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Size dependency of spatial and temporal patterns of marine migration of sea trout (Salmo trutta L.) and Arctic char (Salvelinus alpinus (L.)) in Repparfjord Northern Norway

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Table of Contents

Summary

Acoustic telemetry was used to study the movements and habitat use of sea trout (*Salmo trutta* L.) and Arctic char (*Salvelinus alpinus* (L.)) in Repparfjord in Northern Norway during July until October 2010. In total, 18 trout and 8 char was internally tagged with acoustic depth temperature-tags (ADTT), and 6 trout and 3 char with identification-tags. Detected fish ranged in size with an average (mean±SE) of 27.8±1.6 cm for trout and 29.1±1.8 cm for char. All fish was monitored by 32 stationary hydrophones placed in zones over the fjord system during the whole time period in addition to manual tracking. Concerning temporal aspects results indicated that trout ascend earlier than char, contradicting other findings in areas close to the study area. However, no statistical analysis were carried out due to all fish were captured at sea so no descend time was recorded. Concerning spatial usage data showed results on distance to land and temperature preferences with fish length. However, species had a trend on distance to land and temperature, where char was observed closer to shore and in colder waters. Concerning zone there was a significant difference in spatial habitat usage on interaction between fish length and species as well as on species. There was a trend with a negative relationship on fish length and zone usage for char indicating that smaller fish seek further out in the system in addition to differences between species where trout occupied inner areas and char was detected more often in the outer areas of the system. This is in accordance with earlier studies that states species will exploit different areas of the system. Data collected from the ADTT-tags showed that trout on average preferred slightly warmer (0.7°C warmer) and shallower water (0.59 m. vs. 0.75 m.) than char. However, the only significant here was on temperature with a positive relationship over fish length.

1   Introduction

Competition for resources has lead to the evolution of behavioural differences between species that share similar ecology by minimising the effect of intra- and interspecific competition (Brannas, 2008). Here the term niche differentiation is applied in ecology. This refers to the process which in time lead natural selection to drive species into different niches. Niche relate to multidimensional habitat usage (Crow *et al.*, 2010), where similar species exploit different resources, so neither of the species outcompete the other i.e. competitive exclusion principle (Hardin, 1960). Coexistence will be achievable through their differentiation of their respective realized ecological niches (Armstrong & Mcgehee, 1980), hence sympatric species are expected to exploit different habitats which allows a stable coexistence between species (Crow *et al.*, 2010).

Arctic char (*Salvelinus alpinus)* and sea trout (*Salmo trutta)* are along with the Atlantic salmon (*Salmo salar*) found along the Norwegian coast. But of the three salmonids char is distributed further north and can be described as Arctic circumpolar (Beddow *et al.*, 1998; Klemetsen *et al.*, 2003). Anadromous Arctic char are predominantly found in its northern part of distribution (Beddow *et al.*, 1998; Rikardsen *et al.*, 2004).

Both trout and char have a high variety of life history, both between and in populations. Some of the most conspicuous strategies involve migrations to marine environments (Finstad *et al.*, 1989; Fleming & Gross, 1989; Jonsson & Jonsson, 1993; Beddow *et al.*, 1998; Rikardsen *et al.*, 2004; Urke *et al.,* 2010). They both reproduce and overwinter in fresh water, and normally first migrate out to sea as smolts (3-6 years). Thereafter they typically undertake two or three annual migration trips to sea before reaching the age of maturation (6-9 years) (Berg & Berg, 1993; Jensen *et al.*, 2005; Rikardsen *et al.*, 2007b). It is of significant importance that they grow fast to be able to withstand predation pressure, enhance their ability to manage harsh migration environments and achieve a body size that makes them more resistant to parasites etc. (Jonsson & Jonsson, 1993; Rikardsen *et al.*, 2000; Rikardsen & Elliott, 2000; Jensen *et al.*, 2005; Rikardsen *et al.*, 2007a; Rikardsen *et al.*, 2007b). To better understand their behaviour and ecology it is vital to obtain detailed overview on movements and habitat usage both temporal and spatial while they are out at open sea (Block *et al.*, 2002; Teo *et al.*, 2004).

The anadromous Arctic char and sea trout complete important parts of their growth while at sea over one or two months in summer in northern Norway where they feed in shallow areas

near shore (Klemetsen *et al.*, 2003; Jensen *et al.*, 2005; Rikardsen & Amundsen, 2005; Rikardsen *et al.*, 2007b). Both species are known to be opportunistic feeders in fresh and salt water, although there is some variation in their choice of prey. Where trout is reported to feed mainly on different fish species but can also feed crustaceans, insects and polychaetes, char is reported to feed more on planktonic crustaceans when feeding in the littoral zone (Berg & Berg, 1993; Rikardsen *et al.*, 2002a; Klemetsen *et al.*, 2003; Jensen *et al.*, 2005; Rikardsen & Amundsen, 2005; Rikardsen *et al.*, 2006; Rikardsen *et al.*, 2007a). However, their feeding pattern has been reported to be correlated with body length, with a change in preferred food after reaching a certain length (Berg & Berg, 1987b; Dempson *et al.*, 2002).

Few studies have investigated marine migratory pattern of sympatric trout and char, especially over vertically distributions in the sea. A study over marine migratory pattern of Icelandic sea trout in 1996 by use of Data Storage Tags (hereafter DST) that recorded depth, reported that fish spent most of their time in shallow waters (0-5 m) near shore with exceptions to a few dives down to 26 m (Sturlaugsson & Johannsson, 1996). Their results were supported in a study done by Rikardsen *et al.* (2007b) in Hals River in the Alta-fjord system in Finnmark located 85 kilometres south east from Repparfjord. They used DST-tags that recorded temperature and depth and found that trout moved in average 0.6 m deeper in the water and in 1.3°C warmer waters than char. Rikardsen hypothesised that the optimal areas for char were the cooler outer parts whereas trout preferred the warmer inner parts of the fjord-system. Other than this very little information exists for sympatric vertical distribution over the sea trout and Arctic char in other areas, especially considering the differences in habitat usage over differences in fish size.

There have been studies on differences in feeding patterns and habitat usage between the two species. Most of the research has been based on fish captures in the littoral zone, studies on stomach content and capture re-capture rather than studies of marine movements, and the marine phase has only been superficially investigated concerning instant depth/temperature measurements and location (Rikardsen *et al.*, 2002b; Jensen *et al.*, 2005; Rikardsen & Amundsen, 2005; Rikardsen *et al.*, 2007a; Rikardsen *et al.*, 2007b). It is hypothesised that the post-smolt distribution for at least sea trout at sea can be explained by the general preferences for shallower water.

Concerning temporal scale of the migratory pattern between species, early studies from Vardnes River in Northern Norway suggest that there is a different pattern for species

regarding the timing of migration, duration of sea residence, smolt-size at first migration and growth pattern during the migration (Berg & Berg, 1987a; 1989a; 1993; Jensen *et al.*, 2005).

The aim of this study was to examine and compare differences in temporal and spatial marine habitat usage of sea trout and Arctic char. The goal was to investigate differences between and within both species, in areas where they are present over the same time period. The difference in habitat use with fish size and species was specifically examined to look for contrasts between and within species. The expected result was findings of differences both between and within species concerning habitat usage, temperatures and depth. It was expected that trout would occupy areas closer to the river mouth and obtain higher temperatures than char. It was also expected that trout operate in deeper waters than char, and had a later retirement from their respective sea residence than char. Analysis was performed on information collected from tags with information on real time location, depth and temperature of the surrounding waters of fish collected during summer 2010 in the Repparfjord area.

2   Materials and methods

2.1   Study area

The study was conducted from July to October 2011 with wild fish collected from Repparfjorden, northern Norway (Fig. 1). Repparfjorden is located on 70° N; 24° E in Northern Norway and stretches 14 km south east of the island Kvaløya. The fjord-system consists of many small watercourses with anadromous fish present; however, the most important inlet of freshwater is Repparfjord River. Repparfjord River has a protected status as a national salmon river in Norway, and is reported to be among the top ten rivers in Norway regarding salmon. There are also sea trout and Arctic char stocks here, and the char are fully protected with a no-fish status (Anonym, 2007; Anon., 2010a; b).
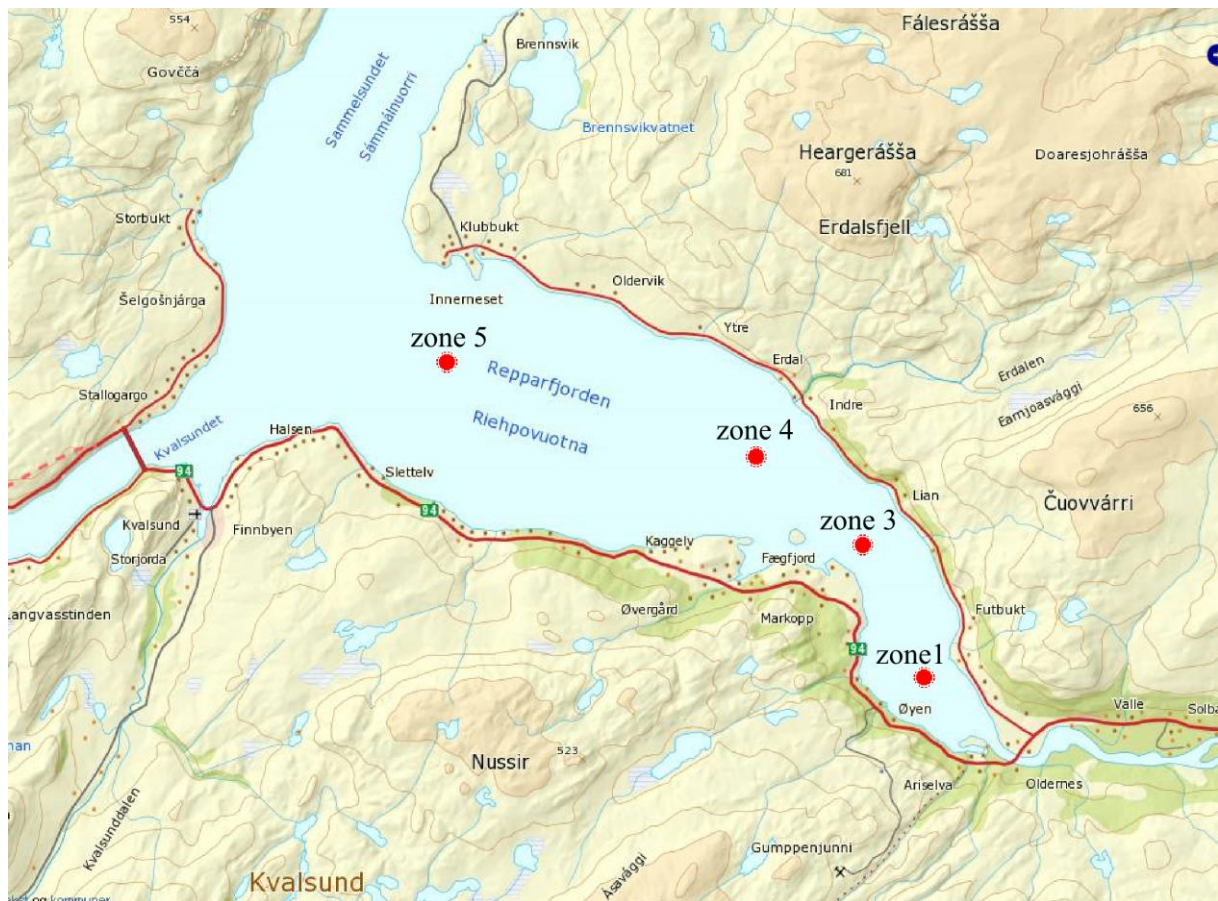
Figure 1. The Repparfjord area with CTD stations.

2.2 Fish collection and tagging methods

Fish was captured at sea using nets supplied from boat in order to catch the near-shore going fish during 20th – 21st July. The catch site was located approximately 1 km from the river mouth of Reppafjordelva on the northern side of zone 1 (Fig. 1).

The collected fish was internally tagged with acoustic transmitters, identification-tags (ID-tags) for fish under 23 cm, and Acoustic Depth and Temperature Transmitter (hereafter ADTT) for larger fish. The ADTT-tagged fish recorded the instant temperature and depth of the fish. Experiments involving tagging of fish with acoustic transmitters in combination with passive monitoring receivers have also shown to be a very cost effective way of studying underwater movements among fish, and have found a widespread use because of this (Thorstad *et al.*, 2007; Davidsen *et al.*, 2009, Urke *et al.* 2009).

In this study 18 trout and 8 char were tagged with ADTT-tags. In addition 3 char and 6 trout were tagged with ID-tags (Table 1). Size varied with 27.8±1.6 cm for trout and 29.1±1.8 cm for char (mean±SE).

Each ADTT-transmitter sent out two different IDs, with instant depth (range from 0-130 m) associated with even IDs and instant temperature (range 0-25.5°C) associated with odd IDs with transmission intervals on 180/240 sec. The transmitters weighed 6.9 grams in water, had a cylindrical shape with measures 13x40mm, manufactured by Thelma BioTel AS (Trondheim, Norway). The ADTT-tags had a spherical range of 450 m with battery capacity has been tested to 14.5 months.

Fish under 23 cm was marked with acoustic ID-tags (Thelma BioTel AS , Acoustic Smolt Transmitter, 7.3 mm). Transmitters were programmed with an individual semi-random delay/transmit sending schedule (transmission intervals 30/90 sec) with an average sending rate of 60 transmissions per hour to buoys moored in the fjord and river mouths. The transmitters had a spherical range of about 150 meters and battery capacity of 5.5 months.

All captured fish was kept in partly covered tanks in shady areas before operation. The surgical protocol for implanting acoustic tags followed the general recommendations given by Mulcahy (2003). Fish were pre-anaesthetised (0.5 mg*L^{-1} Metomidate, MarinilTM, Wildlife Labs., Inc., Fort Collins, CO, USA) for minimum 1.5 minutes. Fish were then transferred to an anaesthetic bath containing 60 mg L^{-1} Metacanium (MS 222, tricaine methane sulphonate). Fish reached surgical anaesthesia within 4 minutes, and was transferred to a V-shaped operating table with a continuous flow of water with 40 mg L^{-1} constantly pumped over the gills. A midline ventral incision of 1.5 cm enabled the placement of the tag into the coelom of the fish. The incision was closed with a single-layer, simple interrupted stitch pattern using a monofilament suture material (Resolon, 3/0 usp). The incision area was sealed by the use of a tissue adhesive (Histoacryl, Braun). Total length and weight of all fish were recorded. The whole procedure was completed within 5 minutes. After implantation functionality of the tag and fitness of fish was controlled by placing the fish in recovery tanks. Fish regained balance ability and showed active swimming ability within 1-2 minutes of recovery. After 1 hour the fish was released at the catch-site.

Table 1: Overview over number of tagged fish, and type of tag:

Species:	Number/type of tagged fish:	
	ID:	ADTT:
Char	3	8
Trout	6	18

2.3   Data collection

A network of passive receivers (VR2W, VEMCO Division AMIRIX Systems Inc. Halifax, Canada, www.vemco.com) was moored in the fjord with the acoustic protocol S256 at 69 kHz. The network consisted of 32 passive sonar buoys placed in transects with high resolution across the fjord (Fig. 2). Receivers continuously scanned for tag-signals and recorded date, time and codes from ID and ADTT-tags. In the fjord there was 4 zones with very high resolution (zone 1 through 4), in addition to near-shore buoys further out in the system (zone 5, Fig. 2). This was supplemented with manual tracking by the use of a portable receiver (VR100, VEMCO) in the fjord by use of motorboat in the time periods late May – Early July and early September –end September.
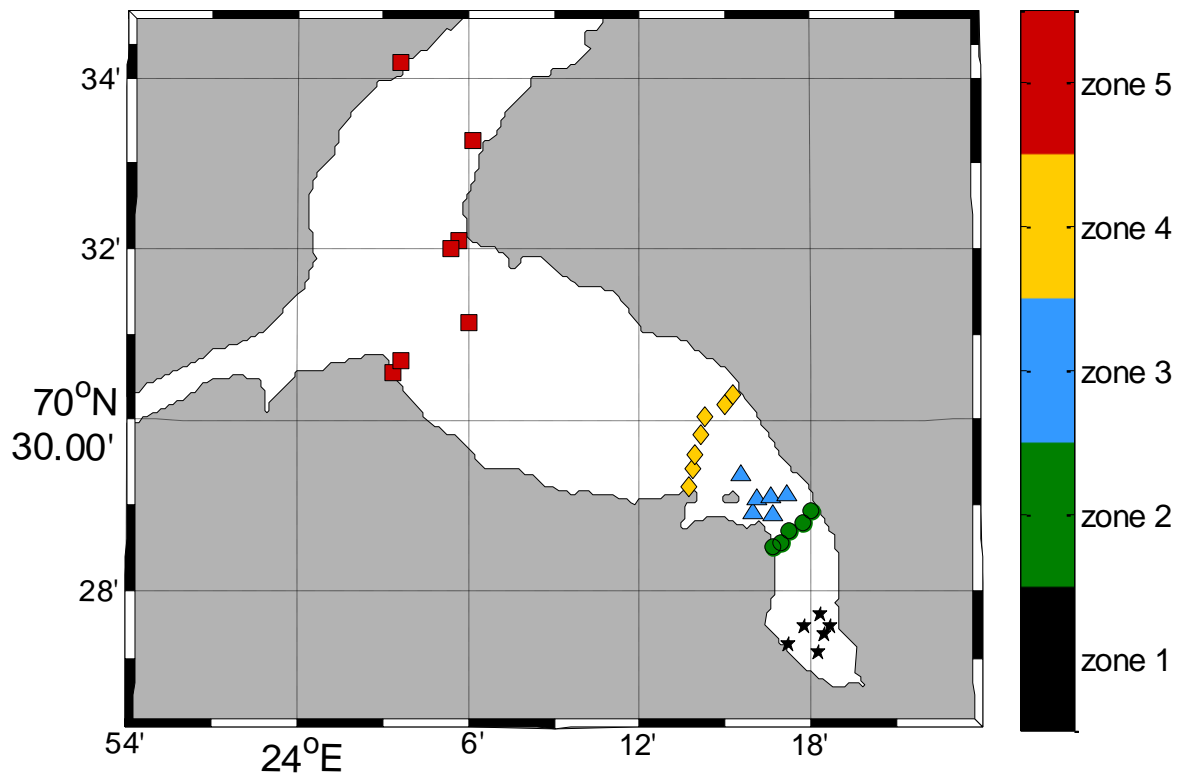

Figure 2: Map over the passive receivers placed in Repparfjorden with different zones (Zone 1:black stars, Zone 2: green circles, Zone 3:blue triangles, Zone 4:yellow upright squares, Zone 5: red squares.

2.4   Environmental information

Conductivity-Temperature-Depth (CTD) measurements in the fjord were recorded May 26th, June 26th, July 28th, August 3rd, August 10th and September 13th on zones 1, 2, 4 and 5 (Fig. 1) by the use of SAIV SD204 (www.saivas.no).

The sensor specifications (resolution and accuracy) for the different parameters were:
Temperature 0.001±0.01°C, salinity (from conductivity) 0.01±0.015 ppt., pressure 0.01 dbar
(m) ± 0.01% FS. The conductivity profiles together with temperature data were then
converted to salinity profiles using standard methods (Farmer & Freeland, 1983; Fofonoff &
Millard, 1983).

Temperature-loggers at three depths (1 m, 3 m, and at bottom: 55-65 m) were placed at
midfjord stations in zone 1 and 3 (Fig. 1) from May until mid-October.

Temperatures were plotted for zone 2 mid-fjord in the period from 20th July until 20th
September 2010 (Fig. 3). Temperature varied highly over depth and time at sea. There is a
clear variation in temperature concerning depth and it is obvious that there is a shift in the
stratification layers after the 15th August, where the system stabilises more and the
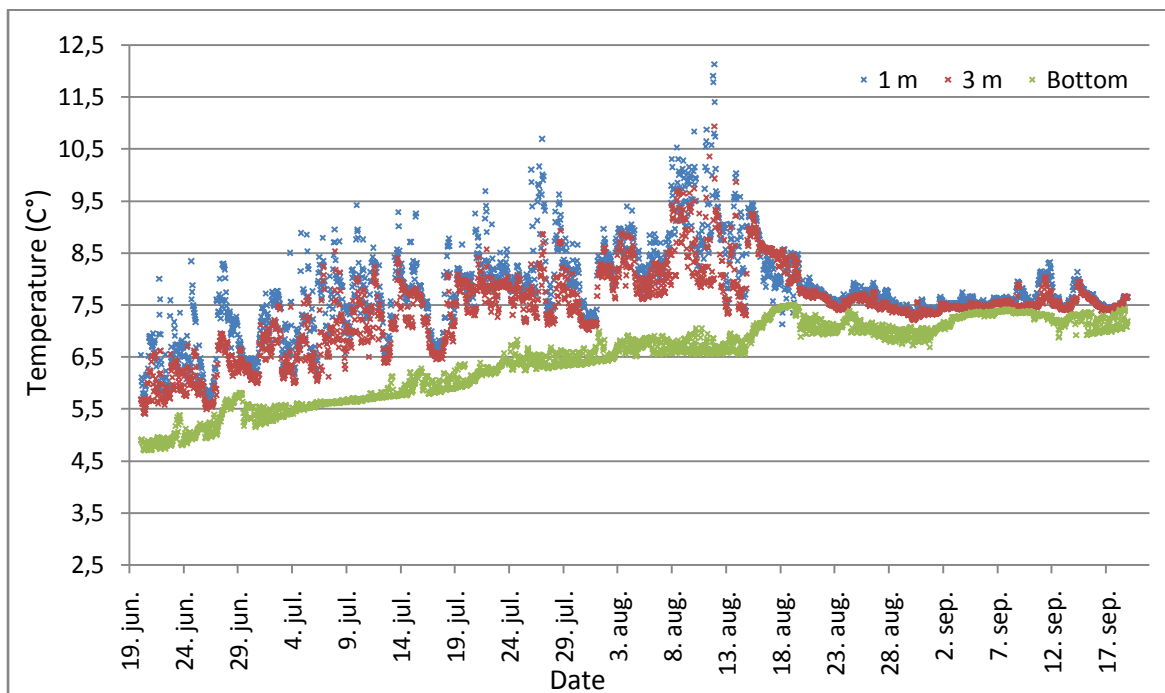temperature and salinity gradient is more uniform over depth (Appendix VI; VII).

Figure 3. Temperature variation 20th July – 20th September mid-fjord zone 2 in Repparfjord measured
on 1m, 3 m and bottom 55 m.

2.5 Statistical analysis

All statistics was analysed with the software R 2.10.0 (R Development core team, 2007). A p-value < 0.05 was considered significant results.

In order to estimate effects from species and fish length on spatial and temporal aspects, linear mixed effect models (LME) was fitted to the data. All models included fish length and species as fixed effects and were fitted to distance to land, distance to river, zone, temperature and depth as response variables. Individual ID was modelled as a random effect in order to account for observational dependency caused by repeated measures of the same individual. Data was checked for homogeneity of variance and normality of residuals by visual inspection of plots of residuals against fitted values. Response variables and fixed effects were log-transformed to better meet the assumptions of the model. The best model was determined by model selection based on all possible nested models of the full model. All model selection was done by the use of the Akaike Information Criterion (AIC) (Anderson & Burnham, 2002). The best model was the most parsimonious model with lowest AIC value.

Due to assumed high predation pressure on smaller fish in the system, fish ≤ 25 cm was tested for spatio-temporal changes. For this LME was used to test whether there was an effect of fish length ≤ 25 cm on distance to land or zone.

LME models were fitted for the time period 5th-15th August, since this period showed a variation in contrast to the rest of the period. Here models were fitted to distance to land/river, zone, temperature and depth.

Concerning sea residence, migration from sea was defined by last tag-detection in sea. Fish was present during the whole investigation period; however, the last trout was detected in the sea at the 20th September whilst char was detected until last day of investigation when equipment was removed from the sea on 15th October. In order to compare the two species concerning statistical analysis on spatial aspects, only detections from the period when both species was present was included, i.e. during period from 22nd June until 20th September

A total of 99 575 detections from 35 different fish (ADTT: 18 trout and 8 char, IDs: 6 trout and 3 char) was detected in the passive buoy network or by manual tracking during the time period from 22nd June until 20th September. Fish with less than 20 observations was omitted due to large variances within samples.

10

3 Results

3.1 Temporal aspects:

Concerning sea residence there was a clear difference between species (Fig. 4). Trout had a more uniform residence time, where tagged fish ascended over the same time period whereas char had a more scattered ascend within species. Trout had a large portion of detected fish leaving sea in just a two week period where 40 % of all tagged trout left during $17^{th} - 31^{st}$ August (Fig 4). There was no such pattern for char where there was an incline in fish migrating from sea over a longer time period than for trout during August until mid-October. There was no clear indication in data on differences in fish length on sea residence for species.
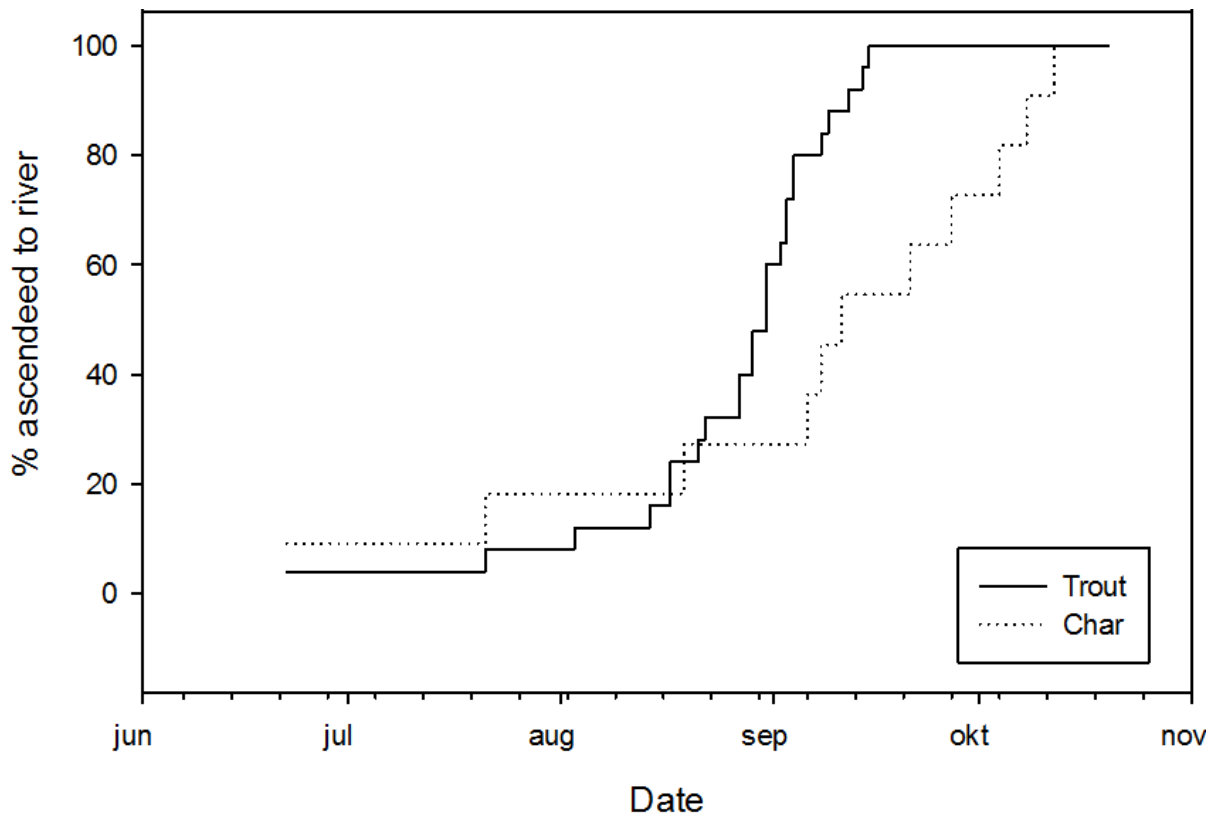

Figure 4. Cumulative ascent to river recorded for trout and char.

3.2   Spatial aspects:

3.2.1   Distance to land:

Concerning distance to land the best model contained only fish length (Appendix I). There was a positive relationship on distance to land of fish length ($\beta=0.24\pm0.09$, t=2.74, p=0.008, Appendix II). Larger individuals were more often observed further from shore. This relationship can be illustrated using average values for the whole period (Fig. 5). This indicated that smaller fish seek shallower areas whereas larger fish roam more around in the fjord system.
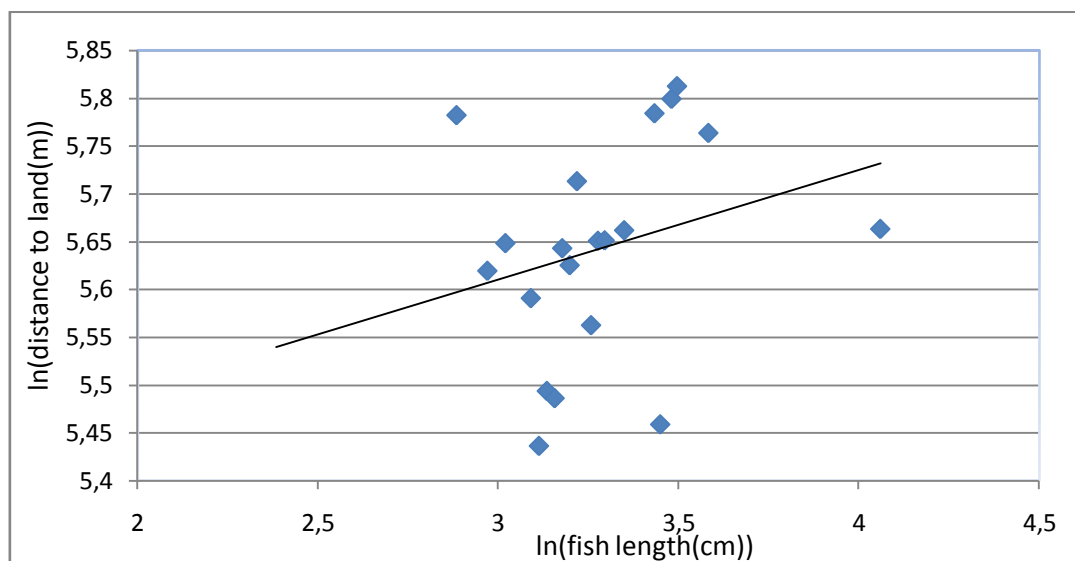

Figure 5. Log-transformed distance to land compared to fish length for all fish from 21st June until 20th September. $\beta=0.12$, $R^2=0.07$

3.2.2   Zonal variance between species:

The best model for zone usage contained fish length, species and interactions (Appendix I). There was a significant interaction effect between species (t=-2.61, p<0.05). For trout zone usage had no relationship on fish length ($\beta=-0.11\pm0.15$) whereas char had a negative relationship ($\beta=-0.94\pm0.36$), indicating smaller fish seek further out in the system (Appendix II). This could be illustrated by average fish size on all detection in different zones for both species (Fig. 6a). However, data points on zone 5 on char were represented only by 7 detections of one fish on 27 cm.

Concerning species there was a significant effect of zone usage (t=2.68, p<0.01, Appendix II). This suggested that char overall stayed further out in the system and was more often

represented in zones 2-5 than trout (Fig. 6b). 89.2% of all trout and 74.9% of all char detections were in the innermost zone closes to the river outlet. There was a higher detection rate in the outermost parts of the system by char, but the pattern indicated that both species favour the inner parts of the system (Fig. 6b).
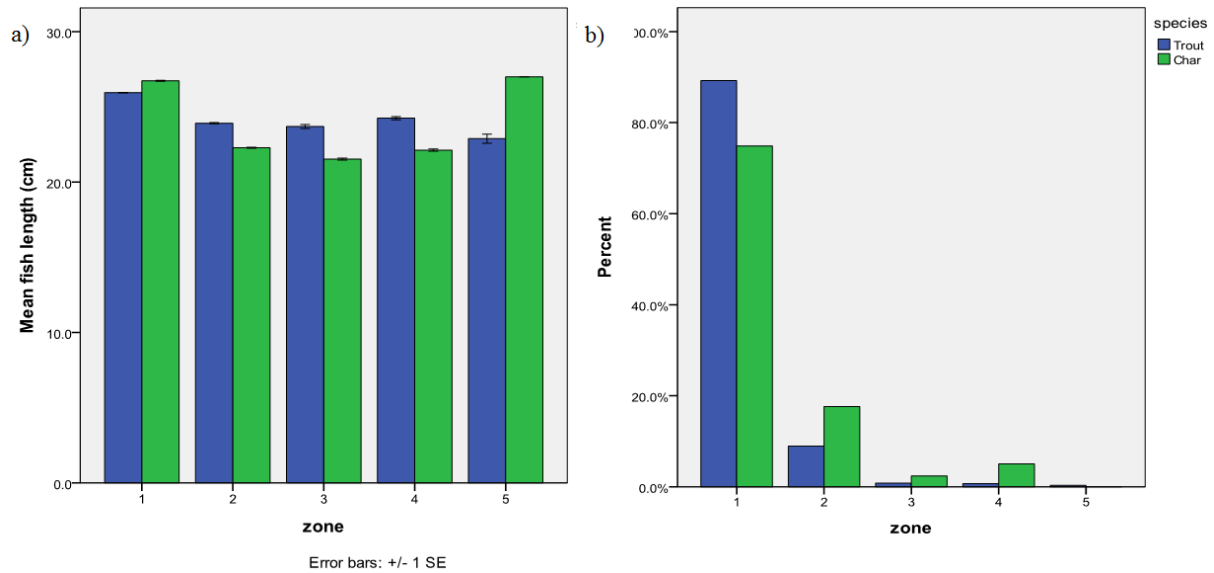

Error bars: +/- 1 SE

Figure 6. Overview of zones and differences between species. **a)** Mean fish length (cm) for the different zones (± SE). **b)** Total detection rates over zones for whole period.

The second best model included only fish length (Appendix II). There was a trend concerning zone-habitat usage of fish length (β=-0.279±0.146, t=-1.91, p=0.06, Fig 6a), where larger fish stay close to river outlet and smaller fish are more often detected on the outer zones (Zone 1: 26.16±0.016 cm, Zone 2: 23.16±0.027 cm, Zone 3: 22.47±0.076 cm, Zone 4: 22.64±0.066 cm, Zone 5: 23.02±0.30 cm).

3.2.3 Spatio-temporal variation for fish under 25 cm:

For fish ≤ 25 cm there was a significant change in distance to land over elapsed days. There was a positive relationship between elapsed days and spatial habitat-usage concerning distance to land (β=0.0029±0.0002, t=19.07, p<0.001, Appendix III). This relationship was also present when analysing the average values for all fish ≤ 25 cm (Fig. 7).
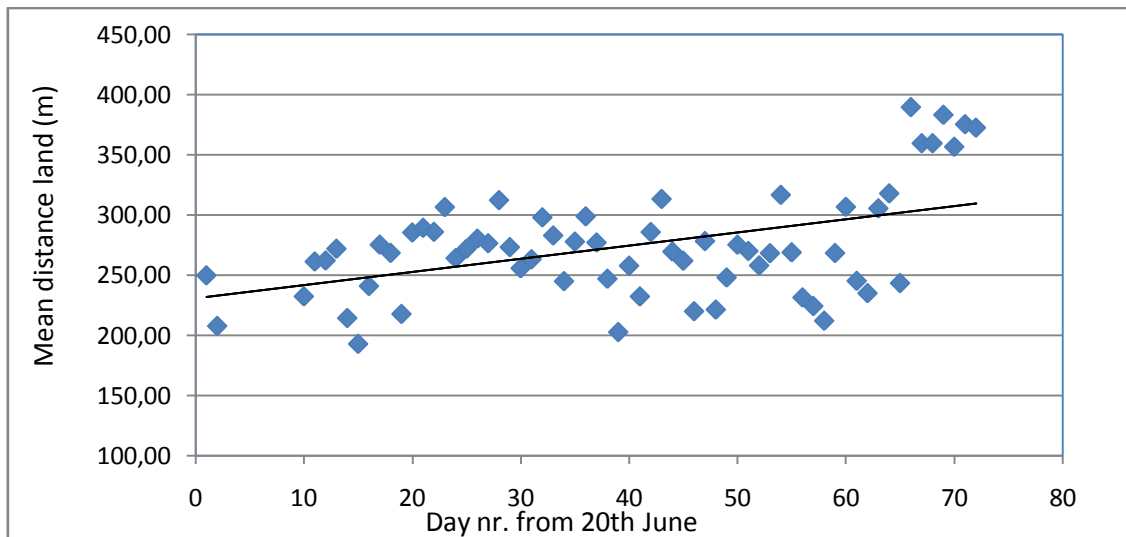
Figure 7. Fish ≤ 25cm. Mean distance to land over whole time period (β=1.09, R^2=0.22).

Concerning zone usage, there was an interaction effect between fish length and species for fish ≤ 25 cm (t=-2.78, p<0.05, Appendix III). For trout there was no relationship between zone use and fish length (β=0.56±0.76) whereas char had a strong negative relationship (β=-2.64±0.95). There was also an effect of species (t=-2.87, p<0.05) where trout preferred the innermost areas and char stayed further out. Trout had 86.4% of its total detections in the innermost zone whilst only 59.2% of all char detections were found here (Fig. 8). Concerning fish length, there was no clear effect of zone usage for fish ≤ 25 cm. This suggested that differences in zone habitat usage were mainly explained by species and interactions between species and fish length rather that fish length directly.
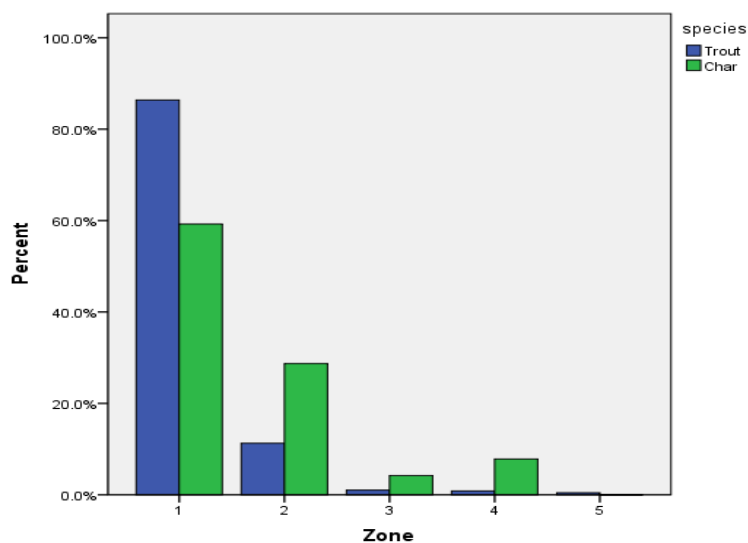

Figure 8. Total detection rates over zones for whole period for fish ≤ 25 cm.

14

3.2.4 Distance to river.

The best model on distance to river for all fish included fish length, species and interactions (Appendix I). There was a significant effect of fish length (t=3.45, p=0.001) which indicated a negative relationship between distance to river and fish length (Appendix II). There was also an interaction effect between species and fish length (t=-3.37, p<0.005). For trout there was no relationship between distance from river and fish length (β=-0.08±0.12) whereas char had a negative relationship with larger fish staying closer to the river outlet (β=-0.75±0.22). Plotting average values for all data point supported this analysis, however, with a sligth positive pattern for trout due to repetative measurements that were accounted for in the LME-models (Fig. 9).
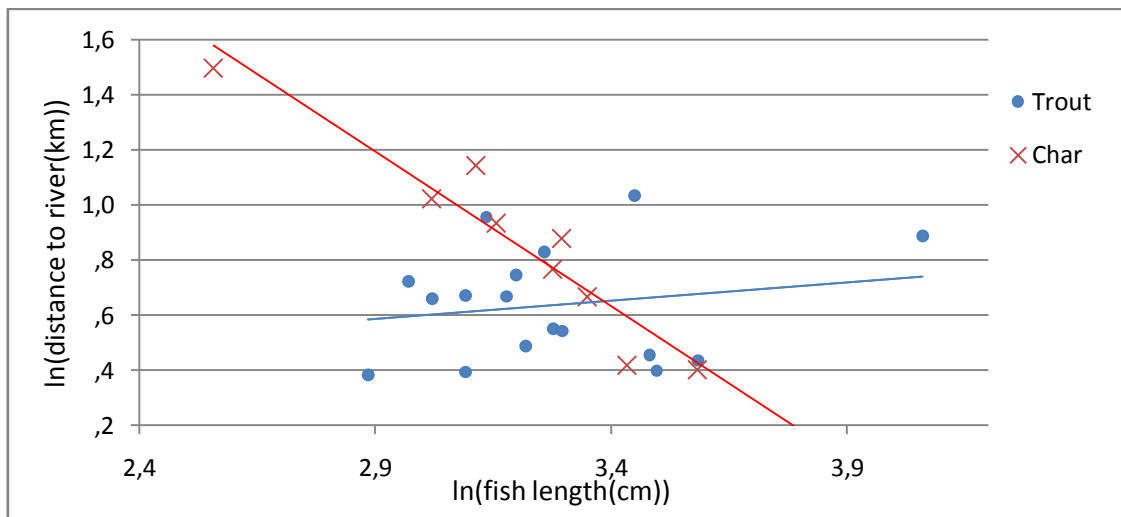
Figure 9. Average distance to river values on fish length. Log-transformed for graphical enhancement. Trout: β=0.13, R^2=0.03, char: β=-1.12, R^2=0.9.

3.2.5 Temperature and depth:

For temperature, the best model included just fish length, where there was a significant effect over the whole time period (t=2.25, p<0.05). A positive relationship between temperature and fish length (β=0.23±0.10) was detected, where larger fish had an overall higher temperature preference than smaller fish. Plotted with average values the relationship is still showing (Fig. 10). Concerning species there was a slight difference in average values (10.74±0.02°C and 10.03±0.03°C for trout and char respectively). However, the effect of species was not significant (β=-0.07±0.04, t=-1.59, p=0.13) when analysing the second best model (Appendix I; II).

15
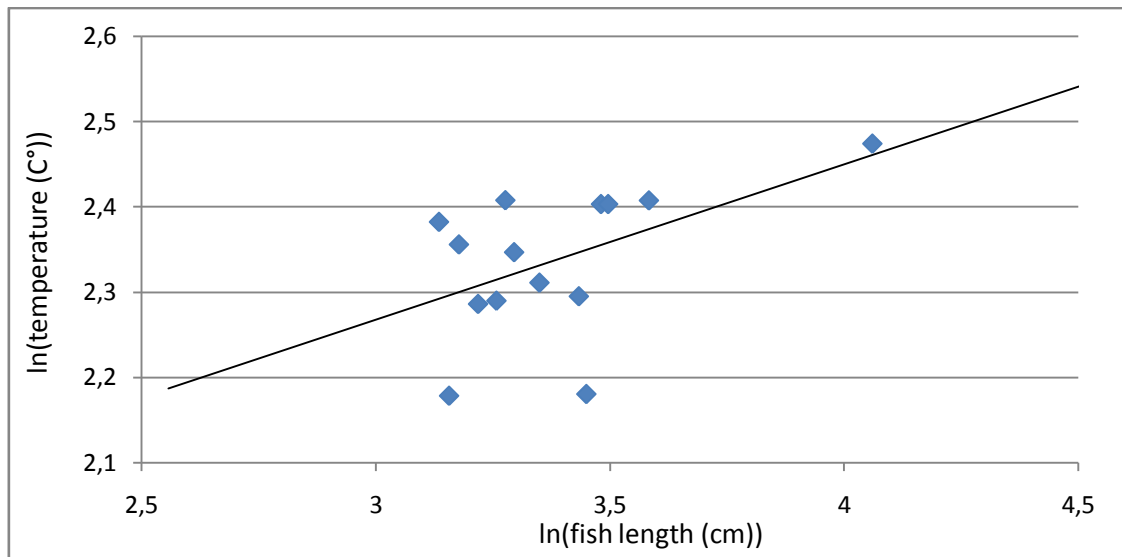
Figure 10. Log-transformed mean temperature from 21st June until 20th September compared to log-transformed fish length. (β=.18, R^2=0.26)

For depth, trout preferred on average more shallow areas than char (0.59±0.01 m vs. 0.75±0.01 m). The best model contained only species (Appendix I), but the effect was not significant (β=0.061±0.038, t=1.6, p=0.12, Appendix II). There was a similar non significant relationship when analysing the second best model which contained only fish length (β=0.05±0.11, t=0.43, p=0.67). This indicated that there were no apparent differences between species concerning depth preferences during the whole investigation period.

3.3 Temporal variation in temperature and depth preferences:

Over the whole data collection period there was a general good accordance between species concerning temperature and depth preferences; however, there was large variation between species in the period 5th-15th August (Fig. 11). During this period there was a distinction between species concerning habitat usage with different temperature and depth preferences. In order to seek out the causes for this differences data collected during this period was analysed further.

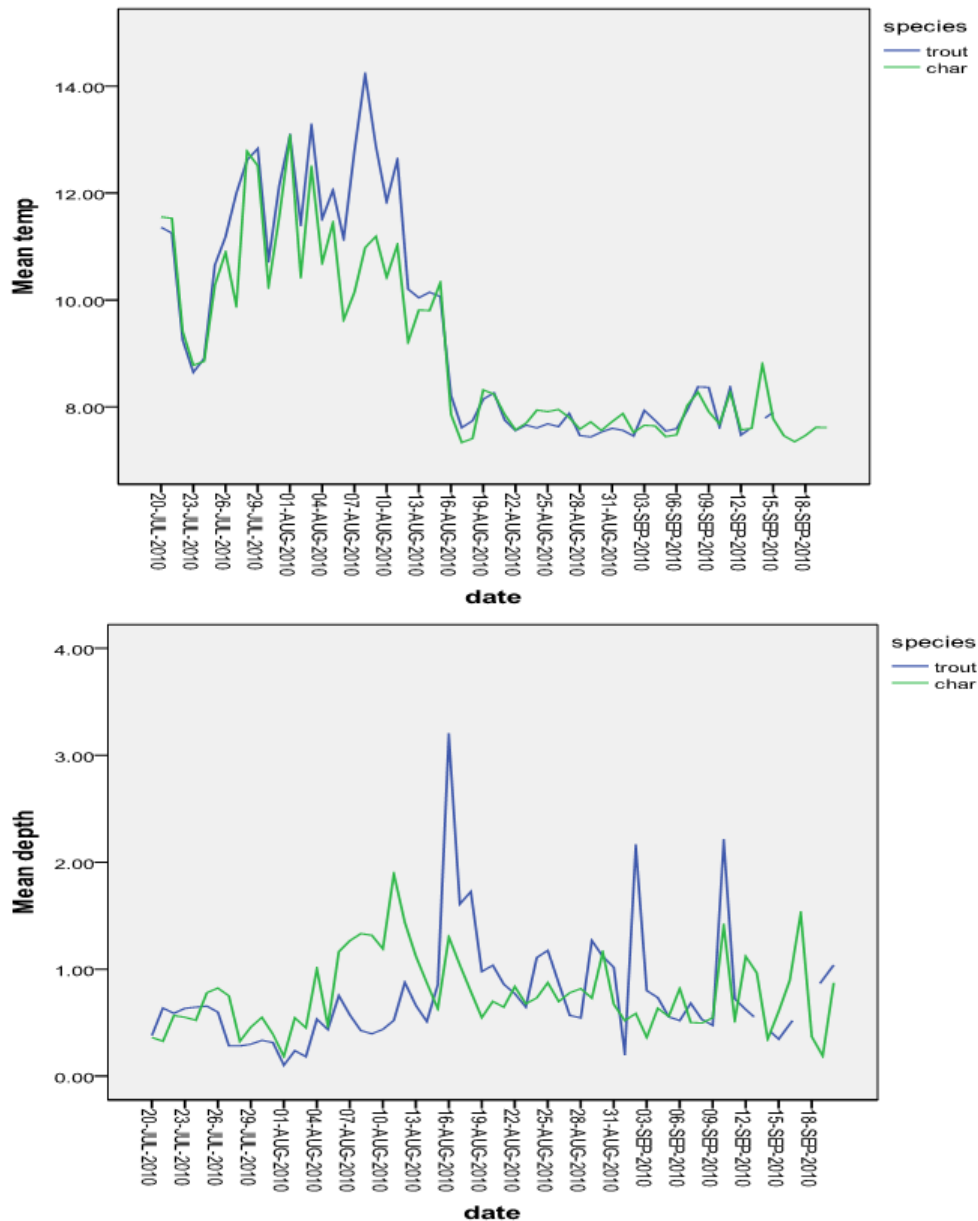**Figure 11.** Mean depth and temperatures recorded by ADTT-tags for over whole data collection period.

3.3.1 Distance to land 5th-15th August:

Concerning distance to land the best model included fish length, species and interaction effects (Appendix IV). There was a significant effect of species (t=-4.04, p<0.001) and interaction between species and fish length (t=3.85, p<0.001, Appendix V). For trout there was no significant relationship concerning distance to land on fish length on (β=-0.02±0.19) whereas char had a strongly negative relationship (β=-1.30±0.37). This was illustrated by plotting the average values for all fish over distance to land and fitting a linear regression lines (Fig. 12). However, this figure was plotted with simple regression analysis on average values, so the relationship for trout are incorrectly negative due to repeated measurements that was accounted for in the LME-models. This is in contrast to results from the whole time period where there was no significant interaction effect between species and the only significant factor was fish length. During 5th - 15th August there was no significance effect of fish length (t=-0.11, p=0.91). However, this might be explained by the interaction effect between species (Fig 12).
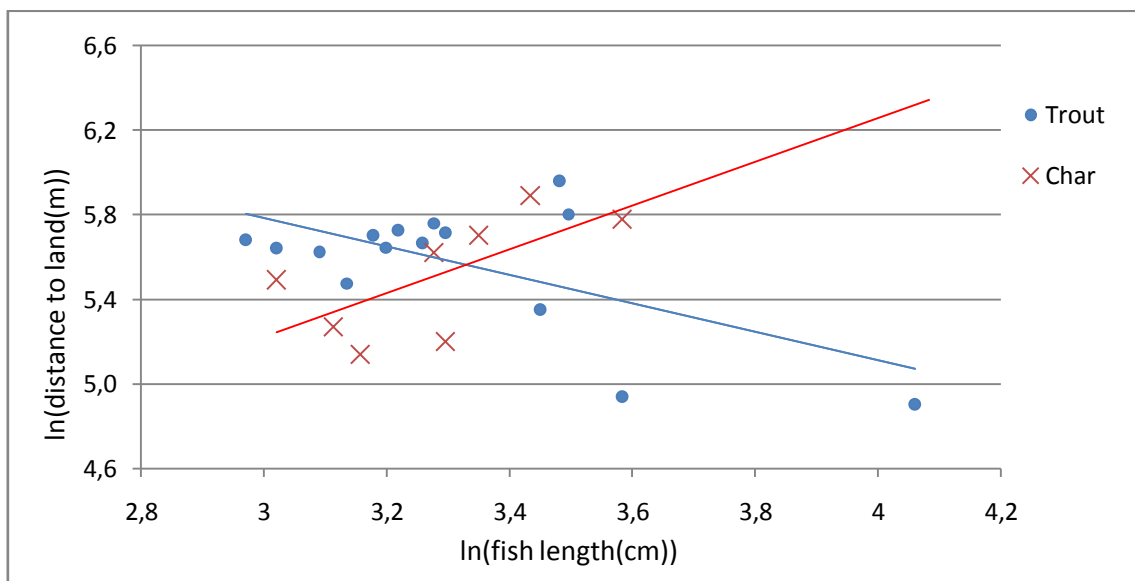
Figure 12. Log-transformed distance to land over fish length 5th-15th August with simple linear plotted regression lines. Trout β=-0.67, R^2=0.44, char β=1.03, R^2=0.38.

3.3.2 Zone 5.-15th August

Concerning zone, the best model contained fish length, species and interaction (Appendix IV). There was a clear effect of species (t=7.31, p<0.001, Appendix V), where trout had 90.8 % and char had 61.3 % of all their detections in zone 1 during the period. Char had 24.3 % of all detection on zone 2, a much higher proportion than for the rest of their sea residence. It was

apparent that char had a higher proportion of their detection further out in the sea. Trout could mainly be found in the 2 innermost zones, whereas char were frequently detected in the outermost zones (fig. 13).
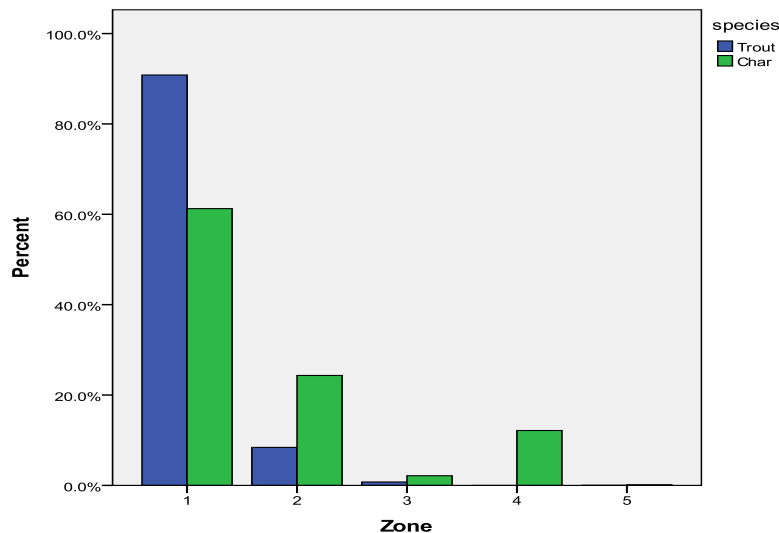
Figure 13. Total percentage of all detections showed over zones between species 5th -15th August.

The interaction effect between species was strongly significant (t=-7.04, p<0.001) as well as the effect of fish length (t=3.56, p<0.001). However, the latter results was highly influenced by one trout (ID#43) on 58 cm which was the only trout in the outer areas with 2 detection in zone 5 whereas there were no trout detections in zone 4.

3.3.3   Distance to river 5th -15th August

Concerning distance to river, the best model contained fish length, species and interactions (Appendix IV). There was a good accordance with results from the whole period with a significant effect of fish length (t=3.42, p<0.001), species (t=6.84, p<0.001) and interactions between these two (t=-6.63, p<0.001). For trout there was a positive relationship between distance to river and fish length (β=0.73±21) , while char have a negative relationship (β=-3.01±0.45). This indicated that larger trouts and smaller char are found closer to the river mouth.

3.3.4   Temperature and depth 5th-15th August

The best model for temperature included only fish length (Appendix IV). Here there was a significant negative relationship between temperature and fish length (t=-2.1, p<0.05, Appendix V). This suggested that larger fish seek colder areas than small fish in this period (β=-0.29±0.14). The relationship also apparent when plotting a simple regression on average

19

values for detection in period from 5th-15th August period (Fig. 14). This was contradicting the results from the rest of the study period which indicated that larger fish seek warmer water.
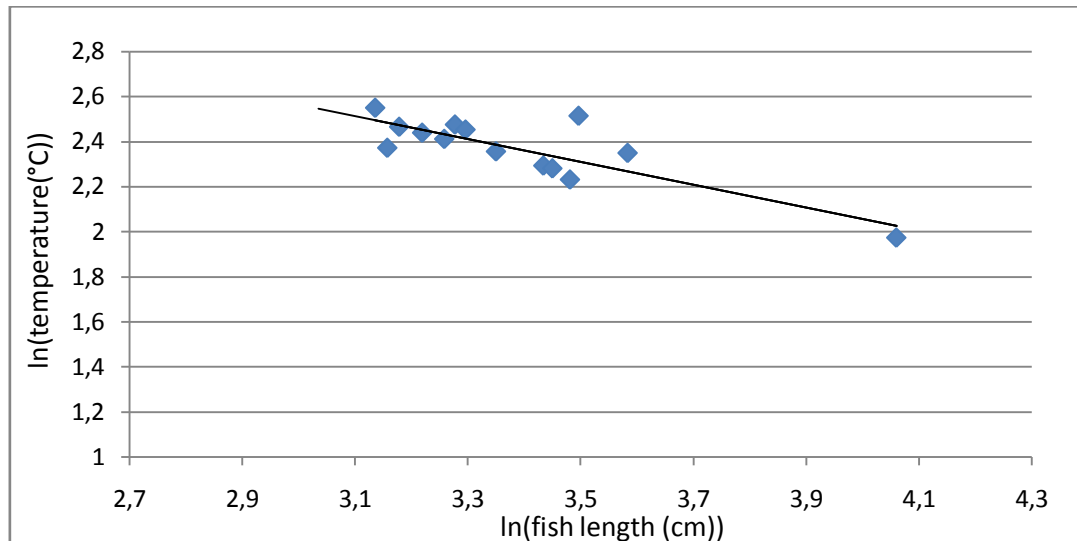
Figure 14. Log-transformed temperature on fish length 5th-15th August (β=-0.51, R^2=0.69)**.**

Concerning differences in temperature between species there was a mean of 11.87±0.03°C for trout and 10.36±0.04°C for char. The second best model included just species (Appendix IV), and showed a trend in the temperature data on preferences between species (β=-0.08±0.04, t=-2.01, p=0.058, Appendix V). This indicated char preferred colder areas. This refleced the results from the rest of period, but were more obvious during this period (Fig. 15a).
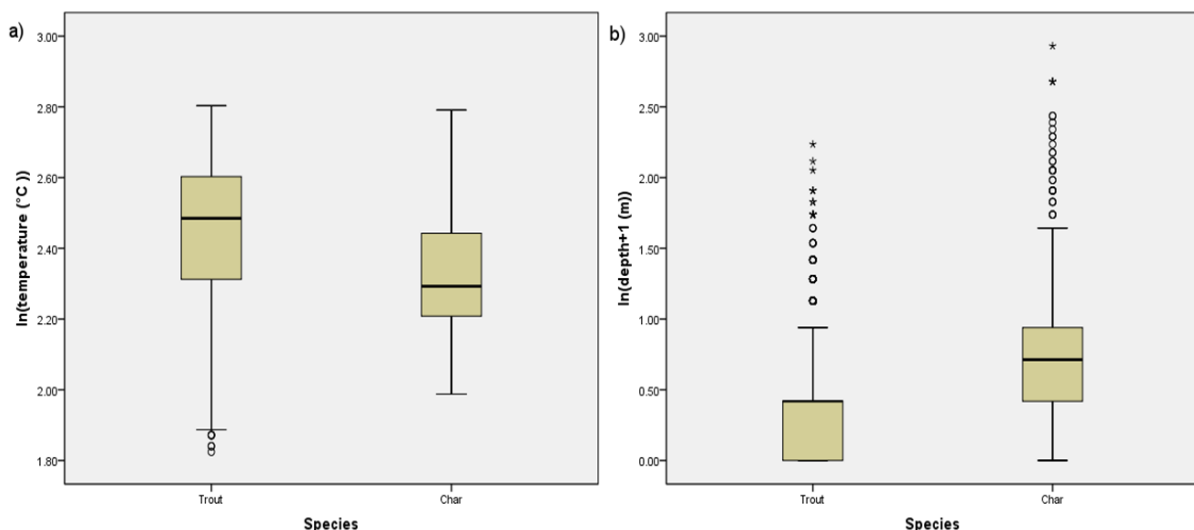
Figure 15. a) log-transformed temperature for species 5th-15th August. **b)** log-transformed depth +1 for species 5th – 15th August. Each box-plot shows the median (black line) of coefficients of variation, the interquatile (25%-75%) range, 1.5 times this range (brackets), and outliers (circle and stars)

On depth preferences, the best model included fish length, species and interactions (Appendix IV). Here species had a significant negative effect on depth preferences (t=-2.63, p<0.05, Appendix V). Simple average values indicate that char (1.18±0.03 m) stayed overall deeper in the water than trout (0.58±0.01 m) (fig. 15b). Outliers here was caused by occational deep dives for both speceis. Results indicated that there was a difference between species where char preferred deeper waters (Appendix V). This was in accordance with temperature differences on depth during this time period (Appendix VI). There was also an interaction effect between species and fish length (t=2.77, p<0.05), where trout had no relationship between depth and fish length (β=0.12±0.19) whereas char had a positive relationship (β=0.98±0.35). This was still apparent when plotting average values with a simple regression (Fig. 16). However, effect of fish length was non-significant (t=0.65, p=0.052).

Figure 16. Log-transformed depth+1 compared to fish length. Trout (β= -0.003, R^2=0.0001) char (β=1.37, R^2=0.78).

4   Discussion

This is one of the first studies that assess both horizontal and vertical distribution of sympatric sea trout and Arctic char. Earlier studies have either been on horizontal distribution by use of capture-recapture methods (Berg & Berg, 1987a; Berg & Jonsson, 1990; Berg & Berg, 1993), or on vertical distribution concerning the species by the use of data storage tags (Sturlaugsson & Johannsso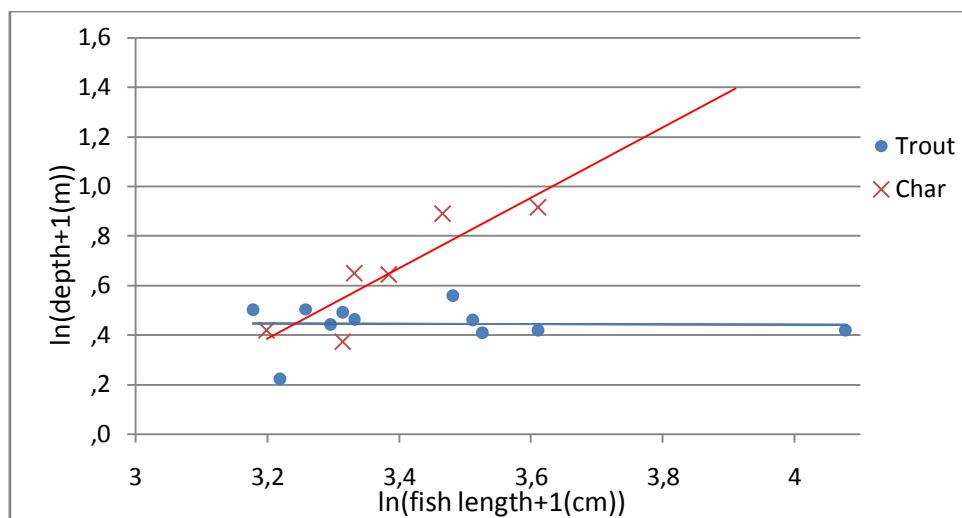n, 1996; Rikardsen *et al.*, 2007b). However, none of these studies could determine the location of the fish, and hence make it possible to directly compare the two species living sympatric in the same locality during their annual summer migration. The resolution of the buoy-network made it possible to assess differences in behaviour and analyse instant data concerning temperature, depth and position that were logged during time period from 20th July until 15th October 2010.

Results indicated that the main factors to explain differences between anadromous trout and char were interaction effects between fish length and species on spatial preferences, rather than just species. Fish length was the only explanatory factor concerning distance to land and temperature. Species was the only explanatory variable on distance to river during the whole time period, but there were also interaction effects between species and fish length. The results suggest a divergence between species on habitat usage. During 5th until 15th of August there was a shift in the overall trend where species and interactions between species and fish length are the explanatory factors on distance to land and depth. Here only temperature variation was best explained by fish length. This indicated that abiotic factors such as temperature and salinity explain much of the variation seen over time.

4.1   Temporal aspects:

Studies on capture- re-capture methods indicate longer marine residence for trout than char, with a divergence concerning size, where maturing fish tend to leave sea first, followed by non-maturing fish and then juveniles (Berg & Berg, 1989a; Johnson, 1989; Beddow *et al.*, 1998; Klemetsen *et al.*, 2003; Jensen *et al.*, 2005; Rikardsen *et al.*, 2007a; Rikardsen *et al.*, 2007b). However, Berg and Berg (1993) conducted a study in Vardnes River located in northern Norway and found no such correlation in char. Other studies also shows earlier descends for veterans than smolts in iteroparous salmonids, making the effective sea residence time for veterans equal as for non-maturing individuals and smolts (Jonsson *et al.*, 1990; Morita *et al.*, 2009). Also, recent studies have suggested that at least some trout individuals

overwinter in sea water and estuaries also in northern areas (Knutsen *et al.*, 2004; Jensen & Rikardsen, 2008).

Results indicated that char, in contrast to other studies, emigrated from sea later than trout. As all fish used in the analysis were captured at sea, there was no data on total sea residence for the respective species. There was only descriptive data on fish terminating sea residence, so no statistical analysis could be performed concerning duration of sea residence. However, the findings suggested that trout had a more uniform emigration from sea, with fish leaving sea in batches. This might be due to abiotic factors. As the temperature in sea stabilised over time it may become unprofitable for trout concerning optimal growth temperatures whereas the char might endure harsher environments on temperature on optimal growth as hypothesised by Rikardsen *et al.* (2007*b*). This is supported by the fact that char are a coldwater species with a circum polar distribution and hence well adapted to cool temperatures. It has also showed high growth rates at low temperatures (Berg & Berg, 1987b; 1989b; 1993; Klemetsen *et al.*, 2003). Jensen *et al.* (2005) concluded that sea residence for both species are highly influenced by sea temperature in June for the Alta system (85 km from Repparfjord). High June temperatures prolong the sea stay whereas warm August temperatures lead the species to ascend up river. This is in accordance with data for trout where there were relative high temperatures until the 15th August with a rapid temperature shift after this period. Here 40 % of all tagged trout disappeared from sea in a two week period (17.08 – 31.08). However, there was no such data on char in this period that supports this hypothesis. Here there was a steady incline of char ascending to river. This might indicate that char are not influenced by temperature in the same magnitude as trout, and are capable of utilising the resources at sea in cold temperatures. Because of these capabilities char might be able to exploit the marine environment for a longer time period than trout where the sea is cold rather than in warmer areas (Berg & Berg, 1987b; 1989b; 1993).

4.2   Spatial aspects:

Previous studies on sympatric behaviour between species have hypothesised that there will be differences in niches concerning habitat usage and feeding habitat between the two species (Jensen *et al.*, 2005; Rikardsen *et al.*, 2007b). Their research states that the differences can be explained by preferences on optimal feeding temperature between species. However, there is a lack of research that says anything about preferences on habitat usage concerning distance to land between sympatric trout and char.

23

In this study analysis on distance to land showed that the only significant factor was fish length. There was also a trend between species, but most of the differences in habitat usage could be described by fish length rather than species. The fact that distance to land was explained by fish length is logical considering predation pressure in the system. The expected result here was a positive relationship on fish length in accordance to habitat usage on shore-near areas versus more remote areas. This was supported in the data where there was a consistent pattern with larger fish feed further out from shore than fish ≤ 25 cm.

On the spatio-temporal variation over time for fish ≤ 25 cm there was a positive relationship between distances to land over elapsed days. This was expected since predation pressure might restrict the smaller fish closer to the shore. During their respective sea residence predation pressure might be more influential in the beginning of the time period. As fish grows over time there was a trend where they use areas further away from shore and thus have a niche shift in diet in accordance to earlier studies (Berg & Berg, 1987b; Dempson *et al.*, 2002). There was no interaction between fish length and species, this is supported by Jensen *et al.* (2005) who states both species have approximately the same growth rate whilst at sea (1.8% per day) and hence make both species capable to utilise areas further away from shore in accordance with day number concerning predation pressure.

Concerning spatial habitat usage, earlier studies indicated a difference between species, where trout occupied the innermost areas and char roam further out in the system (Jensen *et al.*, 2005; Rikardsen & Amundsen, 2005; Rikardsen *et al.*, 2007b). Results from this study suggested a difference in zone usage between species and an interaction effect on fish length over species. Concerning interaction effects there were no relationship for trout and a negative relationship for char. This suggested smaller char seek further out in the system. There was also a significant effect of species, with char utilising the outer zones in a larger degree than trout. The latter result supports earlier DST studies in nearby areas in Alta fjord-system (Rikardsen *et al.*, 2007b) which states that char will seek further out in the system to optimise feeding, where it is speculated that char have a lower temperature for optimal feeding (Jensen *et al.*, 2005). However, results indicated that fish length, at least for char, is an important factor concerning habitat utilisation in a fjord system.

Findings on zone usage were supported by analysis on distance to river. Distance to river was measured in kilometres, and because distance from river was measured as shortest linear distance, results here might deviate from analysis done on zones. However, there was a clear

24

interaction between species with no specific relationship for trout and a negative relationship for char. This suggests the two species have a difference in preferences not just between species, but over length as well. These findings support Rikardsen *et al.* (2007b) DST experiment from the Alta-system where they concluded that the two species operate in different parts of the fjord on their respective sea residence. Here it is thought that trout will occupy the warmer parts of the system, close to the river outlet whereas char go further out in the cooler areas of the system. However, they did not conclude anything concerning respective fish length and interaction here. From the data collected in this study there was an indication that behaviour concerning habitat usage in the fjord is controlled by length in interactions with species.

Concerning temperature the only significant explanatory factor found were fish length. There was a positive relationship where larger fish preferred higher temperature. Data revealed a difference between species (10.7±0.02C° for trout and 10.0±0.03C° for char), but there was no indication of a significant variation between specie. This is in contrast with earlier research which hypothesises that char prefer the cooler water to optimize their feeding behaviour (Jensen *et al.*, 2005; Rikardsen *et al.*, 2007b). There is supportive research that states that there is a higher temperature preferences concerning thermal limits for survival etc. (Berg & Berg, 1993; Lyytikainen *et al.*, 1997; Thyrel *et al.*, 1999; Larsson *et al.*, 2005; Elliott & Elliott, 2010), however, there is no evidence there is a difference in optimal temperatures for growth whilst at sea (Elliott, 1994). Larsson *et al.* (2005) conducted laboratory experiments where they found that trout on average preferred a higher optimal feeding temperature concerning growth (16°C) than char (11°C) which supports other studies in the nearby areas (Berg & Berg, 1993). However, the data Larsson *et al.* (2005) extracted was on freshwater habitats and no such data could be found on the two species whilst at sea. Also, the non-significant results here indicated that the differences while at sea are not so explicit.

Concerning depth preferences the expected result was a difference between species where char stayed in shallower areas than trout i.e. Rikardsen *et al.* 2007b. Results indicated a difference in mean depth on respectively 0.59±0.01 m. for trout and 0.75±0.01 m for char. However, there was no significant effect of fish length or between species during the whole time period. This is in contrast to other studies on sympatric behavior at sea between trout and char in the Alta-system located just 85 km south east from Repparfjord (Rikardsen *et al.*, 2007b). They concluded that trout on average lay deeper in the water column than char.

However, the results may be influenced by habitat differences concerning temperature stratification differences in the system. There was a wide variety on temperatures on depths over time in the system, with a heterogenic environment during July and beginning of August that changed rapidly after the 16th of August. After this period there was a larger degree of homogeneity on temperature concerning depths from 0–5 m (Appendix VI). This may explain some of the unexpected behavior that was observed on depth between species. Because of the large temperature variation on depth, char may seek deeper areas to optimize their feeding as the system shows great variance in temperature in early August in accordance to Jensen *et al.* (2005) and Rikardsen *et al.* (2007b).

4.3 Temporal variation in temperature and depth preferences:

There was a temperature shift from the 15th of August where the surface temperatures rapidly declined with about 4 C° over a period of just 3 days. This was succeeded by a shift in habitat usage between species with a vast difference between species concerning depth (Fig. 11). The system changed rapidly in August to a more homogeneous distribution concerning both salinity and temperature gradients over depths from 0-5 m (Appendix VI; VII). These are all explaining factors for the niche shift during the period, as well as a good indication that trout seem to terminate their sea residence due to these abiotic changes.

4.4 Differences between species in habitat usage 5th – 15th August:

The temperature shift after 16th August was caused by a hail storm (40 mm) (www.met.no). There was observed an change in behaviour during these day, where fish overall stayed deeper in the water coloumn. During the whole period data indicated a good correlation between species on temperature and depth preferences. However, the expected result was to see a larger variation between species on both temperature and depth in accordance with earlier research (Berg & Berg, 1987b; 1989b; Jensen *et al.*, 2005; Rikardsen & Amundsen, 2005; Rikardsen *et al.*, 2007a; Rikardsen *et al.*, 2007b).

For the whole period distance to land was best explained by fish length with a trend on differences between species. However, during the period from 5th until 15th August the pattern changed, here there was a clear interaction effect between fish length between species. Trout had a negative relationship concerning fish length and distance to land with large fish seek nearer shore whereas char had the opposite relationship with larger fish roamed further away

from shore. This might be an effect of differences in choice of prey, where the abundance of prey controls habitat usage of species.

Zone usage in the period from 5th until 15th of August illustrated a difference between species with trout having over 90% of all its detection in the innermost zone, whereas char only had 60% (Fig. 13). Here there were different preferences between species in accordance with earlier studies conducted in Alta (Rikardsen *et al.*, 2007b). This supports their hypothesis that char will seek further out in the system over their annual migrations than trout, which are known to keep close to the river outlet (Berg & Berg, 1987b; 1989b; Elliott, 1997; Dempson *et al.*, 2002; Rikardsen *et al.*, 2002a; Jensen *et al.*, 2005; Rikardsen & Amundsen, 2005; Rikardsen *et al.*, 2007a; Rikardsen *et al.*, 2007b). However, char have been reported to grow considerably better than trout at low water temperatures (Berg & Berg, 1987b; 1989b; 1993). This might partly explain the observed behavior where char seek further out because of less competition for resources and the differences on growth over temperature come into effect.

Zone usage in this period was supported by data found on distance to river, where there was a clear indication that char had a different preference concerning habitat measured in distance from river on fish length with a steep negative correlation that indicated smaller fish seek further out in the system. However, this relationship was not significantly expressed for trout. Here all fish seemed to obtain more or less the same areas during the whole period. This might be due to preferences for lower salinity gradients and higher temperatures in the inner parts of the system i.e. Rikardsen *et al.* (2007b) in addition to differences in prey choice.

Concerning temperature preferences during this period, the only explanatory factor was fish length as for the whole period. However, there was a shift here, where there was a positive relationship between fish length and temperature for the whole period, data suggested a negative relationship during $5^{th} – 15^{th}$ August. There was also larger variation between species, and a trend that indicated char had an overall lower temperature than trout. Concerning species it reflected the overall results during the whole period, but was more evident during this ten day period. This supports earlier research on temperature preferences concerning the species (Jensen *et al.*, 2005; Rikardsen *et al.*, 2007b; Elliott & Elliott, 2010). However, they had no data on differences over fish length for species.

Concerning depth there was detected significance between species as well as an interaction effect on species and fish length. Here char preferred deeper water than trout, which supports

temperature data found during this period. Stratification layers had a high variance concerning temperature in the beginning of August (Appendix VI). During this period char stayed further out in the system, this indicated char stay in waters with higher salinity gradients (Appendix VII). This indicates that char have a lower temperature and higher salinity tolerance than trout as reported from studies in Alta (Jensen *et al.*, 2005; Rikardsen *et al.*, 2007b). This result may also be explained by nutrition access and differences in diet over their sea residence i.e. Rikardsen *et al.* (2007a). The interaction effect found here with no relationship for trout and a positive relationship for char may be due to differences in prey preference over size. Here earlier studies indicate that trout change to an all-fish diet when reached 25 cm, where char have a more varied diet and switch to all-fish diet $\geq$ 40 cm (Rikardsen *et al.*, 2000; Knutsen *et al.*, 2001; Rikardsen & Amundsen, 2005; Rikardsen *et al.*, 2006). However, samples from trout (n=8, length range 18-23 cm) sampled July 21st at the marking site in Repparfjorden revealed 99 percent fish diet for this size group (Urke *et al.,* 2011). This indicates that there might be differences in areas in close approximation on diet over fish length. However, no data was collected on char.

Conclusion:

Concerning temporal habitat usage in marine migrations it has been hypothesised that species are the explaining factor. Here it is hypothesised that trout on average have an overall longer sea residence, with a later ascend to river than char. However, this study showed a uniform ascends for trout and later retirement for char.

Concerning spatial habitat usage earlier research indicate that trout have an overall higher temperature preference, stay closer to the river mouth as well as more often utilises deeper areas in the system than char. However, this study indicated that interactions between species and fish length are of importance concerning spatial usage of the system. There was a clear pattern where char preferred the outer parts of the system i.e. Rikardsen (2007b), however, there was also a negative relationship between distance to river and fish length for char. This indicates that fish lengths are an important explanatory factor concerning spatial habitat usage.

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6 Appendix:

Appendix I:

AIC-models of log-transformed variables on distance to land, temperature, zone and depth preferences concerning fish length and species.

Distance to land

Model:	Factors	AIC	ΔAIC	$e^{(-\Delta AIC/2)}$	Weight
1	Fish length	163784,4	0	1,00	0,87
2	Fish length + species	163789,5	5,1	0,08	0,07
3	Fish length * species	163791,0	6,6	0,04	0,03
4	Species	163791,2	6,8	0,03	0,03

Distance to river

Model:	Factors	AIC	ΔAIC	$e^{(-\Delta AIC/2)}$	Weight
1	Fish length * species	86684,7	0,0	1,00	0,77
2	Fish length	86687,3	2,7	0,26	0,20
3	Fish length + species	86692,1	7,5	0,02	0,02
4	Species	86695,0	10,3	0,01	0,00

Zone

Model:	Factors	AIC	ΔAIC	$e^{(-\Delta AIC/2)}$	Weight
1	Fish length * species	159434,1	0	1,00	0,48
2	Fish length	159434,5	0,4	0,82	0,39
3	Species	159437,9	3,8	0,15	0,07
4	Fish length + species	159438,4	4,3	0,12	0,06

Temperature

Model:	Factors	AIC	ΔAIC	$e^{(-\Delta AIC/2)}$	Weight
1	Fish length	-5029,9	0,0	1,00	0,77
2	Species	-5025,8	4,1	0,13	0,10
3	Fish length + species	-5025,7	4,2	0,12	0,10
4	Fish length * species	-5023,6	6,3	0,04	0,03

Depth

Model:	Factors	AIC	ΔAIC	$e^{(-\Delta AIC/2)}$	Weight
1	Species	21380,5	0,0	1,00	0,48
2	Fish length	21380,7	0,3	0,88	0,42
3	Fish length + species	21384,9	4,4	0,11	0,05
4	Fish length * species	21385,4	5,0	0,08	0,04

Appendix II:

Summary tables over log-transformed distance to land, zone distance to river, temperature and depth for whole period.

Distance to land

	Estimate ± SE	DF	t-value	p-value
(Intercept)	4.73±0.28	99481	16.72	<0.001
log(fish.length)	0.23±0.09	56	2.74	0.008

Zone

	Estimate ± SE	DF	t-value	p-value
(Intercept)	1.57±0.50	99330	3.12	0.002
log(fish.length)	-0.11±0.15	54	-0.75	0.458
as.factor(species)2	3.20±1.19	54	2.68	0.010
log(fish.length):as.factor(species)2	-0.94±0.36	54	-2.61	0.012

Distance to river

	Estimate ± SE	DF	t-value	p-value
#(Intercept)	0.87±0.41	99516	2.12	0.034
log(fish.length)	-0.08±0.12	55	-0.68	0.499
as.factor(species)2	2.51±0.73	55	3.45	0.001
log(fish.length):as.factor(species)2	-0.75±0.22	55	-3.37	0.001

Temperature

	Estimate ± SE	DF	t-value	p-value
(Intercept)	1.53±0.35	24932	4.43	<0.001
log(fish.length)	0.23±0.10	21	2.26	0.035

Depth

	Estimate ± SE	DF	t-value	p-value
(Intercept)	0.20±0.35	25464	0.57	0.567
log(fish.length)	0.05±0.11	20	0.51	0.615
as.factor(species)2	0.06±0.04	20	1.60	0.126

Appendix III:

Summary tables for distance to land and zone usage for fish ≤ 25 cm.

Distance to land over elapsed days for fish ≤ 25 cm

	Estimates ± SE	DF	t-value	p-value
Intercept	5.30±0.04	55453	125.07	0
Daynr.	0.0048±0.0001	55453	27.80	<0.001

Zone difference for fish ≤ 25 cm

	Estimates ±SE	DF	t-value	p-value
Intercept	-0.53±2.42	55357	-0.22	0.828
log(fish.length + 1)	0.56±0.76	17	0.73	0.475
Species	8.54±2.97	17	2.88	0.011
log(fish.length + 1) : species	-2.64±0.95	17	-2.79	0.013

Appendix IV:

AIC-table for model selection on log-transformed data extracted on $5^{th} - 15^{th}$ August.

Distance to land

Model:		AIC	ΔAIC	e(-ΔAIC/2)	Weight
1	Fish length * species	44574,14	0	1,00	0,994
2	Fish length + species	44585,63	11,49	0,00	0,003
3	Species	44585,96	11,82	0,00	0,003
4	Fish length	44592,21	18,07	0,00	0,000

Distance to river

Model:		AIC	ΔAIC	e(-ΔAIC/2)	Weight
1	Fish length * species	13969,58	0	1,00	1,000
2	Species	13999,05	29,47	0,00	0,000
3	Fish length + species	14001,07	31,49	0,00	0,000
4	Fish length	14005,58	36	0,00	0,000

Zone

Model:		AIC	ΔAIC	e(-ΔAIC/2)	Weight
1	Fish length * species	1109,02	0,00	1,00	1,000
2	Species	1140,37	31,36	0,00	0,000
3	Fish length + species	1143,01	34,00	0,00	0,000
4	Fish length	1150,51	41,50	0,00	0,000

Temperature

Model:		AIC	ΔAIC	e(-ΔAIC/2)	Weight
1	Fish length	-3992,61	0,00	1,00	0,721
2	Species	-3989,23	3,38	0,18	0,133
3	Fish length + species	-3988,88	3,73	0,15	0,112
4	Fish length * species	-3986,51	6,10	0,05	0,034

Depth

Model:		AIC	ΔAIC	e(-ΔAIC/2)	Weight
1	Fish length * species	5561,57	0,00	1,00	0,836
2	Fish length + species	5566,14	4,58	0,10	0,085
3	Species	5566,78	5,21	0,07	0,062
4	Fish length	5569,32	7,76	0,02	0,017

Appendix V:

Summary tables for log-transformeddistance to land, zone distance to river, temperature and depth for 5th – 15th August.

Distance to land 5.-15. August

	Estimates ± SE	DF	t-value	p-value
Intercept	5.60±0.63	24803	8.90	<0.001
Fish length	-0.02±0.19	50	-0.12	0.908
Species	-4.49±1.11	50	-4.04	<0.001
Fish length : species	1.30±0.34	50	3.85	<0.001

Zone 5.-15 August

	Estimates ± SE	DF	t-value	p-value
Intercept	-1.71±0.51	24765	-3.34	<0.001
Fish length	0.55±0.16	50	3.56	<0.001
Species	7.83±1.07	50	7.31	<0.001
Fish length : species	-2.28±0.32	50	-7.04	<0.001

Distance to river 5.-15. August

	Estimates ± SE	DF	t-value	p-value
Intercept	-1.83±0.71	24803	-2.58	0.010
Fish length	0.73±0.21	50	3.42	0.001
Species	10.28±1.50	50	6.84	<0.001
Fish length : species	-3.01±0.45	50	-6.63	<0.001

Temperature 5.-15. August

	Estimates ± SE	DF	t-value	p-value
Intercept	3.37±0.46	5967	7.26	<0.001
Fish length	-0.29±0.14	20	-2.10	0.049

Depth 5.-15 August

	Estimates ± SE	DF	t-value	p-value
Intercept	-0.03±0.63	6149	-0.05	0.961
Fish length	0.12±0.19	19	0.65	0.524
Species	-3.09±1.18	19	-2.63	0.017
Fish length : species	0.98±0.35	19	2.78	0.012
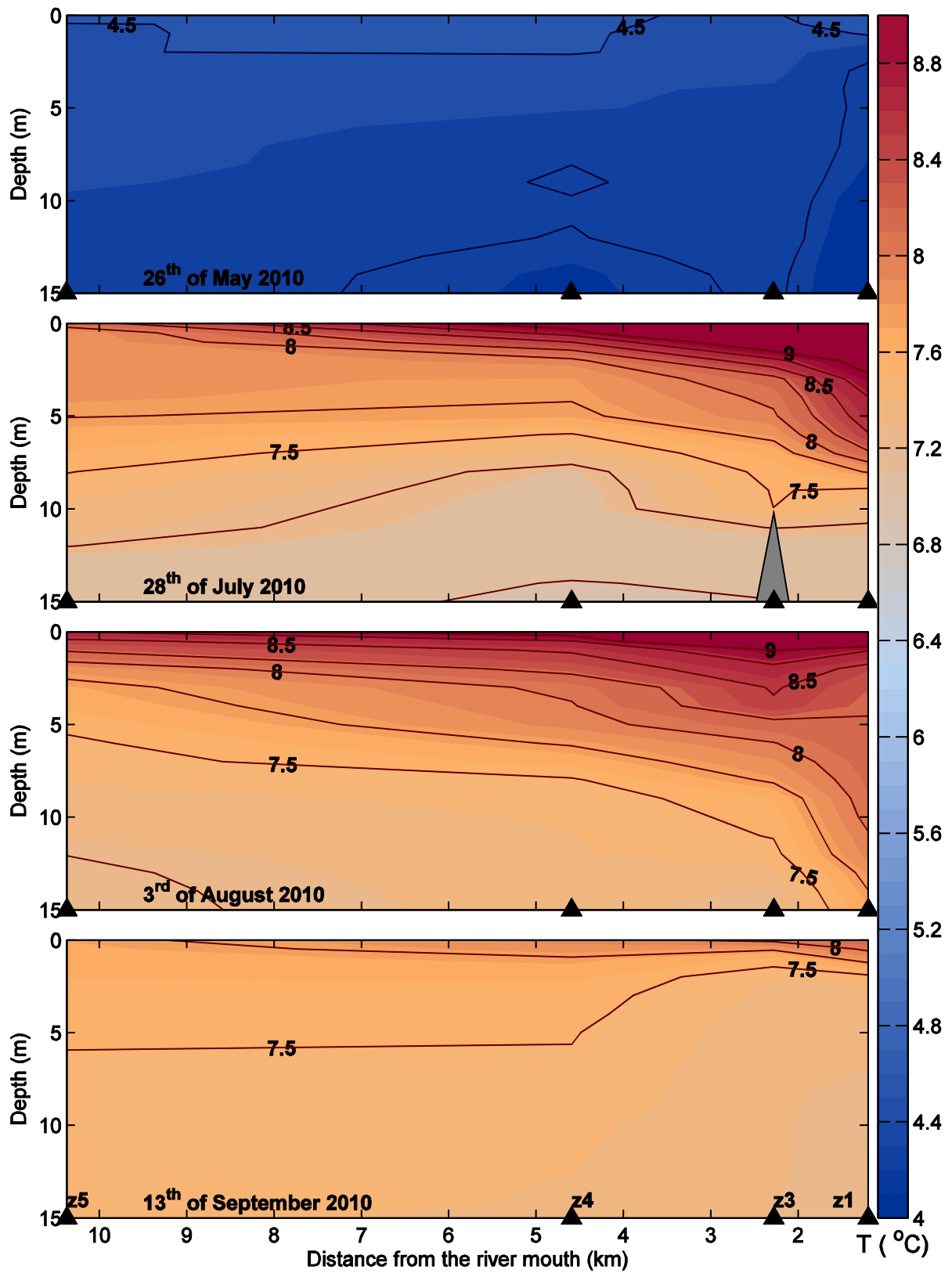
Contour plot of temperature of the fjord lengthwise over four time intervals. Color scale indicates salinity-values. Gray field marks depths where measurements failed. Black triangles indicate zones.
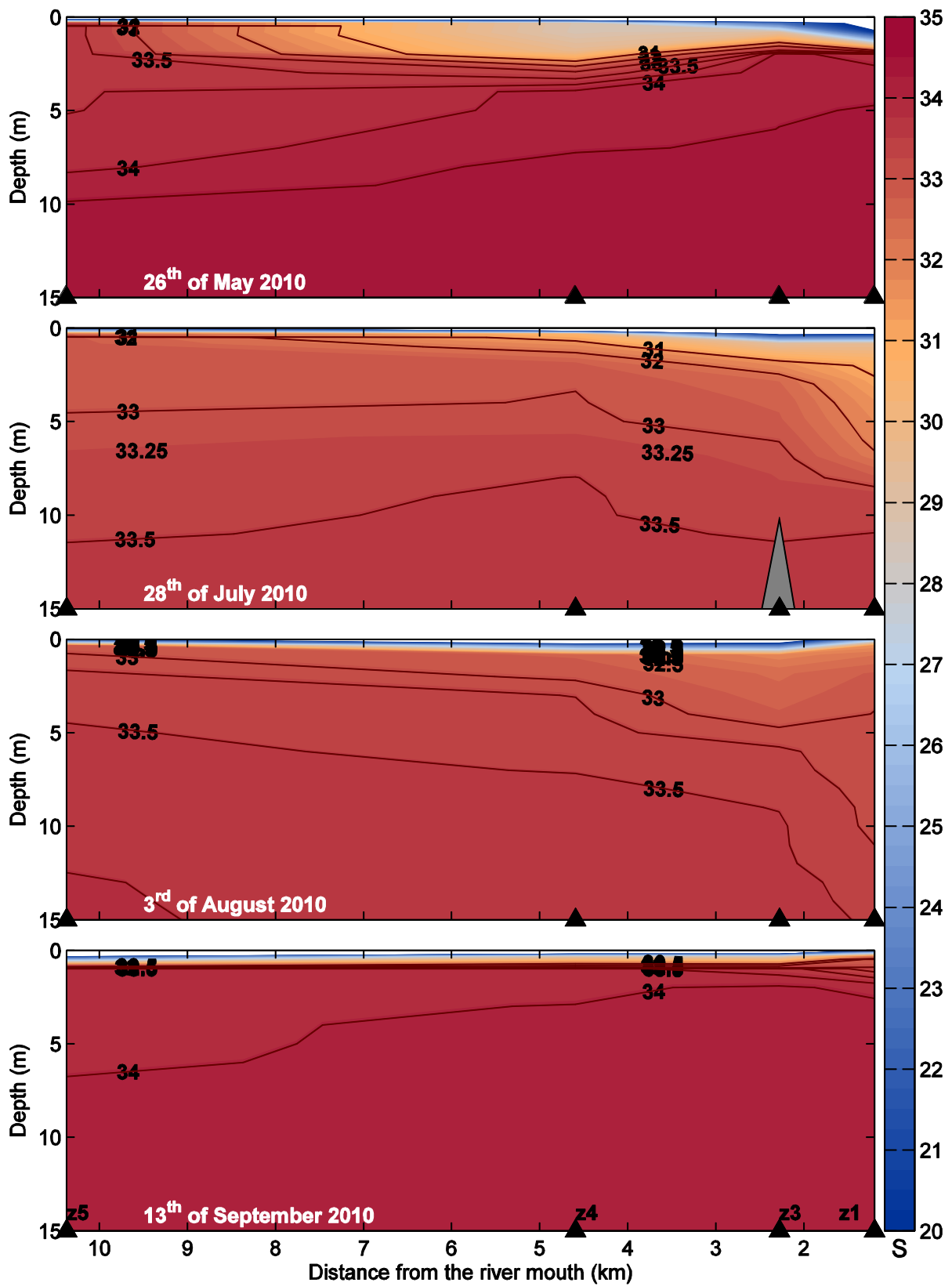
Contour plot of salinity in the fjord lengthwise over four time intervals. Color scale gives salinity-values. Gray field marks depths where measurements failed. Black triangles indicate zones (Fig. 2).