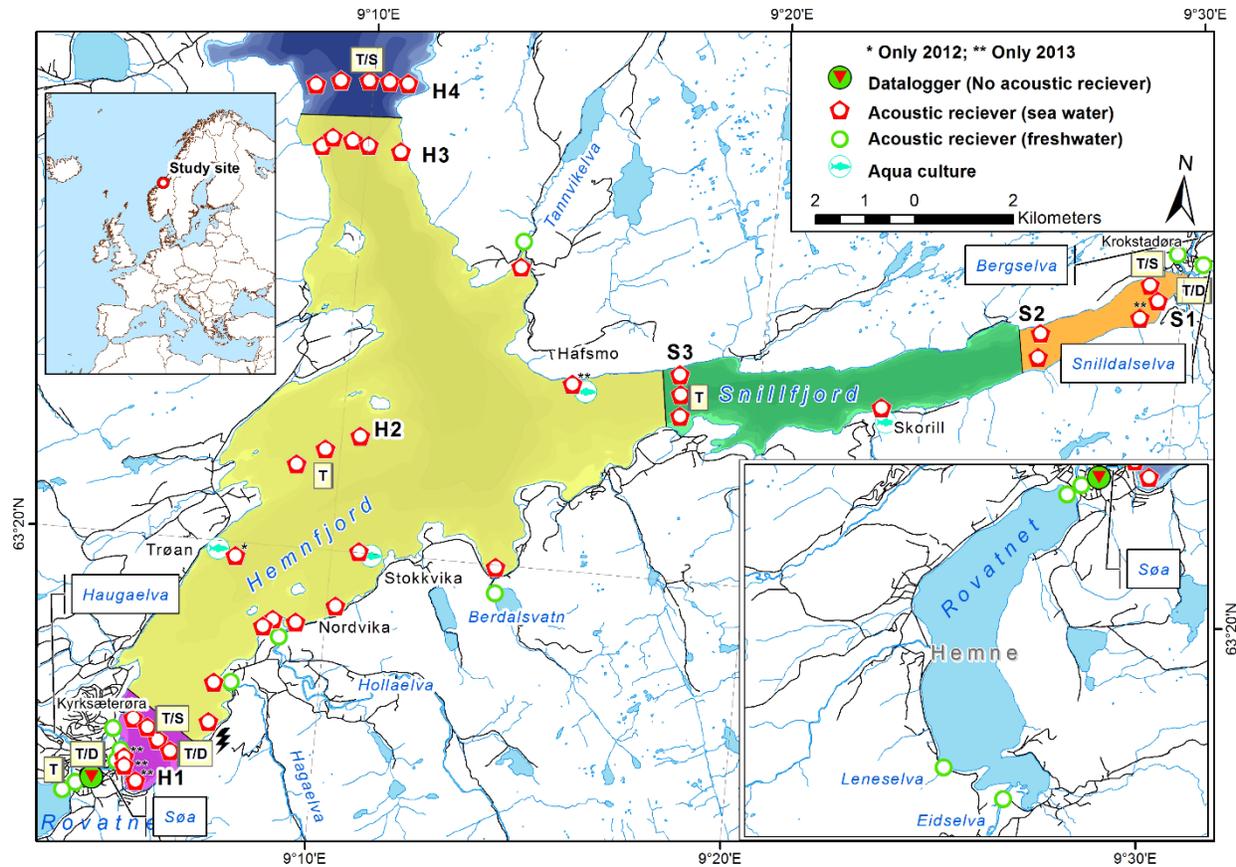
Figure 2: Defined marine area zone codes for ALS deployed in the fjord system; inner Hemnfjord (zone 1, pink area), inner Snillfjord (zone 2, orange area), central Snillfjord (zone 3, green area), central Hemnfjord (zone 4, yellow area) and outer areas (zone 5, blue area). Red pentagon symbols represent marine ALS, green circle symbols represent ALS deployed in freshwater.

2.7.4 Calculating marine residence time

Residence time at each station was calculated as the time from the registration at a given ALS to the next registration on any ALS. The calculation was carried out using the following set of rules:

1. Transition to a new zone occurred when the fish was registered at a station within the nest zone.
2. 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 an ALS in the previous zone.
3. If transition to a zone further into the fjord, the residence time in the next zone started at the time of the first registration at an ALS in the next zone.
4. If transition into freshwater, the freshwater residence started at the time of the last registration at a marine ALS.
5. If transition from freshwater to fjord zones, the fjord residence started at the first registration in the fjord zone.

The chosen rules for calculating residence time implied a set of assumptions. First, all fishes were assumed to be registered by the ALS arrays when passing. Furthermore, the fishes were assumed to be registered at an ALS when moving into a new fjord zone. ALSs in the estuaries and river mouths were considered as part of the fjord. The registrations at the ALS at the Søa power plant were excluded from residency analyses, due to its artificial nature of hydro peaking and water flow.

In order to apply the described rules for estimating zone residence, the transaction time between different zones had to be addressed to the correct zone. Using the defined area zone codes (fig 2), Microsoft Access were used to select the last registrations were the fish moved from one to another zone, of higher zone code number. The ALS ID of these (933 registrations) were transferred to the ID of the next ALS, in order to allocate the residence time of the transition time interval according to the estimation rules listed above.

The residence time was used to calculate total marine residence time, as well as the residence time in the different fjord zones for the fishes during the summer. Individuals that were lost during the study period 1 April – 1 October, in either 2012 or 2013, were excluded from the residence time analysis. In order to be considered as not lost, the fish had to either be registered after the study period at any ALS, or seen migrating to Søa or another watercourse after its marine migration. For the HS13 and the SS13 tagging group, the estimated marine residence were considered as minimum estimates, due to capture and tagging in the estuary of Søa (HS13) and the estuary of Snilldalselva (SS13).

2.7.5 Investigating the use of pelagic water masses

The arrays containing both pelagic and near shore ALS (array H1, H3, H4 and S3 fig. 1) were used to investigate the importance of pelagic water masses for the tagged sea trout. Here, the proportional number of registrations across the ALSs at the array were investigated for each fish. This was considered to give a rough estimate of relative preference between littoral or pelagic water masses, and was investigated both for the period 1 April – 1 October either in 2012 (HS12 tagging group) or 2013, and furthermore for the monthly variation within this period.

2.7.6 Defining habitat at ALS locations

The habitat surrounding each ALS (the area within its range) was categorised as either freshwater habitat, estuarine habitat, littoral habitat, cliff habitat, pelagic habitat or salmon farm, see figure 3. All ALSs deployed in freshwater with no influence of seawater, were defined as freshwater habitat (fig. 3, green circles). ALSs placed near river- and stream mouths in the fjord, likely to influenced by freshwater, where categorized as estuarine habitat (fig 3. green pentagon). ALSs deployed near the shore, or in areas with shallow water (< 10 meters) where the sea trout was likely to feed close to the bottom within the range of the ALS, were defined as littoral habitat (fig. 3. yellow pentagon). ALSs deployed over deep water with steep cliffs along the shoreline within the ALS range, were described as cliff habitat (fig. 3, pink pentagon). ALSs deployed over deep water, without coastline or shallow areas (< 25 meters) within the ALS range, were defined as pelagic habitat. ALSs deployed at aquaculture locations were categorized as salmon farm, and excluded from habitat specific analysis due to low number of fish detections (HS13, 1 May – 1 October 2013, $n = 3$, mean number of registrations = 3.7). The Søa power plant was defined as estuary habitat, due to its output of freshwater within the range of the ALS.
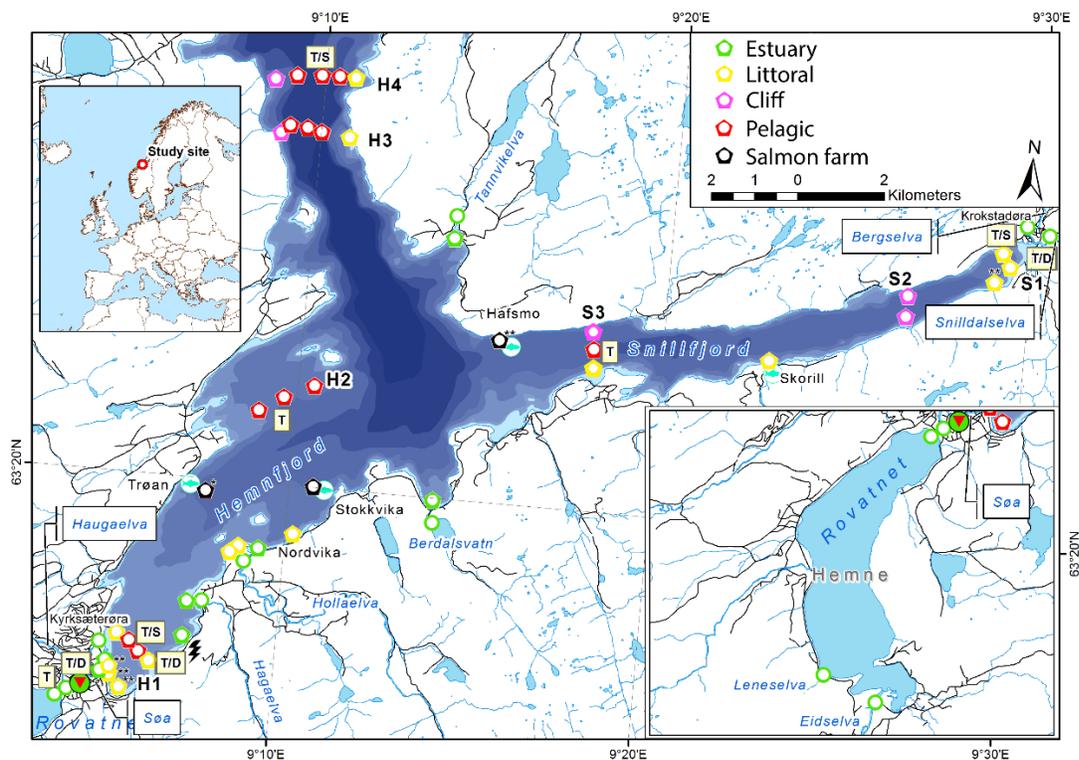
Figure 3: Defined habitat type at ALSs deployed in marine and estuarine waters. Pentagon symbols represent ALSs deployed in estuarine (green), littoral (yellow), cliff (pink), pelagic (red) and salmon farm (black) habitat. Green circle symbols represent ALSs deployed in freshwater habitats.

2.7.7 Swimming depth of tagged fish

The data of swimming depth of the SS13 tagging group was investigated during the period of 1 April – 1 October 2013. For the HS13 tagging group, the data collected on swimming depth was investigated from the time of tagging to 1 October 2013. The swimming depth was compared for the different defined habitats, and for day and night. Day time was defined as the time between sunrise and sunset. The timing of sunrise and sunset were calculated using the sunrise/sunset calculator of the Astronomical Applications Department of the US Naval Observatory (aa.usno.navy.mil) for the coordinates 63°22'00.0"N 9°13'00.0"E. The calculated daily timing of sunrise and sunset were imported to Microsoft Access and linked with the ALS registrations of the SS13 and HS13 tagging group.

The temperature measurements from the temperature and salinity loggers was used to calculate correlation between water temperature and the swimming depth of the fishes tagged during spring 2013, for the period 1 May – 1 October 2013. Here, the average daily temperatures from the loggers was combined to a mean daily temperature, which were correlated to the median average swimming depth each day by making a linear model using R.

The swimming depth of short, medium and long distance migrants was compared when the fishes were recorded in littoral or pelagic habitat. In these analyses, the average swimming depth for the period 1 May – 1 June was applied.

2.7.8 Defining tagged fish as short, medium and long distance migrants

The tagged fish were categorised as either short, medium or long distance migrants according to witch ALSs they were registered at during the period 1 April – 1 October in either 2012 (HS12 tagging group) or 2013, see figure 4. Short distance migrants were only registered in the innermost part of the fjord near its tagging location (fig. 4, green area). Medium distance migrants were registered stations at stations in the central parts of its inner tagging fjord (fig. 4, yellow area), while fishes observed outside this area were considered as long distance migrants (fig. 4, blue area or neighbouring fjord area). Fishes that were lost prior to 1 July in either 2012 or 2013, or were not detected at any ALSs described as long migration distance, were excluded from the analysis considering short, medium and long distance migrants. For residence time analysis for short, medium and long distance migrants, the same individuals as in the general analysis of residence time were used.
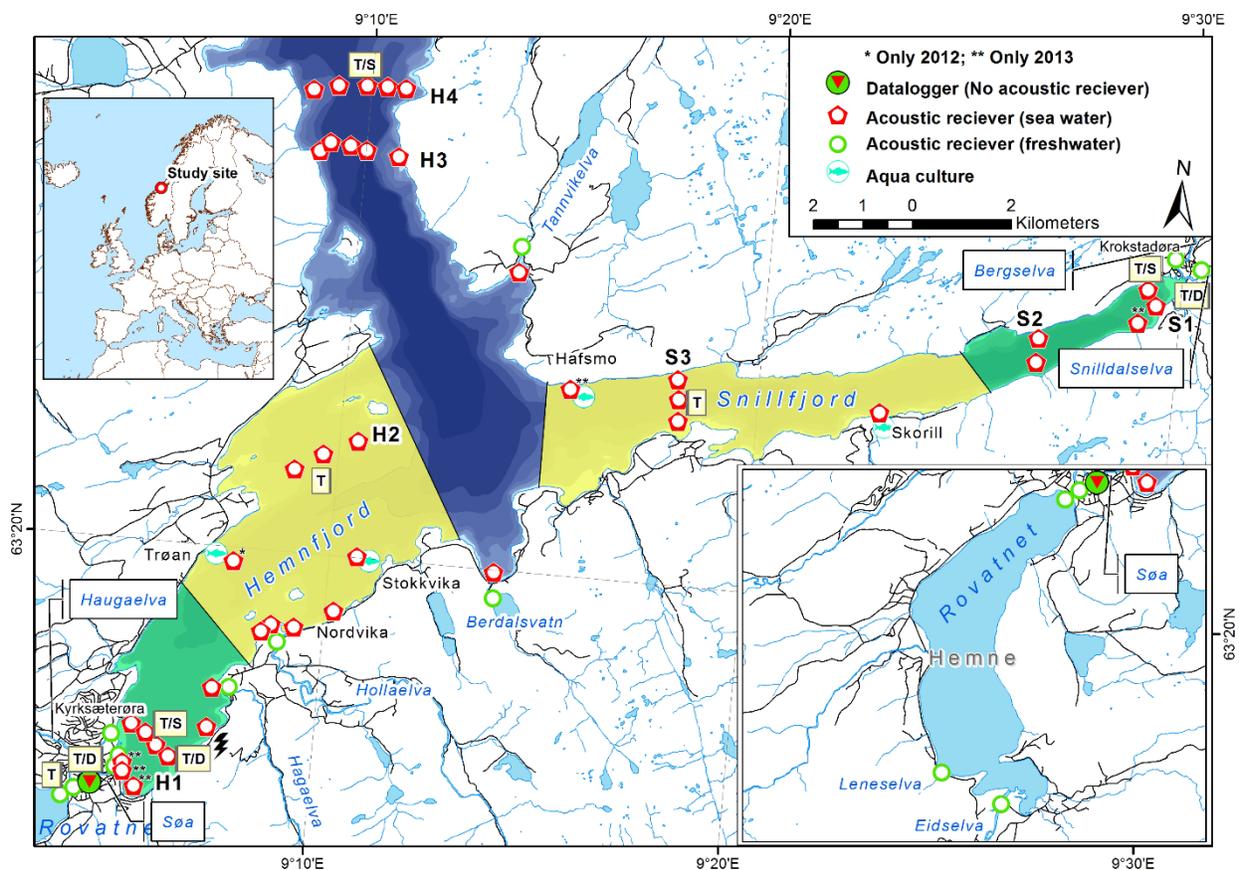
Figure 4: ALSs in green zone in fjord of tagging defined as short migration distance. ALSs in yellow zone in fjord of tagging defined as medium migration distance. ALSs deployed outside green and yellow zone in fjord of tagging defined as long migration distance.

3 Results:

3.1 Environmental parameters

The deployed salinity and temperature loggers at one meter depth revealed that the water temperatures in the outer part of the study area (mean = 10.58 °C, SD ± 2.57 °C) generally had lower water temperatures than the inner part of Hemnfjord (mean = 11.00 °C, SD ± 3.00 °C) and Snillfjord (mean = 11.05 °C, SD ± 3.04 °C) during the period of 1 May – 1 October 2013 (fig. 5). The water salinity was relatively high in both the outer areas (mean = 23.81 ‰, SD ± 2.04 ‰), the inner Hemnfjord (mean = 26.80 ‰, SD ± 7.64 ‰) and the inner Snillfjord (mean = 22.15 ‰, SD ± 4.75 ‰) during the study period.
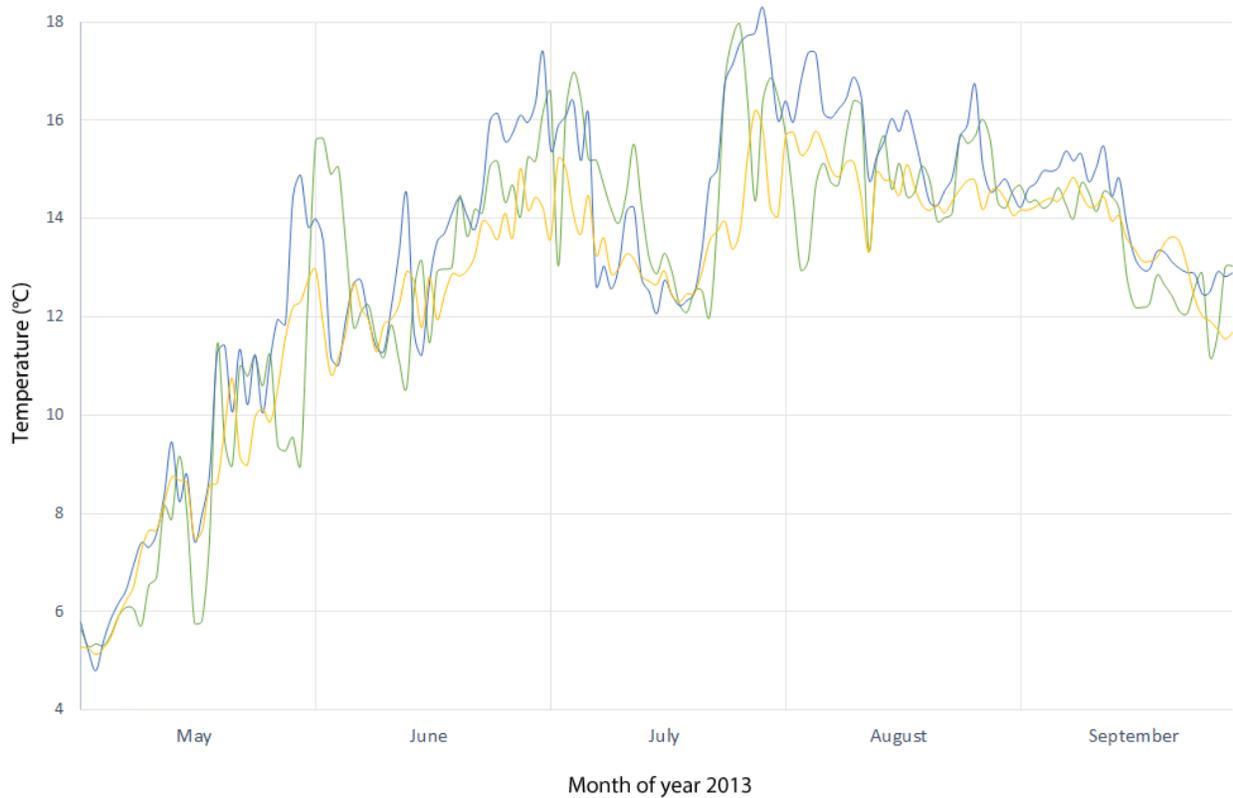
Figure 5: Mean daily temperatures (°C) at 1 meter depth in inner part of Hemnfjord (blue), inner part of Snillfjord (green) and in outer part of the study area (yellow) in the period 1 May – 1 October.

3.2 Biological characteristics

During the study period 1 April – 1 October, in 2012 for the HS12 tagging group, and in 2013 for the other tagging groups, 51 of the initial 115 tagged fishes were lost. The reasons for loosing track of these individuals were in most cases not known. However, 15 individuals were reported captured and killed by local anglers. Furthermore, 8 individuals tagged in the lake Rovatnet were never recorded to leave the lake post tagging, while 4 individuals from the tagging groups migrated out of the study area and were never recovered.

There was no significant difference in natural body length among tagging groups at capture (ANOVA, $n = 64$, $P = 0.091$), for the fish tracked throughout the period 1 April – 1 October in either 2012 (HS12 tagging group) or 2013, see figure 6. However, combining groups revealed that fishes tagged in Søa had a significantly longer natural body length than the fishes tagged in Snilldalselva (*t*-test, $n = 64$, $P = 0.019$).
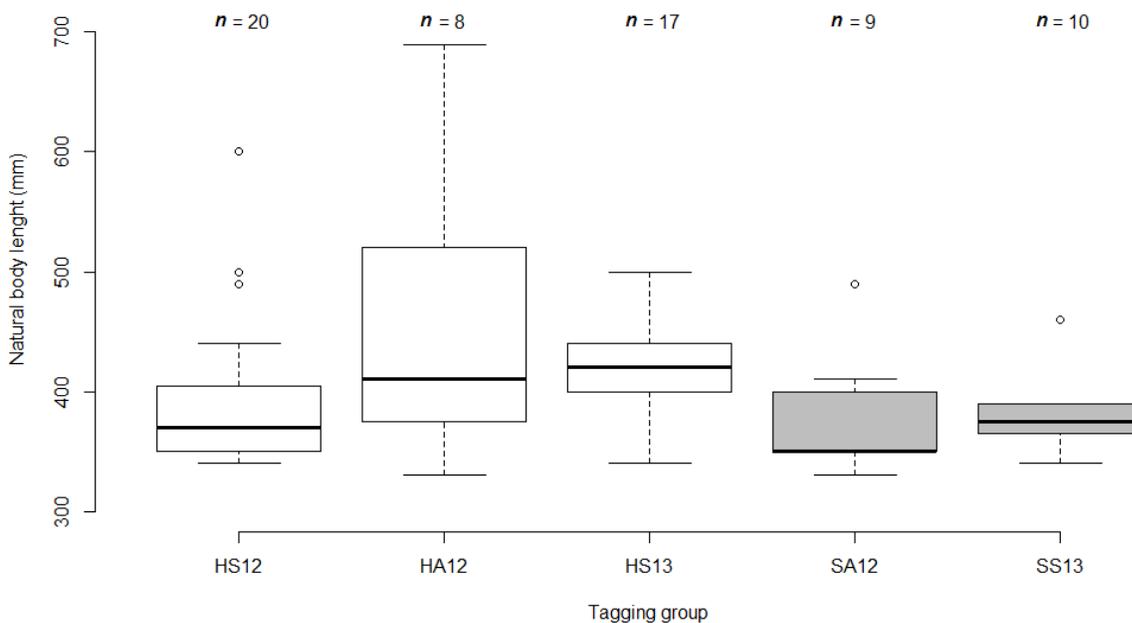
Figure 6: Natural body length (mm) of tagged fish in tagging groups from Søa (white) and Snilldalselva (grey) tracked throughout the period of 1 April – 1 October 2012 (HS12) or 2013. The box-and-whisker plots show median values (black lines), the interquartile ranges (boxes) and the 5th and 95th percentiles (whiskers). Circles indicate outliners.

Significant variation in Fulton's body condition was observed between tagging groups (ANOVA, $n = 64$, $P = 0.004$), for the fish tracked throughout the period 1 April – 1 October in 2012 (HS12 tagging group) or 2013, see figure 7. The SS13 group, tagged in the estuary of Snilldalselva during spring 2013, had significantly higher body condition at tagging than the HS12 (Tukey ANOVA, $n = 30$, $P = 0.003$), SA12 (Tukey ANOVA, $n = 19$, $P = 0.011$), and HS13 (Tukey ANOVA, $n = 27$, $P = 0.011$) tagging group (fig. 7). The SS13 group furthermore tended to have higher body condition than the HA12 tagging group (Tukey ANOVA, $n = 18$, $P = 0.081$).
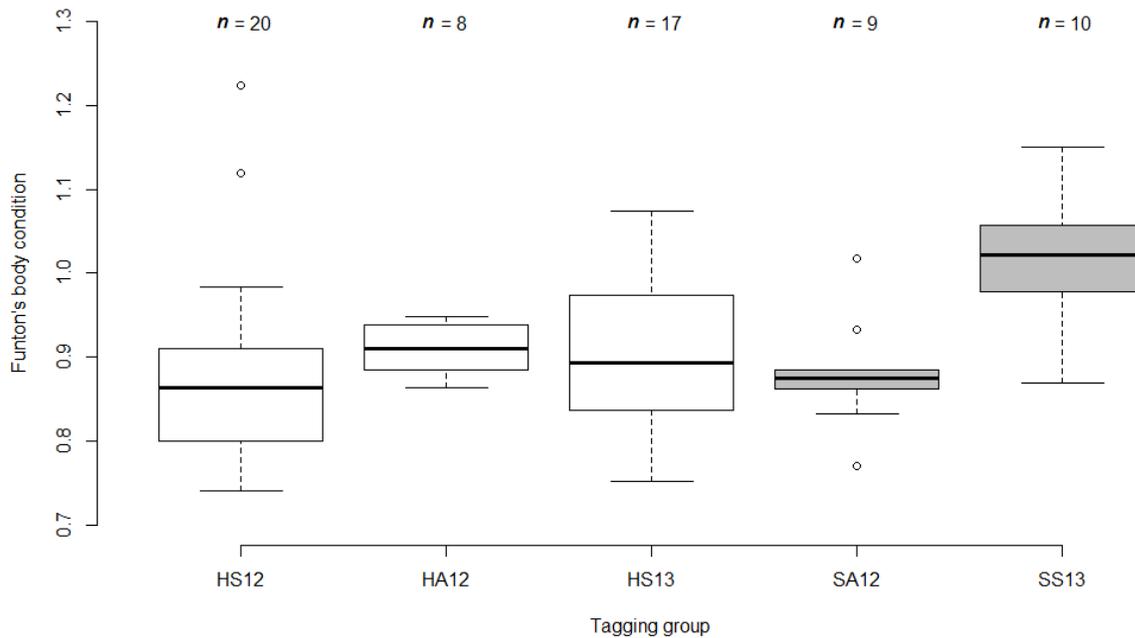
Figure 7: Fulton's body condition of tagged fish in tagging groups from the Hemnfjord (white) and the Snillfjord (grey) tracked throughout the period of 1 April – 1 October 2012 (HS12) or 2013. The box-and-whisker plots show median values (black lines), the interquartile ranges (boxes) and the 5th and 95th percentiles (whiskers). Circles indicate outliners.

Due to variable scale sample quality, the scale analysis resulted in a 75 % cover of smolt length, 67% cover of smolt age, 59 % cover of number of previous marine seasons and a 52 % cover of the age at tracking determination of the fishes tagged and tracked throughout the period 1 April – 1 October in either 2012 (HS12) or 2013, see table 2. The cover varied among groups, with the weakest cover in the HA12 group, with 25 % cover of smolt age and age at tracking, and 38 % cover of smolt length and previous marine seasons estimates, see table 2.

There was considerable variation among tagging groups, both regarding smolt length, age at smoltification, number of previous marine seasons and age at tracking, see table 2. The combined tagging groups of fish tagged in Søa watercourse had significantly greater smolt length (*t*-test, $n = 48$, $P = 0.023$), and had a tendency of older age at smoltification ($n = 43$, $P = 0.099$) compared to the fishes tagged in Snilldalselva. The fishes from Søa watercourse had furthermore significant higher number of previous seasons at sea ($n = 38$, $P = 0.018$) and were nearly significant older at the time of the tracking ($n = 33$, $P = 0.061$) compared to the individuals tagged in Snilldalselva.

Table 2: Scale reading result of tagged individuals tracked 1 April – 1 October either in 2012 (HS12 tagging group) or 2013. Mean, standard deviation (SD), and number and percentage cover of smolt length, age at smoltification, previous marine seasons and age at tracking determinations are given. Mean values as boldface.

	Tagging Group	HS12	HA12	HS13	SA12	SS13	Total
	n	20	8	17	9	10	64
Smolt lenght (mm)	mean	**161**	**199**	**131**	**111**	**140**	**143**
	SD	± 37.5	± 71.9	± 33.6	± 11.9	± 39.4	± 41.4
	n (cover)	14 (70 %)	3 (38 %)	15 (88 %)	7 (78 %)	9 (90 %)	48 (75 %)
Age at smoltification (years)	mean	**2.64**	**4**	**2.13**	**2**	**2.38**	**2.37**
	SD	± 0.81	± 0.00	± 0.35	± 0.00	± 0.74	± 0.69
	n (cover)	11 (55 %)	2 (25 %)	15 (88 %)	7 (78 %)	8 (80 %)	43 (67 %)
Previous marine seasons	mean	**3.45**	**4.67**	**3**	**3.17**	**2.38**	**3.16**
	SD	± 1.44	± 2.31	± 0.67	± 0.41	± 0.52	± 1.17
	n (cover)	11 (55 %)	3 (38 %)	10 (59 %)	6 (67 %)	8 (80 %)	38 (59 %)
Age at tracking (years)	mean	**5.63**	**8**	**5.2**	**5.17**	**4.86**	**5.39**
	SD	± 1.85	± 2.83	± 0.63	± 0.41	± 0.90	± 1.34
	n (cover)	8 (40 %)	2 (25 %)	10 (59 %)	6 (67 %)	7 (70 %)	33 (52 %)

(Left vertical label: Scale reading estimates)

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3.3 Marine residence and spatial use of study area

3.3.1 Total marine residence time during summer

Significant individual variation in the total residence time in marine habitats was calculated during the period 1 April to 1 October either in 2012 (HS12 group) or 2013, see figure 8. Among all of the tagged fishes tracked throughout these periods, the mean marine residence time was 100.5 days (SD 51.5 days, range 7.1 - 183 days). Highest variation was found in the HS12 group, tagged in the spring 2012 and tracked the following summer, where a mean residence of 90.8 days (SD 58.5 days, range 7.1 - 170.8 days) was observed. The HA12 group, tagged at in the outlet of spawning streams in the lake Rovatnet during autumn 2012 and tracked during summer 2013, had the lowest intragroup variation with a mean marine residence time of 53.4 days (SD 14.6 days, range 27.3- 71.8 days).

When comparing marine residence time of the tagging groups, there was found a significant difference between the HA12 tagging group and the HS13 tagging group (Tukey ANOVA, $n = 25$, $P = 0.049$), and between the HA12 tagging group and SA12 ($n = 17$, $P = 0.0105$). No significant variance was found between the other groups.
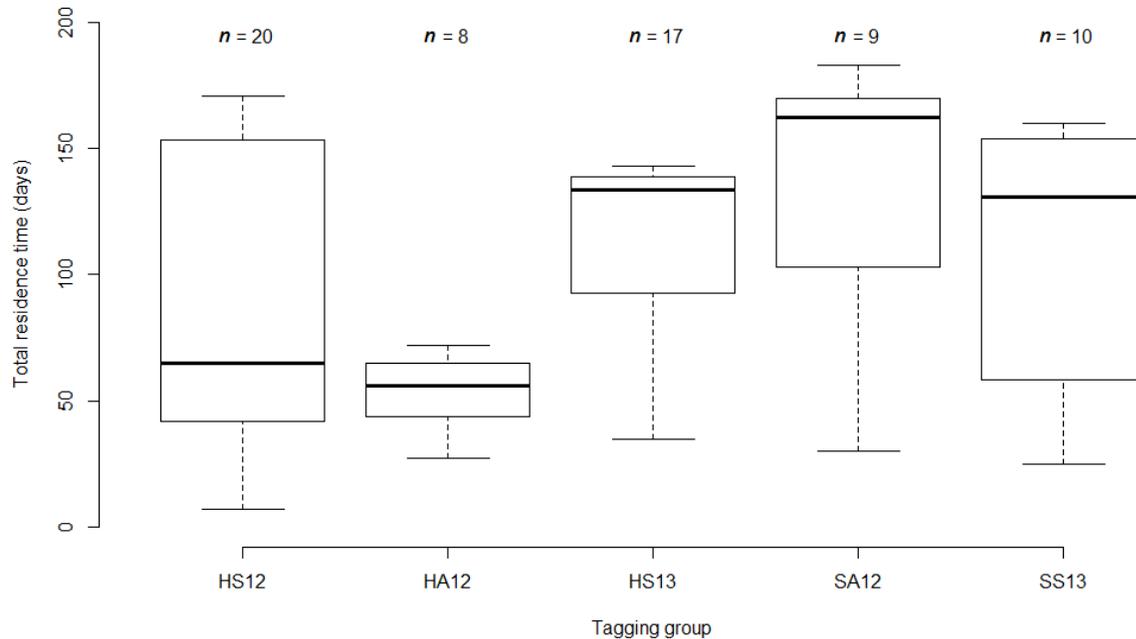
Fig 8: Total residence time (days) in the marine environment during 1 April – 1 October 2012 (HS12) or 2013 for Hemne (white) and Snillfjord (grey) for tagging groups HS12 (Hemnfjord spring 2013), HA12 (Hemnfjord autumn 2012), HS13 (Hemnfjor spring 2013), SA12 (Snillfjord autumn 2012) and SS13 (Snillfjord spring 2013). The box-and-whisker plots show median values (black lines), the interquartile ranges (boxes) and the 5th and 95th percentiles (whiskers).

3.3.2 Time spent in different parts of the fjord system during summer

There was observed large individual variation in the residence time in different fjord zones for the fishes tagged and tracked throughout the period 1 May - 1 October in either 2012 (HS12 group) or 2013, see figure 9. Fishes tagged in Søa spent significantly longer time in the innermost part of Hemnfjord (zone 1, fig 2) than in other parts of the fjord system (Tukey ANOVA, zone 2; $n = 55$, $P = < 0.001$, zone 3; $n = 55$, $P = < 0.001$, zone 4; $n = 55$, $P = < 0.001$, zone 5; $n = 55$, $P = < 0.001$), see fig. 9. Similar trends were observed for the fish tagged in Snilldalselva, where the innermost part of Snillfjord (zone 3, fig. 2) tended to have the highest residence time (Tukey ANOVA, zone 1; $n = 20$, $P = 0.65$, zone 3; $n = 30$, $P = 0.006$, zone 4; $n = 25$, $P = 0.172$, zone 5; $n = 22$, $P = 0.83$), see figure 9. However, individual residence time in the innermost zone varied widely, ranging from 0.2 days to 170.8 days for tagged fishes from Søa (mean 71.1 days, SD 49.5 days), and from 0.002 days to 183.0 days for tagged fishes from Snilldalselva (mean 92.6 days, SD 69.1 days).

When comparing the residence time in innermost areas in Hemnfjord (zone 1, figure 2) and Snillfjord (zone 2, figure 2), no significant difference was found between the two areas (Two-sided *t*-test, $n = 64$, $P = 0.123$). Neither were any significant differences in residence time for the fishes Søa found for the areas of central Snillfjord (zone 3, figure 2, $n = 25$, $P = 0.33$), central Hemnfjord (zone 4, figure 2, $n = 39$, $P = 0.46$) or outer areas (zone 5, figure 2, $n = 18$ $P = 0.39$) compared to the fishes tagged in the Snilldalselva. However, while 15 individuals tagged in Hemnefjord were observed in outer areas (zone 5, figure 2) and returning to the study area, only 3 individuals tagged fish from Snillfjord were observed in this part of the fjord and successfully returning in the end of the summer season.
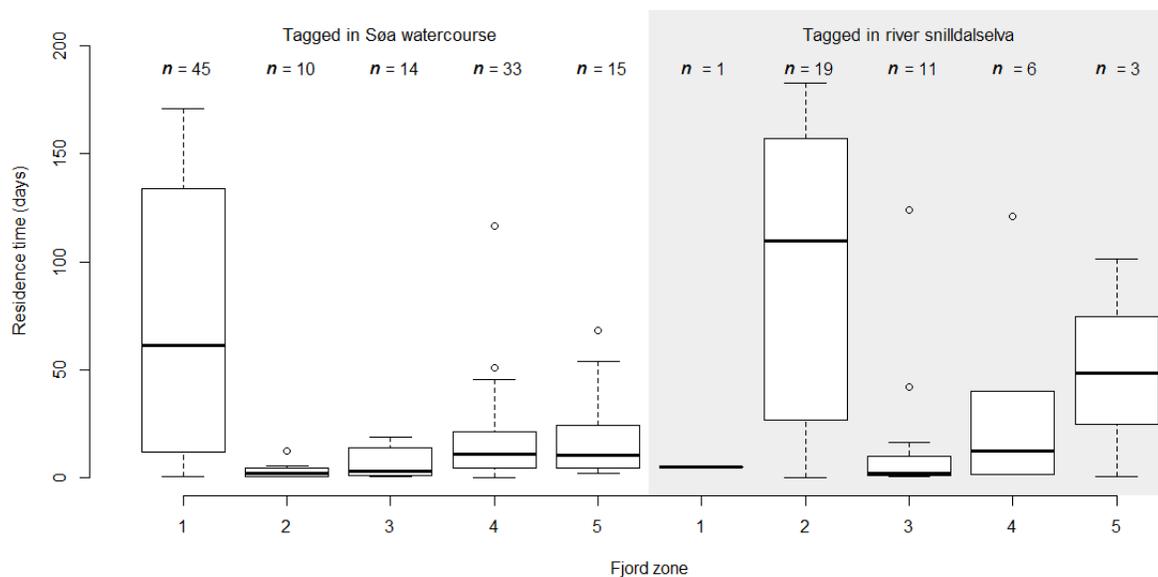
Fig 9: Residence time in fjord zones during the period 1 April - 1 October in either 2012 or 2013 for fish tagged in Søa (Hemnfjord, white background) and from Snilldalselva (Snillfjord, grey background). The box-and-whisker plots show median values (black lines), the interquartile ranges (boxes) and the 5th and 95th percentiles (whiskers). Circles indicate outliners.

3.3.3 Distribution of detections across ALS arrays

The tagged individuals had significantly higher proportions of their registrations at array H1 (fig 10) at ALSs deployed near the shore (littoral habitat) compared to ALSs deployed in pelagic habitat in pelagic water masses (t-test, $n = 122$, $P = <0.001$). Similar trends were seen at array S3, with a significantly higher proportion of the registrations at ALSs along the shore (littoral or cliff habitat) compared to ALSs in pelagic water masses (fig. 10, $n = 58$, $P = <0.001$). At array H3 individuals also had the largest proportions of their registrations at ALSs along the shore (littoral or cliff habitat) compared to the ALSs in pelagic water masses (fig. 10, $n = 50$, $P = <0.001$). At the outermost ALS array called H4 (fig. 10) there was found no significant difference in proportions of registrations between ALSs near the shore (littoral or cliff habitat) compared to ALSs deployed in open water masses (two sided t-test, $n = 56$, $P = 0.42$).

Array H1 (fig. 11) was the only ALS array containing monthly variations of the individuals proportions of pelagic registrations (ANOVA, $n = 191$, $P = <0.001$), throughout the period April – October in 2012 or 2013. April had significantly higher proportions of pelagic registration than both May (Tukey ANOVA, $n = 80$, $P = <0.001$), June ($n = 67$, $P = <0.001$), July ($n = 51$, $P = <0.001$), August ($n = 43$, $P = 0.006$), September ($n = 43$, $P = 0.006$) and October ($n = 33$, $P = <0.001$) at array H1. Even though no significant monthly variation was found at array H3 (ANOVA, $n = 45$, $P = 0.78$), array H4 ($n = 43$, $P = 0.15$) and array S3 ($n = 42$, $P = 0.088$), few individuals were observed at these arrays after the month of June, see fig. 11.
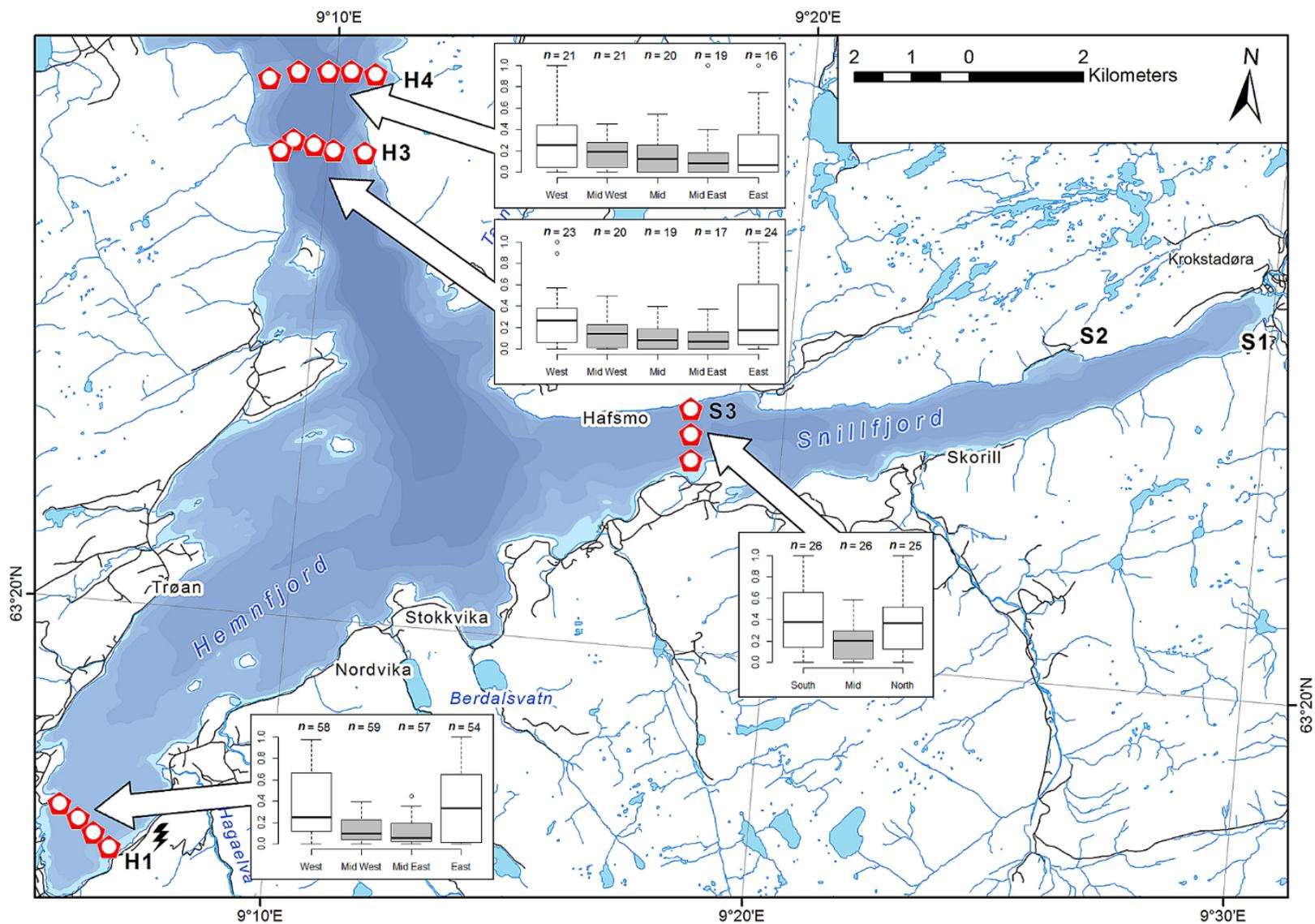
Fig 10: Proportions of individuals registrations at near shore (white) and pelagic (grey) ALS at array H1, H3, H4 and S3. The box-and-whisker plots show median values (black lines), the interquartile ranges (boxes) and the 5th and 95th percentiles (whiskers). Circles indicate outliners.
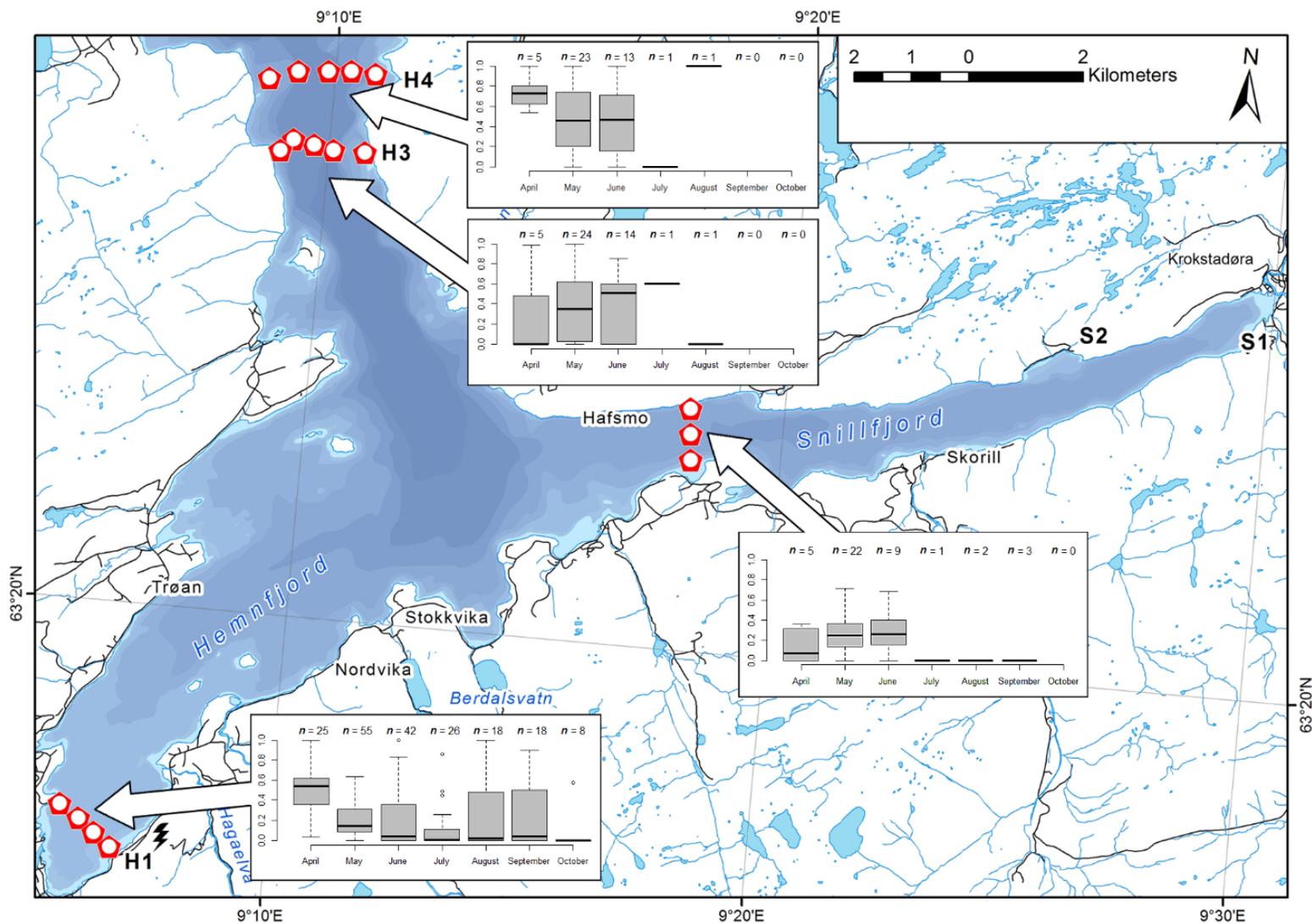
Figure 11: Monthly pelagic proportions of individuals registrations at ALSs across array H1, H3, H4 and S3 from fish tracked either in 2012 (HS12) or 2013. The box-and-whisker plots show median values (black lines), the interquartile ranges (boxes) and the 5th and 95th percentiles (whiskers). Circles indicate outliners.

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3.4 Vertical distribution and swimming depth of study fish

The median average swimming depth was 1.46 meters ($n = 40$, range $0.55 – 6.35$ meters) for the fishes tagged with depth-sensing transmitters during the period 1 May – 1 October 2013, see fig. 12. When recorded at littoral ALSs, there was a tendency towards deeper swimming patterns in august, which had a positive linear relationship with the water temperature ($n = 153$, $r^2 = 0.42$, $P = < 0.001$), see figure 5 and 12. A positive linear relationship was also found between swimming depth and the water temperature when fishes were recorded in pelagic areas ($n = 142$, $r^2 = 0.15$, $P = < 0.001$), see fig. 12.
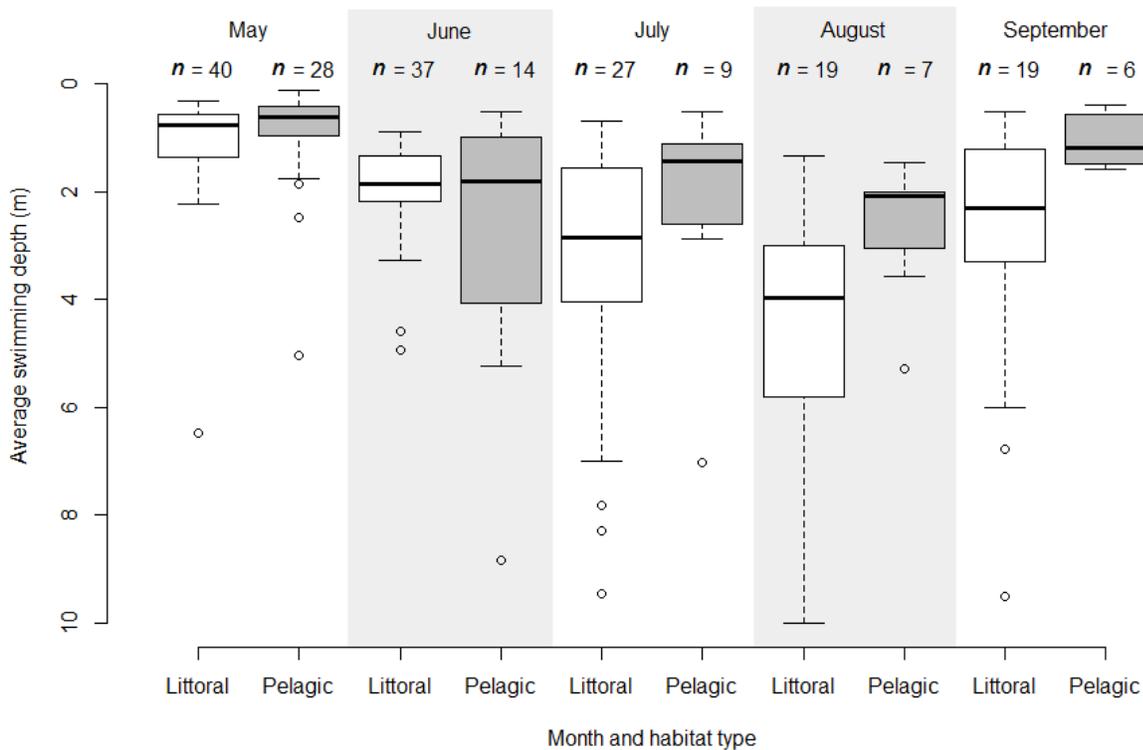
Figure 12: Monthly average individual swimming depth in littoral (white) and pelagic (grey) ALS habitat in the period 1 May – 1 October 2013. The box-and-whisker plots show median values (black lines), the interquartile ranges (boxes) and the 5th and 95th percentiles (whiskers). Circles indicate outliners.

Significantly deeper swimming patterns were found in all defined ALS habitats during day than night (t-test, $n = 24 - 80$, $P = < 0.022$, table 3), see figure 13. The median difference in swimming depth between day and night varied with habitat, ranging from 0.11 meters in estuarine habitat to 1.17 meters in cliff habitat (table 3).

Significant variation in average swimming depth between habitats, both during day (ANOVA, $n = 154$, $P = < 0.001$) and night ($n = 143$, $P = 0.014$) was observed, fig. 13. When analysing the inter habitat variation, significant difference in swimming depth between estuarine and littoral habitat both during day (Tukey ANOVA, $n = 69$, $P = < 0.001$) and night ($n = 69$, $P = 0.019$), and furthermore between cliff and estuarine ($n = 44$, $P = < 0.001$) during day were found. The swimming depth in littoral and cliff habitat was highly similar both during day ($n = 55$, $P = 0.80$) and night ($n = 49$, $P = 0.97$). The swimming depth in littoral ($n = 70$, $P = 0.033$) and cliff habitat ($n = 45$, $P = 0.019$) was significantly deeper than the swimming depth in pelagic habitat during day. The swimming depth was furthermore nearly significant deeper in the littoral habitat than in the pelagic habitat during night ($n = 65$, $P = 0.067$).
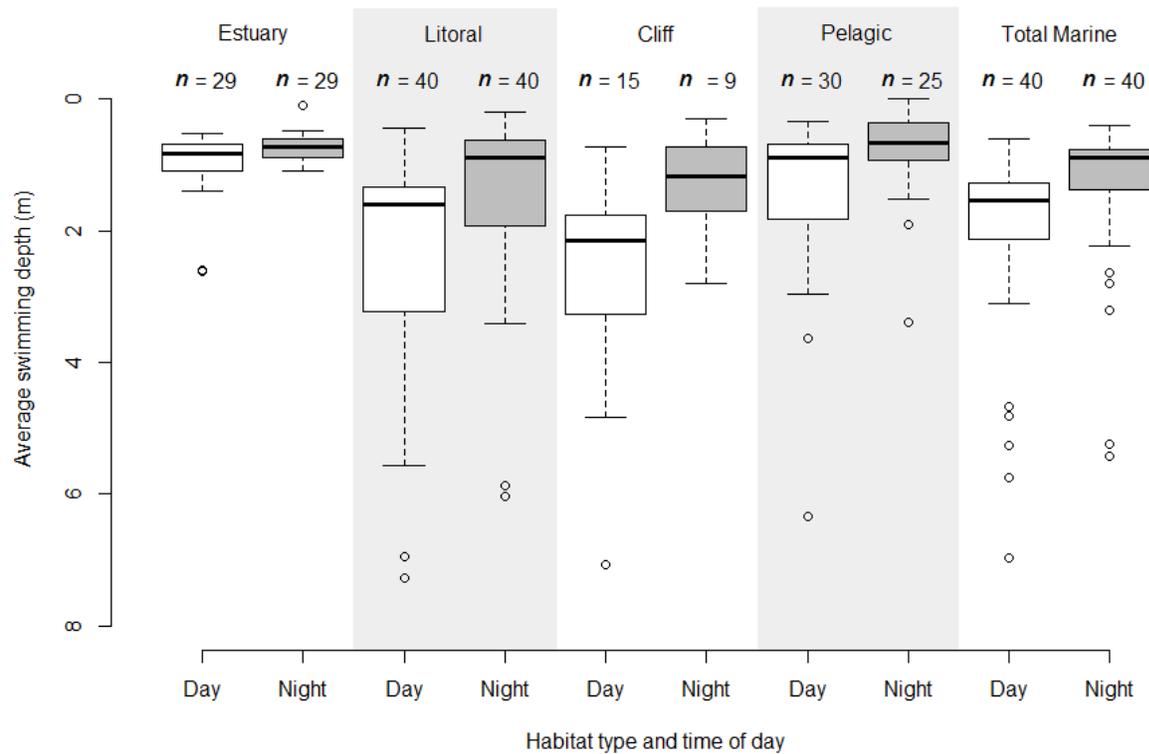
Figure 13: Individual mean swimming depth in different habitats during day (white) and night (grey) in the period 1 May - 1 October 2013. The box-and-whisker plots show median values (black lines), the interquartile ranges (boxes) and the 5th and 95th percentiles (whiskers). Circles indicate outliners.

Table 3: Median average swimming depth of fish tagging group HS13 and SS13 during day and night when recorded in different marine habitats. Welch's *t*-test *P*-values describe level of variance between swimming depth at day and night. Day time was defined as the period from sunrise to sunset.

Habitat	Median average swimming depth (m)			Welch's *t*-test	
	Day	Night	Difference	*n*	Pr(<T)
Estuary	0.84	0.73	0.11	58	**0.010**
Littoral	1.60	0.90	0.70	80	**0.008**
Rock wall	2.14	1.17	0.98	24	**0.006**
Pelagic	0.89	0.67	0.21	55	**0.022**
Total Marine	1.55	0.90	0.65	80	**0.011**

3.5 Characteristics of short, medium and long distance migrants

3.5.1 Morphology and life history of short, medium and long distance migrants

A total of 88 fish were categorized as either short, medium or long distance migrants from tagging watercourse according to figure 4, see table 4. The short distance migrants included 6 individuals from HS12, 19 from HS13, 4 from SA12 and 6 fishes from the SS13 tagging group. The medium distance migrants included 5 individuals from HS12, 4 from HS13, 2 from SA12 and 5 fishes from the SV13 tagging group. The group of long distance migrants included 12 individuals from HS12, 11 from HA12, 4 from HS13, 7 from SA12 and 3 fishes from the SS13 tagging group, see table 4.

Table 4: Tagging group, number of individuals, natural body length and body mass of short, medium and long distance migrants.

Tagging group	Migration distance	n	Natural length (mm)				Body mass (g)			
			Mean	SD	Min	Max	Mean	SD	Min	Max
HS12	Short	6	380	± 35	340	440	500	± 110	350	680
	Medium	5	356	± 9	350	370	444	± 103	370	620
	Long	12	419	± 79	350	600	672	± 385	330	1600
HA12	Long	11	442	± 116	330	690	933	± 775	330	2900
HS13	Short	19	424	± 59	340	580	775	± 387	300	1970
	Medium	4	413	± 33	380	450	590	± 142	420	730
	Long	4	403	± 48	350	460	550	± 196	320	780
SA12	Short	4	368	± 31	340	410	470	± 121	400	610
	Medium	2	350	± 0	350	350	350	± 28	330	370
	Long	7	396	± 56	330	490	577	± 260	310	980
SS13	Short	6	393	± 29	370	450	690	± 258	520	1210
	Medium	5	395	± 60	340	460	686	± 323	390	1120
	Long	3	387	± 57	340	450	597	± 307	400	950

There was significant variation in natural body length within all migration distance groups, see figure 14. The short distance migrants had a median body length of 395 mm, (range 340 – 580 mm), the medium distance migrants had a median length of 363 mm (range 340 – 460 mm) and the long distance migrants had a median body length of 380 mm (range 330 -690 mm). There was no significant difference in body length between the short, medium and long distance migrants (ANOVA, $n = 88$, $P = 0.204$). However, most of the largest individuals (≥ 450 mm, $n = 12$) seemed to conduct long distance migrations ($n = 7$, proportion = 0.58), while few large individuals performed medium ($n = 3$, proportion = 0.25) and short distance ($n = 2$, proportion 0.17) migrations. Among the smaller individuals (≤ 350 mm, $n = 18$), there were found equal proportions of short ($n = 6$), medium ($n = 6$) and long distance migrants ($n = 6$).
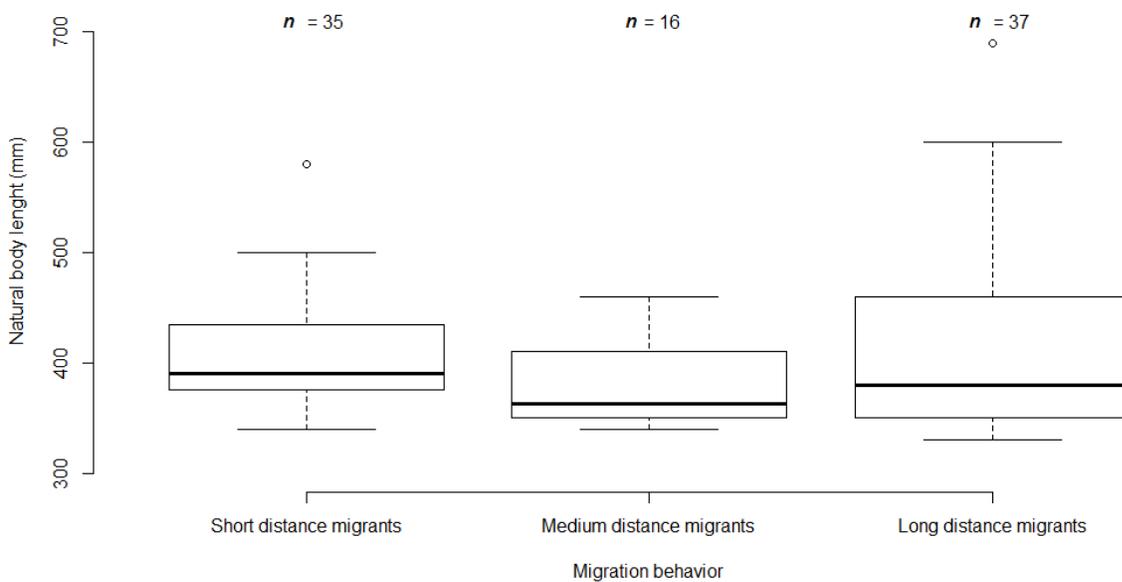
Figure 14: Natural body length (mm) of short, medium and long distance migrants. The box-and-whisker plots show median values (black lines), the interquartile ranges (boxes) and the 5th and 95th percentiles (whiskers). Circles indicate outliners.

Large individual variation in body condition in spring prior to the marine migration was observed, both for the short distance migrants (Fulton's K; median 0.95, range 0.8 - 1.3), the medium distance migrants (Fulton's K; median 0.91, range 0.8 - 1.2) and the long distance migrants (Fulton's K; median 0.87, range 0.7 - 1.1), see figure 15. Long distance migrants had significantly poorer body condition than both short distance migrants (Tukey ANOVA, $n = 29$, $P = 0.013$) and medium distance migrants ($n = 33$, $P = 0.018$). The body condition in spring of short and medium distance migrants were found to be highly similar ($n = 44$, $P = 0.916$).
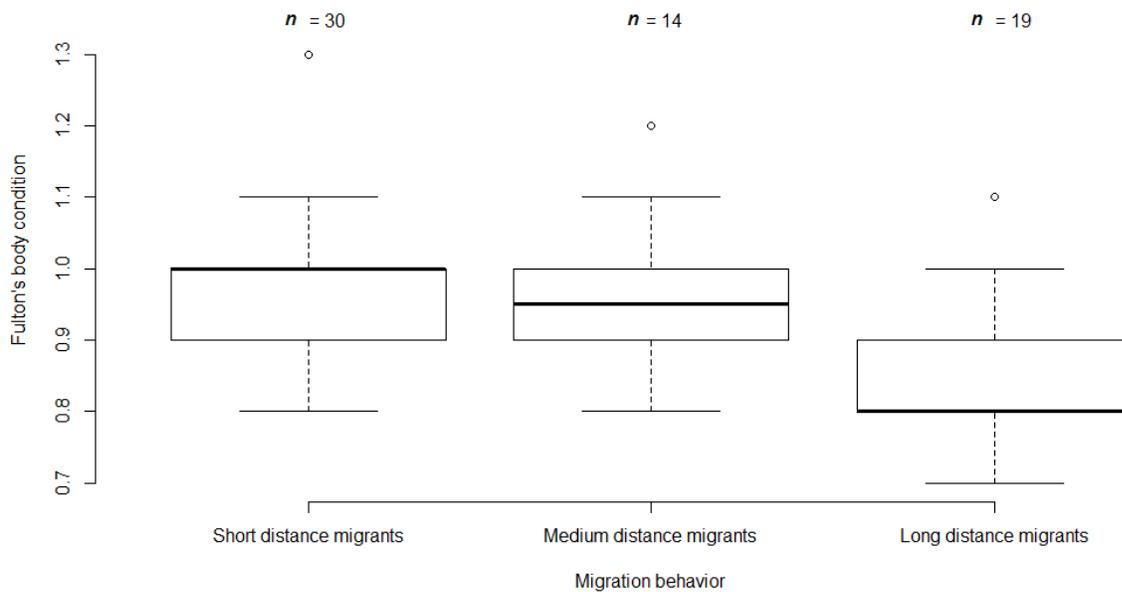
Figure 15: Fulton's body condition in spring prior to migration for short, medium and long distance migrants from. The box-and-whisker plots show median values (black lines), the interquartile ranges (boxes) and the 5th and 95th percentiles (whiskers). Circles indicate outliners.

The percentage cover of smolt length (total 74%, range 73 – 75 %), age of smoltification (total 66 %, range 59 – 71 %), number of previous marine seasons (total 59 %, range 49 – 75 %) and age at tracking (total 52 %, range 46 – 69 %) varied between the groups of short, medium and long distance migrants, see table 5. Long distance migrants had significantly larger smolt length than both short (Tukey ANOVA, $n = 53$, $P = 0.041$) and medium distance migrants ($n = 39$, $P = 0.022$). The long distance migrants had further a nearly significant higher age of smoltification than short distance migrants ($n = 47$, $P = 0.072$) and significant more previous marine seasons than the medium distance migrants ($n = 35$, $P = 0.039$). The age at tracking was significantly higher in the long distance migrants than the medium distance migrants ($n = 30$, $P = 0.033$), and furthermore nearly significant higher than the short distance migrants ($n = 35$, $P = 0.053$).

Table 5: Smolt length, age at smoltification, number of previous marine seasons and age at tracking of short, medium and long distance migrants. Number of available estimates and percentage cover of the scale reading estimates given for each group. Mean values as boldface.

		Migration distance	Short distance migrants	Medium distance migrants	Long distance migrants	Total
		n	*35*	*16*	*37*	*88*
Scale reading estimates	Smolt lenght (mm)	**mean**	**137.40**	**126.60**	**165.00**	**146.90**
		SD	± 34.50	± 36.90	± 46.70	± 42.90
		n (cover)	*26 (74 %)*	*12 (75 %)*	*27 (73 %)*	*65 (74 %)*
	Age at smoltification (years)	**mean**	**2.24**	**2.18**	**2.68**	**2.40**
		SD	± 0.52	± 0.60	± 0.84	± 0.70
		n (cover)	*25 (71 %)*	*11 (69 %)*	*22 (59 %)*	*58 (66 %)*
	Previous marine seasons	**mean**	**3.00**	**2.67**	**3.61**	**3.19**
		SD	± 0.61	± 0.65	± 1.41	± 1.10
		n (cover)	*17 (49 %)*	*12 (75 %)*	*23 (62 %)*	*52 (59 %)*
	Age at tracking (years)	**mean**	**5.13**	**4.91**	**6.16**	**5.50**
		SD	± 0.72	± 0.70	± 1.77	± 1.36
		n (cover)	*16 (46 %)*	*11 (69 %)*	*19 (51 %)*	*46 (52 %)*

3.5.2 Total marine residence time during summer for short, medium and long distance migrants

Long distance migrants had a significantly shorter marine residence time than both short distance migrants (Tukey ANOVA, $n = 50$, $P = 0.05$) and medium distance migrants ($n = 38$, $P = 0.005$), see fig. 16. However, large individual variation in the marine residency was found within both short (median 134.5 days, range 7.1 – 183.0 days), medium (median 141.4 days, range 49.2 – 170.1 days) and long distance migrants (median 60.4 days, range 27.3 – 168.0 days). There was no significant difference in the marine residence time for long migrating individuals between the years of 2012 (HS12 tagging group) and 2013 (two-sided t-test, $n = 24$, $P = 0.99$)
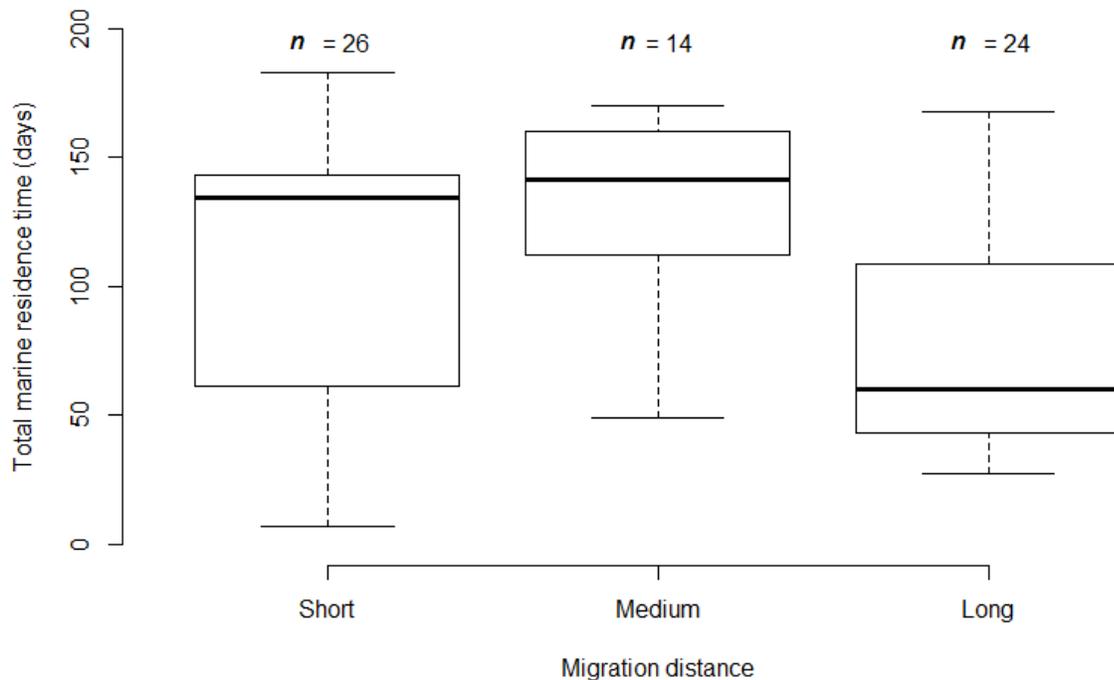
Figure 16: Total marine residence of short, medium and long distance migrants in the period 1 April – 1 October either in 2012 (HS12) or 2013. The box-and-whisker plots show median values (black lines), the interquartile ranges (boxes) and the 5th and 95th percentiles (whiskers).

3.5.3 Marine migration distance and residence in different parts of the fjord system

There was substantial individual variation of the residence time in the different defined fjord zones, see figure 17. For fish tagged in Søa, the long distance migrants had a significant shorter residence time in the innermost part of Hemnfjord (zone 1, fig 2.) than both short distance migrants (Tukey ANOVA, $n = 37$, $P = 0.002$) and medium distance migrants ($n = 26$, $P = 0.008$). Fishes tagged in Snilldalselva had similar trends, as long distance migrants had significantly shorter residence time in the innermost part of the Snillfjord (zone 2, fig. 2) compared to short distance migrants ($n = 13$, $P = 0.039$). Long distance migrants tagged in Snilldalselva also tended to have shorter residence in the innermost part of the fjord than the medium distance migrants ($n = 12$, $P = 0.092$).
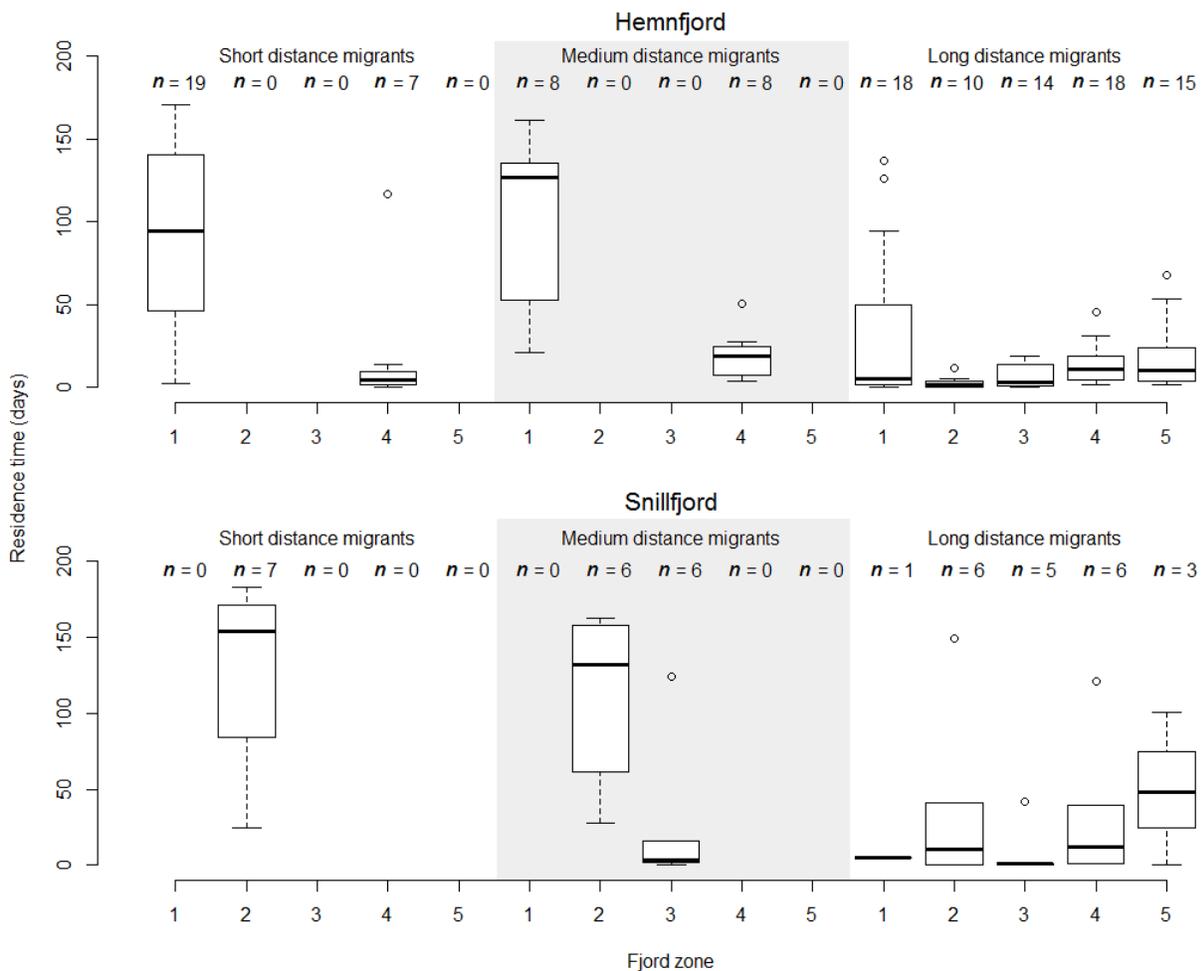
Figure 17: Residence time in fjord zones of short, medium and long distance migrants in the period 1 April – 1 October either in 2012 (HS12) or 2013. The box-and-whisker plots show median values (black lines), the interquartile ranges (boxes) and the 5th and 95th percentiles (whiskers). Circles indicate outliners.

3.5.4 Littoral and pelagic utilization for short, medium and long distance migrants

The ALSs along the shoreline had higher proportions of the individuals detections compared to the ALSs deployed in pelagic water masses at array H1 (fig. 1), both for short (*t*-test, $n = 50$, $P = < 0.001$), medium ($n = 18$, $P = < 0.001$) and long distance migrants ($n = 54$, $P = < 0.001$), figure 18. However, the long distance migrants tended to have higher proportions of pelagic registrations than short distance migrants (Tukey ANOVA, $n = 52$, $P = 0.079$). No significant difference in the proportions of pelagic registrations between short and medium distance migrants ($n = 34$, $P = 0.93$) was observed, neither between the medium and long distance migrants ($n = 36$, $P = 0.43$).
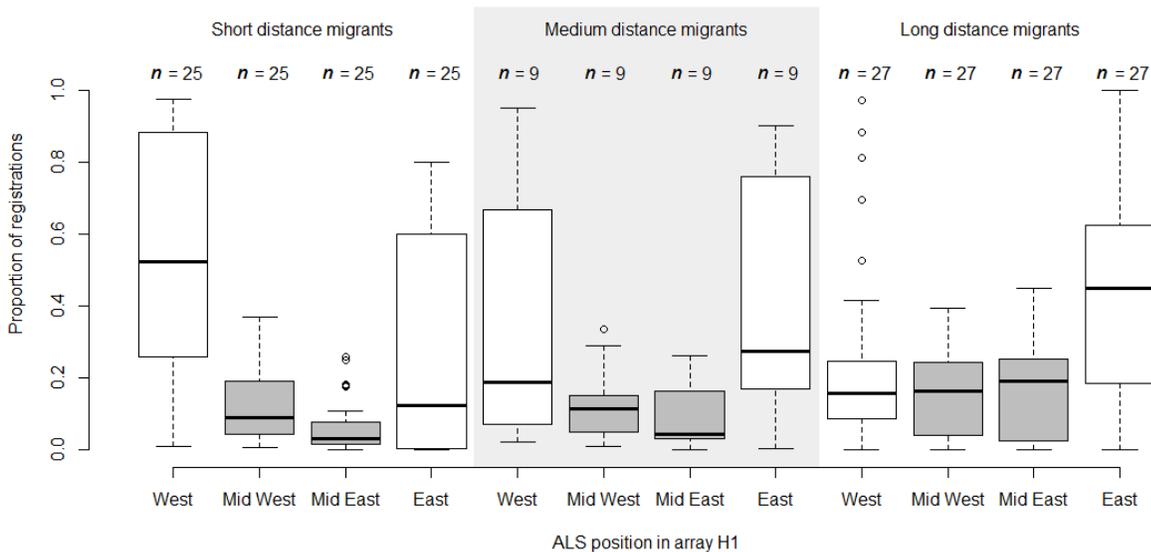
Figure 18: Distribution of individuals registrations recorded on near shore (white) and pelagic (grey) ALSs in array H1 for short, medium and long distance migrants. The box-and-whisker plots show median values (black lines), the interquartile ranges (boxes) and the 5th and 95th percentiles (whiskers). Circles indicate outliners.

A clear trend of higher proportions of pelagic registrations at array H1 was observed for long distance migrants compared to short distance migrants, when investigating the monthly variations within array H1 (fig. 1), see fig. 19. For short distance migrants, the proportion of pelagic registrations in April was significantly higher than both May (Tukey ANOVA, $n = 29$, $P = 0.001$), June ($n = 23$, $P = < 0.001$), July ($n = 19$, $P = < 0.001$), August ($n = 12$, $P = 0.001$), September ($n = 14$, $P = 0.005$) and October ($n = 10$, $P = 0.007$). Similarly, April proved to have significantly higher proportions of pelagic detections compared to the months of June ($n = 14$,

$P = 0.026$), July ($n = 11$, $P = 0.010$), August ($n = 12$, $P = 0.049$) and October ($n = 7$, $P = 0.047$) for the medium distance migrants. Furthermore, the month of April had nearly significant higher proportions of pelagic registrations in than May ($n = 14$, $P = 0.067$). There was no significant variation between months for the long distance migrants (ANOVA, $n = 66$, $P = 0.061$).
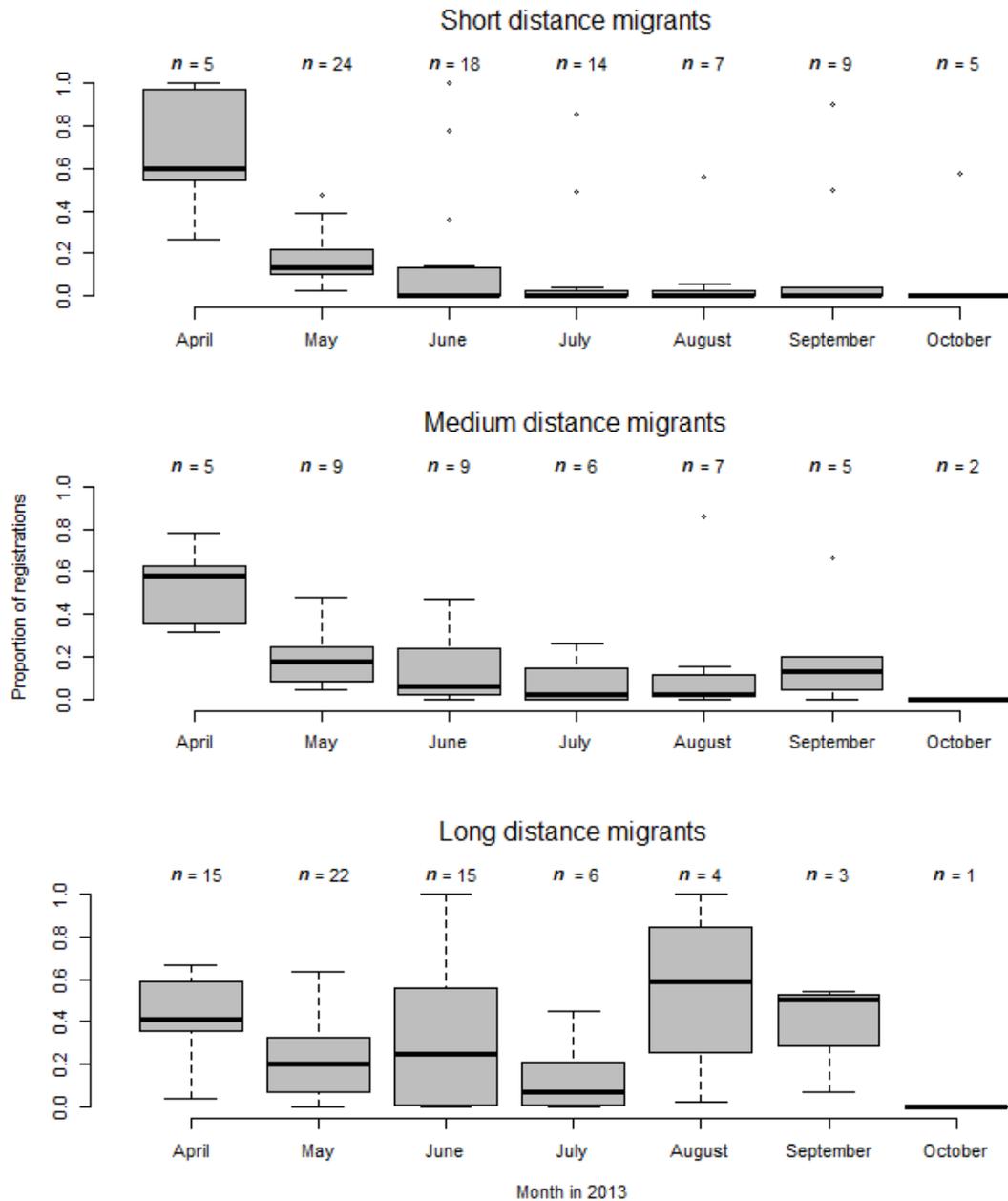
Figure 19: Monthly proportions of pelagic registrations of short, medium and long distance migrants at ALS array H1 in the period 1 April – 31 October. The box-and-whisker plots show median values (black lines), the interquartile ranges (boxes) and the 5th and 95th percentiles (whiskers). Circles indicate outliners.

3.5.5 Vertical distribution differences of short, medium and long distance migrants

Significant differences in average swimming depth between short and long distance migrants (t-test, $n = 31$, $P = 0.013$) was found when recorded at ALSs in littoral habitat in the period 1 May – 1 July (table 6). No significant difference in the swimming depth was found between short and medium distance migrants (two-sided t-test, $n = 33$, $P = 0.58$), neither between medium and long distance migrants (two-sided t-test, $n = 16$, $P = 0.24$), when recorded in littoral habitat in the period 1 May – 1 July 2013.

No significant difference in swimming depth was found between short and long distance migrants (two-sided t-test, $n = 23$, $P = 0.39$), neither between short and medium distance migrants (two-sided t-test, $n = 25$, $P = 0.34$), or between medium and long distance migrants (two-sided t-test, $n = 12$, $P = 0.69$) when recorded in pelagic habitat in the period 1 May – 1 July 2013, see table 6.

Significant deeper average swimming depth was found in littoral habitat compared to pelagic habitat (t-test, $n = 42$, $P = 0.007$) for short distance migrants. No significant difference in average swimming depth between littoral and pelagic habitat was found for medium distance migrants (two-sided t-test, $n = 16$, $P = 0.91$) or long distance migrants (two-sided t-test, $n = 12$, $P = 0.43$).

Table 6: Mean average swimming depth in littoral and pelagic habitat in the period 1 May – 1 July 2013, for fishes tagged during spring 2013.

	Migration distance	n	Average swimming depth (m)		
			mean	SD	range
Littoral habitat	Short	24	1.52	1.03	0.24 - 4.52
	Medium	9	2.05	2.65	0.40 - 8.95
	Long	7	0.93	0.38	0.43 - 6.48
Pelagic habitat	Short	18	0.86	0.61	0.11 - 2.82
	Medium	7	1.89	2.61	0.23 - 7.54
	Long	5	1.41	1.24	0.31 - 3.40

4 Discussion:

4.1 Tagging group characteristics and life history:

Large individual variation in natural body length was found in all of the tagging groups, when comparing individuals tracked throughout the summer seasons 1 April – 1 October in either 2012 or 2013. Despite no significant differences between tagging groups, the fishes tagged in the Søa watercourse were significantly larger than fishes tagged in Snilldalselva when tagging groups were combined. Furthermore, when combining tagging groups, the fishes tagged in the Søa watercourse had significantly higher scores both regarding smolt length and number of previous marine seasons, and had a tendency of older smoltage and higher age at tracking than the fishes from Snilldalselva. The observed difference in smolt length and tendency of older age at smoltification, are probably influenced by the environmental differences between the watercourses of origin. The parr in the watercourse Søa might reside in the lake Rovatnet, enabling them to postpone smoltification. In contrast, the river Snilldalselva offer few deep pools, and have no accessible lake. Hence, it is likely that constraints in food supply or limited availability of appropriate shelter pushes fish in this river towards smoltification earlier than for the parr in Søa. This is consistent with previous studies on how environment influence the smoltification in partly migrating trout populations (Jonsson and Jonsson 1993, Økland et al. 1993, Wysujack et al. 2009). The larger body size of individuals tagged in Søa, probably reflects the tendency of higher age of these individuals and the significantly higher number of seasons in the sea. It may be speculated whether the observed tendency of lower age at tracking of fish from Snilldalselva might be caused by higher mortality due to harsher winter conditions, higher fishing pressure or other unknown causes.

The fishes tagged in the estuary of Snilldalselva during the spring of 2013, were found to have significantly better body condition than the other groups tagged during spring. This is probably reflected by the behaviour during winter of individuals from Snilldalselva, which were mainly found to remain in the inner parts of Snillfjord throughout the winter, in contrast to the fish tagged in Søa, which mainly overwintered in the lake Rovatnet (J.G Davidsen, pers. com.). The marine stay during winter might have offered better feeding opportunities, resulting in better body condition of these fishes at tagging during the spring of 2013. Furthermore, the body

condition might have been influenced by differences in the proportion of non-spawning individuals during the season prior to tagging. Recent bio-telemetric studies have shown that a sea trout population in northern Norway reside in the marine environment during winter (Jensen and Rikardsen 2008, 2012). Furthermore, Jonsson and Jonsson et al. (2009) found that sea trout spending the winter at sea had better growth the first two years after smoltification compared to sea trout overwintering in freshwater.

4.2 Marine residence during summer:

Large intragroup variation in marine residence time during the summer months was observed in most tagging groups. Individuals tagged in the estuary of Søa during spring 2013 had the highest intragroup variation, while individuals tagged at spawning grounds in Rovatnet had the least variable length of residence in the sea. Individuals tagged at the spawning grounds in Rovatnet during autumn 2012 were likely to be individuals of the same population, while the individuals tagged in the Søa estuary were possibly fishes of various origin, either from sub-populations from Rovatnet, or of neighbouring watercourses. This suspicion were strengthen by the fact that a portion of the individuals tagged in the Søa estuary in the spring of 2013 were later observed in neighbouring watercourses during the spawning period in autumn 2013 (J.G Davidsen, pers. com.). Some individuals tagged near the inlet of Søa in Rovatnet during the spring in 2012 were furthermore observed in other watercourses, and two individuals tagged in Snilldalselva migrated to Rovatnet for overwintering (J.G Davidsen, pers. com.). These observations suggest that sea trout populations from other watercourses might use the lake for overwintering, which might have caused fish caught and tagged in the outlet of Rovatnet during the spring in 2012, and in the Søa estuary during the spring in 2013 to be a mix of different populations. Consequently, it is suggested that the large variation in observed marine residence time during summer is partly caused by population variation. Previous studies have revealed that marine stay can vary widely within populations, with a range of factors influencing the duration of the marine residence of an individual, such as age (Nordeng 1977, Jonsson 1985), maturity (Jonsson 1985), environmental conditions in the river (Jensen and Rikardsen 2008) and salmon lice infestation (Birkeland and Jakobsen 1997). The observed marine residence in the present study, is thereby most likely a consequence of both heritage and environment.

4.3 Spatial distribution in the fjord system during summer:

As for the total marine residence time, significant individual variation in marine residence time was observed in different parts of the study area. The innermost parts of the fjords, near the river outlets, demonstrated the longest marine residence time for fishes both from Søa and Snilldalselva. It might be speculated that the sea trout stayed close to the river to ensure access to fresh or brackish water, if they experienced limited seawater tolerance. Previous studies have reported variable sea water tolerance for sea trout post-smolt (Parry 1960, Hogstrand and Haux 1985, Ugedal et al. 1998, Urke et al. 2013), probably influenced by varying water salinities and duration of the sea water exposure. Handeland et al. (2003) found that seawater tolerance varied among strains of Atlantic salmon post-smolt. Hence, there might be variation among both populations and individuals in terms of saltwater tolerance. However, even freshwater resident trout strains tolerate full sea water when acclimated (Jonsson et al. 1994), indicating that marine migrants quickly adapt good osmoregulative capacity when exposed to saline waters. Since all individuals in the present study were considered experienced migrants with one or more previous marine seasons, and the 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 osmoregulative capabilities when entering saline waters. The innermost parts of both Snillfjord and Hemnfjord had high salinity, indicating that salinity probably did not affect the spatial distribution in the fjords to any great extent.

A possible reason for the observed prolonged residency in the innermost parts of the fjords, might be favourable feeding opportunities and suitable habitat in these areas. The large individual variation might be influenced by prey choice or different habitat preferences, as a previous study by Knutsen et al (2001) showed that small individuals mainly fed on shallow water prey, while large individuals fed mostly on pelagic fish. The distribution of the tagged sea trout might furthermore be influenced by seawater temperature, as the deployed data loggers revealed that the water temperatures generally were lower in the outer areas compared to the inner parts of the fjords, throughout the summer season. Jensen et al. (2014) suggested in a recent study that the sea trout's spatial distribution in the inner and outer areas of a fjord was affected by the water temperature, and that the sea trout actively resided in areas with higher water temperatures. Similar findings were also reported in a study by Rikardsen et al. (2007), where the sea trout resided in inner, warmer parts of the fjord. The spatial distribution in the fjord during summer

might furthermore be influenced by spatial variation in possible threats, such as predation (Lyse et al. 1998) or salmon lice infestation (Finstad and Bjørn 2011). It might be speculated that random distribution possibly play a role in the observed distribution. However, random effects are likely to be negligible, as it would imply homogenous environment parameters throughout the study area, or that sea trout do not actively seek desired environment, which seems highly unlikely. The observed variation in marine residence time in areas close to the watercourses, suggest that there are individual differences in feeding behaviour, willingness to migrate or other unknown factors influencing the marine migration. The influence on sea trout's marine behaviour by prey and habitat preferences, water temperature, morphological characteristics, life history, as well as spatial variation in threats such as predation and parasitism, is further evaluated in the next sections.

4.4 Littoral versus pelagic habitat utilization

Tagged sea trout in the present study had higher proportions of registrations near shore compared to pelagic areas. As these results are based on the relative numbers of registrations along the ALS arrays, it cannot be considered as residence time, but provides a rough estimate of relative preference between littoral or pelagic water masses. The results are consistent with findings by Jensen et al. (2014), who showed that sea trout had significantly longer residence time near the shore compared to pelagic areas. The tendency towards littoral habitat utilization is furthermore consistent with previous studies on sea trout feeding behaviour, which suggest that the main feeding habitat of sea trout is in near shore, shallow areas, with crustatians, polychaetes, insects and fish being the main prey types (Pemberton 1976, Lyse et al. 1998, Knutsen et al. 2001). However, the impression that sea trout mainly utilize littoral habitats might be biased, since most studies capture the sea trout near shore as they are harder to catch in open water masses (Rikardsen and Amundsen 2005). Furthermore, the sea trout is probably more dispersed when resident in areas of open water masses, due to larger available areas, and might therefore not only be harder to catch, but also less likely to be recorded on automatic listening stations as in the present study.

Even though most feeding studies on sea trout have been conducted by catching the sea trout in littoral habitat near the shore, or shortly after entering freshwater (Rikardsen and Amundsen 2005), pelagic fish species are often found to be a considerable part of the sea trout diet, with herring (*Clupea harengus* L. 1758) as a key prey species (Pemberton 1976, Knutsen et al. 2001, Rikardsen et al. 2006). A study done by Rikardsen and Amundsen (2005) investigated the prey selection of sea trout in open water masses by using a surface trawl more than 500 meters from the shore. Here a pelagic feeding behaviour was evident, as more than 95 % of the sea trout's prey consisted of herring (Rikardsen and Amundsen 2005).

The present study was not designed to monitor the selection of prey, and due to the long range (300 – 350 m) of the automatic listening stations, it cannot be excluded that the tagged sea trout might have a pelagic feeding behaviour when registered on stations located near the shore. On the other hand, the sea trout is likely to hold a pelagic feeding behaviour when registered at pelagic areas, due to the absence of littoral habitat and prey within the range of these automatic listening stations. Observations in pelagic areas might reflect strictly migratory behaviour without feeding, but this is likely to be negligible, as the sea trout migrate to maximize growth (Jonsson and Jonsson 1993), and therefore should use every opportunity to feed. Pelagic swimming behaviour is furthermore thought to increase the risk of predation (Lyse et al. 1998), which suggest that the sea trout would prefer more shallow areas for migration in order to reduce its exposure to potential predators. Overall, when drawing conclusion on littoral versus pelagic utilization based on the data from the present study, this has to be done with caution.

When discussing the proportional numbers of fish detections across the ALS arrays, it has been assumed that the range of the ALSs within each array is homogenous. ALS range is known to vary and be dynamic according to a range of physical factors, such as underwater topography, chemical and physical properties of the water, and water turbulence (Heupel et al. 2006). Thus, we cannot exclude that the ALSs in the array have different ranges, which might influence and cause biased data recordings. One possibility could be that fishes are less likely to be detected in shallow areas along the shoreline, due to higher risk of signal shielding and absorption of the transmitting signal.

4.5 Variation in vertical distribution with habitat, time of day and season

The sea trout was found to swim significantly deeper in the water column during day than night in all habitats. This vertical swimming pattern called diel vertical migration is a common phenomenon in many aquatic taxa (Hays 2003). The phenomenon is thought to be governed by light (Appenzeller and Leggett 1995), and earlier studies have suggested that this migration behaviour might be triggered by body temperature regulative, feeding or anti-predator behaviour (Clark and Levy 1988). Such vertical movements have probably not been quantitatively recorded for sea trout prior to this study. However, similar swimming patterns have previously been recorded by Davidsen et al. (2008) for Atlantic salmon post-smolt, who suggested that the observed vertical movement was a result of trade-off between avoiding predation by avian and marine predators, feeding or osmoregulative advantages. As the size of the sea trout tagged in the present study is larger than post-smolt of Atlantic salmon, and predation pressure decrease with body size (Dieperink et al. 2001), the tagged individuals in the present study probably had less anti-predator behaviour than the salmon post-smolt in the study by Davidsen et al. However, assuming that the sea trout had deeper swimming patterns during day due to avian anti-predator behaviour, the shallow swimming patterns during night might reflect favourable conditions in the upper water layer due to lower salinity, higher temperature or feeding preferences. A study by Pemberton et al. (1976) witch investigated the sea trout diet during day and night, found an increased intake of mid-water and surface prey, and a decrease in benthic preys during night. Pemberton et al. (1976) suggested that the sea trout were more likely to detect prey which were clear from the substrate and at the surface of the water, and furthermore speculated that there could be varying conspicuousness of the littoral prey between day and night. The observed difference between day and night in the present study can therefore probably be explained by a shift in prey. This is presumably due to changes in the detectability of the prey types, as the sea trout is considered a visual feeder (Klemetsen et al. 2003). It might be speculated the that different prey types conduct similar diel vertical movements, and thus influence the swimming depth of the tagged sea trout. It is also likely that more than one of the mentioned factors might influence the observed swimming patterns simultaneously, or at different times during the marine residence.

A highly significant, positive correlation between swimming depth and water temperature was observed during the summer season, and the fishes increased the swimming depth from April towards late summer. A series of conductivity, temperature and depth-measurements (data not shown) taken throughout the study period, showed decreasing water temperature with increasing depth, suggesting that the sea trout actively regulated its body temperature by seeking water layers of preferred temperatures. This is consistent with a recent study by Jensen et al. (2014), who suggested that sea trout actively seek the warmest areas in the fjord. However, in the present study the sea trout tended to go deeper with rising temperatures, suggesting that it actively moved into colder water during the warmest periods in summer. Rikardsen et al. (2007) reported that the mean ambient temperatures for sea trout ranged between 11.5 ^{0}C and 12.9 ^{0}C during the marine residence in the Alta Fjord, during the months of June and July. Thus, it might be speculated that the preferred ambient temperature for sea trout is around 12 ^{0}C while in the marine environment. If true, it might explain the observed deeper swimming pattern during the warmest periods of the summer season in the present study. The correlated swimming pattern and water temperature was most evident for tagged fishes recorded on ALSs deployed near shore with littoral habitats available within the ALS range. The less obvious pattern in pelagic areas might possibly have been influenced by differences in mixing of the water column in littoral and pelagic areas.

Another possible reason for the observed trend of deeper swimming behaviour towards late summer might be shifting of prey type, or that the prey follow similar depth-trends according to changing water temperatures. If so, the sea trout recorded in littoral habitat might be more likely to change prey during the season, due to a high variability of available prey types (Christie 1997). Stomach analyses of sea trout caught in previous studies have found that polychaetes and marine crustatians are important early in the season, while fish is more important during late summer, suggesting that prey type vary with seasonal changes in the prey availability (Knutsen et al. 2001, Rikardsen et al. 2006).

4.6 Morphological characteristics and life history of short, medium and long distance migrants

Large individual variation in the migration distance was observed, where some individuals remained in the innermost part 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 tagging groups. The low number of long migrating individuals in the groups caught and tagged during spring of 2013 probably reflected that these groups were caught and tagged in the estuaries. Long distance migrants were found to have minor residency in the innermost parts of the fjord compared to the short migrating individuals. Thus, the likelihood of capturing short distance migrants in the estuary were probably much greater than the chance of capturing long distance migrants during the capture and tagging in the spring of 2013. Interestingly, all individuals tagged near the spawning grounds in the lake Rovatnet during the autumn of 2012 which migrated to sea the following summer, conducted long distance migrations. The observed variation in proportions of long distance migrants between tagging groups, suggest that the migration distance varies among populations. This is consistent with previous studies, which have shown a wide range in migration distance among populations (Jensen 1968, Svärdson and Fagerström 1982, Pratten and Shearer 1983, Berg and Berg 1987), which is thought to be caused by both environment and heredity (Klemetsen et al. 2003).

No significant difference in natural body length between short and long distance migrants was found. However, even though all size classes performed long distance migrations, large individuals ($\geq$ 450 mm) seemed to have a greater tendency to conduct long distance migrations than remaining close to the tagging location, while equal proportions of short, medium and long distance migrants were found among the individuals of low natural body length ($\leq$ 350 mm). Jensen et al found (2014) found that large individuals were more likely to conduct long distance migrations than smaller individuals. Berg and Berg (1987) found no such relationship within 2122 recaptures in a capture-recapture study, but this might have been influenced by the fact that recapture position does not necessary reflect the maximum migration distance for the fish, and that the method for measuring length might have varied among the fishermen who recaptured the fish.

Larger individuals need bigger prey (Klemetsen et al. 2003). Consequently, it might be more likely to find higher abundance of suitable prey further out in the fjord, and hence be more likely for larger individuals to perform long distance migrations (Jensen et al. 2014). This is consistent with a study by Knutsen et al (2001), where the author found that small post-smolt individuals fed inshore in shallow water prey communities, while larger sea trout were found further out feeding on pelagic fish. Larger individuals might therefore have a higher probability to perform long distance migrations. Predation risk is considered to be size dependent (Dieperink et al. 2001), and might cause smaller individuals to stay in littoral habitat, were they are probably less exposed to predators (Lyse et al. 1998). However, all individuals in the present study were larger than post-smolt, which is considered as the most vulnerable group for marine predation (Dieperink et al. 2001). Furthermore, as all tagged individuals in the present study were considered experienced marine migrators with one or more previous marine migrations, limited predation pressure is suggested for these fishes. The even distribution of short, medium and long distance migrants among the smaller individuals ($\leq$ 350 mm), furthermore indicate that there was no strong anti-predator behaviour limiting the migration distance for this size group. The selection of prey thus seems to be the most plausible explanation for the migration distance. Fast growing individuals change to a more piscivorous diet at a smaller size and younger age (Klemetsen et al. 2003) than slower growing individuals, which might partly explain why some smaller individuals conduct long distance migrations. Alternatively, it is possible that the smaller individuals of long distance migrants have similar feeding behaviour as the short distance migrants, and are dispersed further out in the fjord due to suitable habitat and conditions in both areas, while the larger individuals experience favourable conditions in outer areas compared to inner areas.

The long distance migrants had a poorer body condition than short distance migrants, suggesting that the individuals having poorer body condition experiences a greater need to maximize feeding, and thus shows greater tendency to migrate. This assumption is supported by a study conducted by Wysujack et al. (2009) on brown trout parr, where the author found that poor body condition promoted migratory behaviour. It is furthermore supported by a rearing experiment by Davidsen et al. (in review), who found that starved sea trout post-smolts migrated further out in the fjord compared to fully fed individuals. It might be speculated that poorer body condition in spring prior to the sea migration, triggers the sea trout to conduct longer marine migrations, as the

instinct for feeding might suppress the instinct to avoid negative effects of marine migrations, such as related cost of osmoregulation and swimming, and elevated risk of predation, pathogens and parasites. Such changes in the risk-taking behaviour have previously been documented by Damsgård et al. (1998) in Coho Salmon (*Oncorhynchus kisuch*, Walbaum 1972), who found that starved individuals had compensative growth after a starvation period, caused by increased boldness and feeding activity in the presence of predators. Compensative growth have furthermore been suggested by Marco-Rius et al. (2012) for sea trout post-smolts, in a study where body size attained in freshwater was found to be negatively related to growth during its first marine season.

Significant variation in the life history of short, medium and long distance migrants was found. Long distance migrants had significantly greater smolt-length than both short and medium distance migrants. Previous studies have revealed that larger brown trout parr is more likely to smoltify and adapt a migratory behaviour (Wysujack et al. 2009, Acolas et al. 2012). Hence, it may be speculated that larger body size of the sea trout smolt might further influence the extent and distance of the first migration, and that the migratory behaviour of the first migration shape the migration patterns the following years. The long distance migrants generally seemed, despite some non-significant differences, to have older age of smoltification, higher number of previous marine migrations, and a greater total age. Hence, it seems that older and more experienced marine migrants tend to migrate longer distance than less experienced migrants. However, the life history is likely to be greatly influenced by the conditions in its natal watercourse and by population characteristics. Thus, the observed differences in life history between short, medium and long distance migrants might be influenced by morphological or genetic traits of the different populations.

As scale reading is influenced by subjective evaluations, such results should be considered with care. The scale readings were based on a relative low number of scales sampled at tagging, and due to high proportions of replacement scales, a portion of the scale samples had to be excluded. Evaluation of individual scales might have been biased towards the general impression of scales in the tagging group. Despite the quantitative weakness of the presented scale readings, the results provided in the present study correspond with a study by Villar-Guerra et al (2013), who

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.

4.7 Behavioural differences between short, medium and long distance migrants

The present study revealed that long distance migrants had a shorter marine residence time than short and medium distance migrants. Possible reasons for the shorter marine stay of long distance migrants are further discussed in a subsequent section. The long distance migrants spent a minimal portion of their total marine residence time in the innermost areas of the fjord, compared to short and medium distance migrants, suggesting that these areas had limited value for long distance migrating individuals. Long distance migrants were found to have a significantly higher proportion of pelagic registrations compared to short distance migrants, when observed at ALSs across the arrays. This suggest that the long distance migrants had a higher degree of pelagic swimming and feeding behaviour. This was furthermore evident when investigating the monthly pelagic utilization of different migration groups at array H1, as short distance migrants tended to have lower proportions of pelagic registrations than long distance migrants in all summer months except April. Interestingly, the month of April had significantly higher portions of pelagic registrations than later in the season for the short distance migrants at array H1. This suggests that the marine behaviour is not determined before entering the sea, but is adapted during the first period in the marine environment, as previously suggested by Villar-Guerra et al. (2013) and Davidsen et al. (in review). Brown trout is known to adapt specialized feeding behaviour at least in parts of its ontogeny (Klemetsen et al. 2003), which might be a plausible explanation for the present observations of developing distinctions between short and long distance migrants regarding pelagic utilization.

The suspicion that there might be different feeding behaviour between the short and long distance migrants is strengthened when looking at swimming depth in the littoral and pelagic areas. Short distance migrants swim significantly deeper than long distance migrants, when recorded at ALSs containing littoral habitat within their range. In pelagic areas, no difference in swimming depth between long and short distance migrants was observed. Furthermore, while significant

difference in swimming depth between littoral and pelagic habitat was found for short distance migrants, no differences in swimming depth between these habitats were found for medium and long distance migrants. The long distance migrants thus seem to maintain a pelagic swimming behaviour even when observed close to the shore, supporting the hypothesis of difference in feeding behaviour between the short, medium and long distance migrants.

4.8 Is salmon lice responsible for reduced marine residence in long distance migrants?

The parasite salmon lice (*Lepeoptheirus salmonis* Krøyer, 1838) has over recent decades gained increasing attention as a threat for sea trout during its marine migration. The abundance of salmon lice is known to vary both in time and space (Tully and Whelan 1993), where high abundance is associated with salmon lice outbreaks in aquaculture intensive areas (Heuch et al. 2005). During the last decades the salmon lice infection rates in wild salmonids have increased (Tully et al. 1993, Tully and Whelan 1993, Bjørn et al. 2011), and salmon lice has been found to cause increased mortality related to sea migration (Skaala et al. 2014). Salmon lice infestation have furthermore caused reduction the marine residence for sea trout post-smolts, as heavily infested individuals tend to seek freshwater (Birkeland 1996). The premature return to the river is induced by osmoregulative failure (Birkeland and Jakobsen 1997), caused by sores in the mycoid and epidermis layer from the salmon lice parasitism (Grimnes and Jakobsen 1996).

In the present study, long distance migrants had significantly shorter total marine residence during the summer season than short migrating individuals. When residing in different areas, the sea trout is likely to experience different environmental conditions, as well as varying exposure to threats such as predators, pathogens and parasites. During the present study, and during fieldwork for another ongoing sea trout study on feeding behaviour in the study area, low infection rates of salmon lice on wild sea trout were observed. However, high infection rates by salmon lice on sea trout outside the study area was reported during the early summer of 2012 (Taranger et al. 2012). During early summer of 2013 lower sea lice infection rates was reported in outer areas compared to the early summer of 2012 (Taranger et al. 2012, 2014), yet the infection rates in outer areas might still have been higher than in the inner parts of the study area. Hence, it might be

speculated that higher salmon lice infestation rates in outer areas is the cause for the observed shorter marine residence for long distance migrants. However, previous studies have revealed that premature return from the sea mainly concerns sea trout post-smolts (Tully et al. 1993, Tully and Whelan 1993), and is thus not likely to have caused the observed difference in marine residency for the older and larger individuals in the present study. Furthermore, the long distance migrants in the present study tended to be older than the short distance migrants. Previous studies have revealed that older individuals generally return earlier from the marine migration (Nordeng 1977, Jonsson 1985), and might thus explain the observed difference in marine residency of short and long distance migrants. The migration further out in the fjord might have resulted in better feeding opportunities, which might have given sufficient growth and energy stores for spawning and overwintering in shorter time compared to short distance migrants, as investigations of feeding behaviour have shown that early summer is of most importance for feeding (Knutsen et al. 2001). Lastly, no significant difference in the marine residence time was observed for the long distance migrants in 2012 compared to 2013. As the reported salmon lice infection rates in outer areas differed greatly between these years (Taranger et al. 2012, 2014), the premature return of the long distance migrants would likely been more pronounced in 2012 than 2013, if salmon lice affected the marine residency of the tagged individuals. Despite the uncertainty whether or not salmon lice caused the reduced marine residence time for long migrating individuals, the groups of short, medium and long distance migrants were likely to experience different exposure to sea lice infestation, which might have caused different costs related to the marine migration, increased mortality rates, or ultimately altered fitness.

4.9 Marine behaviour as a possible conditional response, and its implications for population dynamics and future conservation of Norwegian sea trout stocks.

The present study indicate that there are variables such as genetics, ontogeny, morphological and life history characteristics witch might affect the behaviour of sea trout in the marine environment, both on population and individual level. This implies that sea trout should be managed on population level rather than on regional levels. Furthermore, the apparent mix of populations caught in the Søa watercourse in the present study indicate that some watercourses, might be important for both its own population and for neighbouring sea trout populations, and hence should be managed accordingly. In order for proper management of mixed populations, more research to map the genetics, behaviour as well as important areas for feeding, spawning and overwintering is needed.

While behavioural differences between and within sea trout populations are documented (Klemetsen et al. 2003, Villar-Guerra et al. 2013, Jensen et al. 2014), knowledge on the underlying causes for the observed wide range of marine behaviour is lacking. However, current research on the underlying causes affecting the brown trout to adapt resident or migratory behaviour, suggest a conditional strategy governed by both environmental conditions and heritage (Jonsson and Jonsson 1993). The results from the present study indicate, as previously suggested by Villar-Guerra (2013) and Davidsen et al (in review), that the marine behaviour is a continuum of such conditional response, affecting whether the sea trout remain in the innermost parts of the fjord close to its home watercourse, or migrate far out in the marine system. If such conditional response for the marine behaviour of sea trout exists, it implies that the marine behaviour of the sea trout can be altered, if the conditions in the marine environment change. It may be speculated that unfavourable conditions in the outer fjord areas might trigger residency in areas closer to the home watercourse and visa versa. As sea trout populations depend largely upon marine prey (Knutsen et al. 2001), the marine conditions determine the growth and survival of the individuals in the population. Fjørtoft et al. (2014) estimated a decrease in growth between 20 – 40 % during first two marine migrations for sea trout in the period from 2000 – 2007 compared to the period 1976 – 1982, in a recent study in the River Etneelva in southern Norway. Due to the strong correlation between female size and fecundity (Bagenal 1973, Fleming and

Gross 1990), the marine conditions will have significant effect on the recruiting stock in the population. Moreover, a population containing large individuals is often of higher interest for recreational fishing, and it is therefore desirable to preserve the population structure of such populations.

In terms of conservation of sea trout populations, the present study illustrates the importance of mapping the marine behaviour of sea trout, as the threats to the population depends heavily on the marine areas it utilize. Long-term series of data on environmental parameters will be useful to monitor environmental changes, and the response of the sea trout populations. Furthermore, it could be advocated that more research on the underlying causes for the wide range of the sea trout's marine behaviour is required, as it might prove to be essential for evaluating and modelling sea trout distribution, behaviour and main threats, and identifying necessary conservation measures for Norwegian sea trout stocks.

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