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The behaviour of anadromous Arctic charr during their first marine migration

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Abstract

Climate change-induced alterations of aquatic ecosystems, increased water temperature and human activity are substantial stressors to anadromous Arctic charr, and these are all expected to increase in the future. The knowledge of the marine behaviour of anadromous Arctic charr, especially post-smolts, is limited and few studies has described their residency at sea in detail. Therefore, more studies are needed to get a complete understanding of anadromous Arctic charr's feeding migration and how stressors as climate change and human activity interact with this life-history strategy.

The use of electronic tags in behavioural studies have recently revealed the marine migratory behaviour of Arctic charr, but these studies include almost solely adult individuals. In this thesis, I have investigated the migratory behaviour of 50 Arctic charr first-time migrants (post-smolt) in the Balsfjord, northern Norway, during their first summer at sea. Fish were tagged with acoustic tags with depth sensors and monitored by 76 acoustic receivers in both fresh water (n = 72) and at sea (n = 4) in the period 28th June–08th October 2018.

Arctic charr post-smolts were found to reside between 0–78 days at sea and experienced high survival with 82 % (n = 37) of the fish returning to fresh water. Fish were observed to re-enter their native river for assumed overwintering. Fish detections at four cross-fjord transects indicated the littoral habitat to be the most utilized habitat compared to the pelagic. Post-smolts showed a fidelity to depths between 0–3 m while at sea and a diel shift in depth use was observed. Furthermore, fish depth use varied between fjord sections and throughout the summer. Fish resided within 45 km from their native river, within the fjord system and utilized mostly mid-fjord areas and the eastern side of Balsfjord. Despite within-fjord residency, fish moved distances beyond 300 km during the summer and these total travelled distances correlated positively with fish size.

This study is one of the first to provide a detailed description of the spatiotemporal marine area use of Arctic charr post-smolts. The results presented here provide important information for coastal area management and conservation of anadromous Arctic charr populations and may also act as a reference during the ongoing climate change.

1 Introduction

Many species migrate from one habitat to another to maximize overall fitness (Gross, 1987). Amongst fishes, diadromy is a common migration pattern where individuals move between freshwater and saltwater habitats to feed and spawn (McDowall, 1997). At high latitudes, ocean productivity exceeds freshwater productivity (Gross et al., 1988), and the most common form of anadromy in these regions is anadromy, which is characterized by reproduction in fresh water and feeding in the marine environment (Jørgensen & Johnsen, 2014; Myers, 1949). For anadromous salmonids, the marine feeding migration represents a high-risk high-reward life-history strategy that may result in higher fitness by increased growth and fecundity, despite an increased mortality risk at sea (Jørgensen & Johnsen, 2014).

Arctic charr (*Salvelinus alpinus* L.) has a circumpolar distribution and is known to exhibit diverse life-histories strategies (Klemetsen et al., 2003). Anadromous populations of Arctic charr are present in the northernmost parts of its distribution area, including subarctic regions of Norway and Russia, the Bjørnøya Island, Svalbard Archipelago, Iceland, Greenland and Arctic Canada (Jørgensen & Johnsen, 2014; Klemetsen et al., 2003). Anadromous Arctic charr are partial migrants where one part of the population performs annual feeding migrations to the marine environment and the other part remains in fresh water (Jørgensen & Johnsen, 2014; Klemetsen et al., 2003). The degree of anadromy is related to individual conditional traits such as growth rate, lipid content and body size of juveniles, irrespective of parental phenotype (Rikardsen & Elliott, 2000). The freshwater juvenile stage (parr) varies from 1–9 years depending on latitude and climate (Jensen et al., 2012; Klemetsen et al., 2003; Rikardsen & Elliott, 2000), with juveniles in colder watercourses smoltifying at an older age due to slower growth rates (Bottengård & Jørgensen, 2008). The timing of the seaward migration is regulated by freshwater temperature, waterflow and light and will vary between years (Jensen et al., 2012). After entering the marine habitat, Arctic charr reside 30–60 days at sea depending on fish size and latitude (Jørgensen & Johnsen, 2014). Annual mean sea residency of 23–54 days has been reported for first-time migrants (Berg & Berg, 1993; Jensen et al., 2019), while veterans typically reside a few days longer at sea, between 41–68 days (Berg & Berg, 1993). However, large between-year variations in marine residency occur (Berg & Berg, 1993). At sea, charr mainly reside in the upper 3 meters of the water column in nearshore habitats (Harris et al., 2020; Jensen et al., 2014, 2016; Spares et al., 2012). The

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dispersion distances during the marine migration normally confine within 30 km from the natal watercourse (Rikardsen et al., 2007a), but individuals travelling distances between 100–940 km away from their native river has been reported in northern Norway (Jensen & Berg, 1977). After the first migration to sea, most Arctic charr continue an anadromous behaviour, however some migratory individuals can stay as residents in freshwater over a year or become permanently resident (Jensen et al., 2019). Immature charr migrate up to four times to the sea before they return as sexually mature to reproduce (Gulseth & Nilssen, 2001). After maturation, fish continue to reproduce every year (Jørgensen & Johnsen, 2014). The overwintering mainly occurs in freshwaters as tolerance for combined high salinities and cold sea temperatures is low for Arctic charr (Dempson, 1993), but estuary overwintering has been observed (Jensen & Rikardsen, 2012). Arctic charr exhibit homing to its native watercourse, however straying to nearby rivers and overwintering in other watercourses occasionally occur (Jensen et al., 2015). The high growth obtained at sea correlates with increased fecundity and winter survival (Jensen et al., 2018). However, detailed information of the spatiotemporal distribution of individuals during the marine migration are not well documented.

At high latitudes, aquatic ecosystems are experiencing more rapid climate change than freshwater and marine systems in tropical and temperate regions (Parmesan, 2006). The current temperature increase in oceans and freshwaters has contributed to altered ecosystems and changed behaviour for some species (Parmesan, 2007), including migratory species (Finstad & Hein, 2012; Visser et al., 2009). Anadromous Arctic charr is currently experiencing changes in both marine and freshwater habitats (Andersson et al., 2015; Finstad & Hein, 2012). While increased water temperatures and primary production in river and lakes may increase the abundance of sympatric species more tolerant to warmer temperatures, such as brown trout (*Salmo trutta* L.) (Rolls et al., 2017), little is known of the impacts of climate change on the marine segments of the life-cycle. In addition to climate change, anthropogenic activities impact wildlife (Halpern et al., 2015). Along the Norwegian coast, one of the biggest stressors to anadromous salmonids is the elevated density of salmon lice (*Lepeoptheirus salmonis*, Krøyer) in areas with open-net pen farming of Atlantic salmon (*Salmo salar* L.) (Bøhn et al., 2020; Serra-Llinares et al., 2020; Vollset et al., 2018). Currently, most salmon farming occurs in coastal waters in southwestern and mid-Norway, outside the distribution range of anadromous Arctic charr (Otero et al., 2011). However, the Norwegian aquaculture industry is expected to expand northwards (Vollset et al., 2021). This

will likely increase the densities of salmon lice in the pristine costal feeding areas of the anadromous Arctic charr, potentially impacting their behaviour, growth, and survival in the marine environment. The combined effects of climate change, increasing human activity and increased parasite infection risk at sea could make the marine habitat less profitable and might reduce the degree of anadromy in Norwegian mainland Arctic charr populations (Finstad & Hein, 2012). Therefore, monitoring the marine migration of Arctic charr, including their behaviour and space use at sea, is crucial for the conservation of anadromous populations.

In aquatic environments, a common way to study animal movements is by the use of telemetry (Thorstad et al., 2013). Numerous studies have highlighted novel aspects of the marine migration of anadromous salmonids using a variety of telemetry methods (Eldøy et al., 2015; Jensen & Rikardsen, 2012; Seitz et al., 2019; Strøm et al., 2019). In recent years, the marine migrations of Arctic charr at sea have been documented by acoustic telemetry (Harris et al., 2020; Jensen et al., 2014, 2016) which is often used for studying the spatial ecology of fish in fjords and coastal areas (Kessel et al., 2014). Fish tagged with acoustic transmitters can be detected by acoustic stationary receivers (hydrophones) within a detection range, where fish identity, timestamps, and sensor values (*e.g.*depth and temperature) can be transmitted to the receiver and stored (Thorstad et al., 2013). Thus, fish can be passively positioned in both time and space during the study period. Behavioural studies on anadromous brown trout and Atlantic salmon (*Salmo salar* L.) post-smolts are well represented in the literature (Flaten et al., 2016; Halttunen et al., 2018; Thorstad et al., 2007). However, telemetry studies of Arctic charr include almost solely adults (Harris et al., 2020; Jensen et al., 2014, 2016), and to my knowledge, only one study (Atencio et al., 2021), has described the behaviour and movements of post-smolts (first-time migrants) at sea.

The aim of the thesis is to expand upon the limited knowledge of the behaviour of Arctic charr post-smolts. Here, I investigate freshwater returns, marine space use, depth use and migration distances of Arctic charr post-smolts from the Laksvatn watercourse in northern Norway by testing the following hypotheses:

 1) Arctic charr post-smolts reside close to their native watercourse while at sea.

 2) While at sea, post-smolts utilize the littoral zone more than the pelagic zone.

3) Post-smolts utilize the upper 0–3 meters of the water column at sea.

4) Arctic charr return to their home river to overwinter.

2 Methods

2.1 Study area

Laksvatn watercourse

The Laksvatn watercourse (69.23 N' 19.23 E') is situated in the subarctic Balsfjord in northern Norway (Figure 1). The watercourse has a catchment area of 13.3 km^2 and includes the Lake Laksvatn (0.8 km^2) situated at 6 m above sea level 0.6 km from the sea. The average depth in Lake Laksvatn is approximately 6 m and maximum depth 15 m. The lake is normally ice-covered from November to May. The watercourse holds populations of both anadromous Arctic charr and anadromous brown trout.
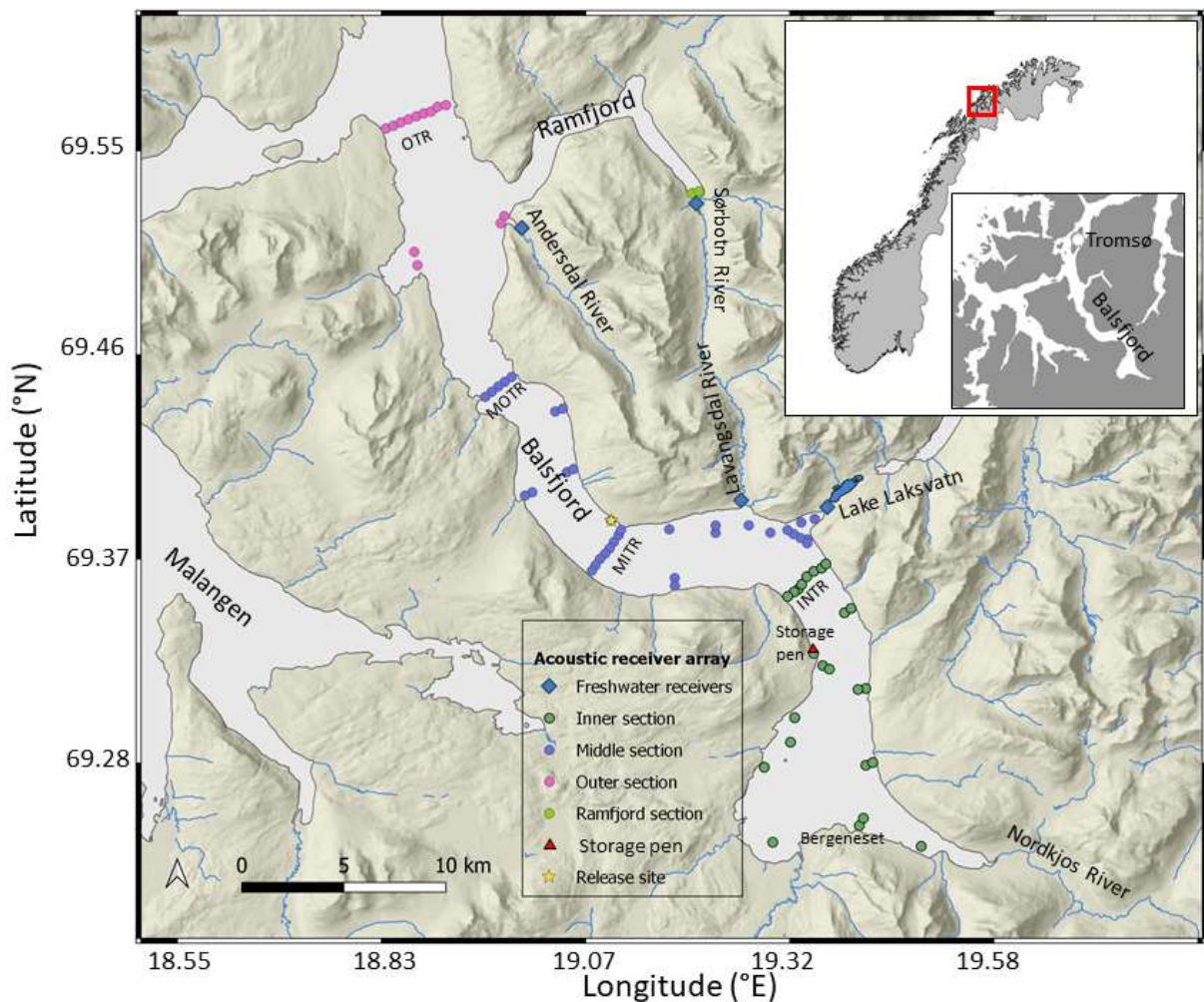

Figure 1. The study area Balsfjord in northern Norway and the acoustic receiver array. Receivers at sea were arranged in fjord sections (coloured dots) including cross-fjord transects (OTR, MOTR, MITR and INTR). Freshwater receivers' positions in rivers (rhombus), the storage pen site (triangle) and the fish release site (star) used during the study period is indicated.

Balsfjord

The Balsfjord (57 km long, 2–7 km width, max. depth 195 m) is separated from the outer coast of Troms by three sounds and is highly influenced by the Norwegian coastal current (Eilertsen & Skardhamar, 2006). Three sills separate Balsfjord from the adjacent fjord Malangen and two shallow sounds surrounding the Tromsø Island (8–30 m depth) (Figure 1). The average tidal difference is approximately 1.3-1.5 m in central Balsfjord, and minor variations in high tide timing (± 30 min) could be observed within few kilometres (Wassmann et al., 2000). Several rivers draining into the fjord system host anadromous populations of mainly brown trout and Arctic charr but also Atlantic salmon. All rivers emptying into the Balsfjord are relatively small and the largest river, Nordkjos River has a mean water flow of 5.65 m s^{-1}. The first 2–4 km outside the Nordkjos River and Sørbotn River normally experience seasonal ice cover. Surface layer salinities are seasonally influenced by the freshwater inputs in the fjord (Eilertsen & Skardhamar, 2006). Seasonal variations in salinity in the upper meters of the water column are typical ranging between 33.5–23.2 ppt, with the lowest salinity observed in August (Wassmann et al., 2000). Stratification of the surface layer starts in June and decreases in August. Annual surface temperature ranges from 1–14 ˚C, and August traditionally appear as the warmest month (Wassmann et al., 2000). A recent study measured the sea temperature in Balsfjord in June 2018 (Barth-Jensen et al., 2020). Balsfjord was stratified and a temperature of 8.0˚C at surface dropping to 5.3˚C at 20 m depth was observed. The thermocline was evident also in August where 10.2 ˚C at surface and 6.8 ˚C at 50 m was recorded (Barth-Jensen et al., 2020).

2.2 Capture and tagging

Capture

Arctic charr smolts were caught in a small fyke net bag (mesh size 10 mm) with two side arms (length 2.5 m, mesh size 16 mm) directed diagonally across the river and closing three fourths of the river width. The fyke net bag was connected on its end to a storage tank from which fish were collected using a fine meshed dip net. The smolt trap was operative in the period 2nd–26th of June 2018. The Arctic charr smolts included in the current study were caught in the period of 03rd–14th of June. The smolt trap was emptied once a day during the catch period and caught fish were relocated to a tank in the river for temporary storage. From

here, fish were transported to Bergeneset (Figure 1) approx. 30 km away by car. Oxygen saturation levels were monitored during transport and kept at saturation level. Fish were then loaded into a tank with circulating water on board a boat. Immediately after recovery from transport, fish were tagged on deck and later transported by boat in the same tank to a storage pen (diameter: 4 m, depth: 2 m) at sea (Figure 1).

Tagging

The Arctic charr smolts (Table 1) were tagged in two events, on the 14th and 19th of June. Fish were first anaesthetized by a 3 min immersion in an aqueous solution of benzocaine ($0.1-0.2$ ml Benzoak® l^{-1}). Immediately after anaesthetisation, fish were placed ventral side up onto a V-shaped surgical table, and biometrics recorded. A $1.5-2$ cm incision was made on the ventral side between the pelvic and pectoral fins. A Vemco (Vemco Inc., Nova Scotia, Canada) acoustic transmitter (V7P model; 19 x 7 mm;1.2 g in water; estimated battery life of 167 days, delay $30-90$ secs random interval) and a PIT-tag (12mm FDX passive integrated transponder (PIT) tag with a unique eight-digit code (Biomark Ltd, Idaho, USA) was inserted into the body cavity. The V7P tags carried depth sensors (resolution 0.15 cm, maximum depth 34 meters) and transmitted a unique individual code train in random intervals ($30-90$ seconds delay). The incision was closed by one or two independent silk sutures (Ethicon 4/0). After tagging, fish were placed back into the tank on board for recovery and transport to the storage pen at sea, were they stayed until the final release. On the 28th of June, fish were transported by boat to the release site and released (Figure 1).

Table 1. Arctic charr fork length (L_F) and mass. Mass were taken from 48 of the 50 tagged individuals.

n	Mean L_F ± SD	L_F range	Mean mass ± SD	Mass range
50	220.8± 16.3 mm	190−260 mm	89.2 ±21.6 g	50−138 g

2.3 Tracking

In June 2018, 76 acoustic receivers (Vemco VR2Tx and VR2AR, Vemco Inc., Nova Scotia, Canada) were deployed in Balsfjord (n = 72) and other four rivers (n = 4) draining to the Balsfjord basin: Laksvatn River, Lavangsdal River, Andersdal River and Sørbotn River. The receivers were deployed in four cross-fjord transects (Outer transect = OTR, middle-outer transect = MOTR, middle-inner transect = MITR and inner transect = INTR) (Figure 1) with several receivers close to shore between the transects. The receiver array was grouped into four main receiver sections, based on their fjord area location, prior to analysis: Inner section, Middle section, Outer section and Ramfjord section (Figure 1). The detection range of VP7-transmitters can reach up to 300−400 meters in good conditions (www.innovasea.com). No range test was performed in this study but the detection range was assumed to be approx. 200 m based on a recent study with similar tags and receivers (Serra-Llinares et al., 2020). Tagged fish were monitored between 28th June − 08th October. Out of the 76 receivers, 6 (8%) receivers were lost at sea, 56 (74%) receivers contained detections from tagged fish and 14 (18%) receivers contained no detections.

2.4 Data analysis

Maps were made in QGIS 3.10. (QGIS Development Team, 2020). Plots were made using either the *ggplot2* (Wickham 2016), *survminer* (Kassambara et al., 2020), *ggpubr* (Kassambara 2020), *actel* (Flávio & Baktoft, 2021) or *RSP* (Niella et al., 2020) packages in RStudio version 1.3.1093 (RStudio Team, 2020).

Filtering

Initial detection filtering was performed in VUE (Vemco User Environment). All detections from tags included in the current study were filtered out and exported as a .csv file. Hereafter, all analyses were performed in R version 3.6.2 (R Core Team, 2019). False detections are erroneous detections occurring in the Vemco VR2 system by code train collision of multiple tags (Simpfendorfer et al., 2015). These false detections could appear as an unknown tag ID (Type A) or as a tag ID included in the study's ID list (Type B). False detections (Type A) were detected and removed by filtering only included tag IDs in VUE (described above) and by using the *min_lag()* and *false_detections*() functions in the *GLATOS* package (Type B) (Binder et al., 2018). The *min_lag()* function was used to calculate the minimum time interval between successive detections. Threshold time was set to 1800 seconds (30 x 60 seconds nominal delay, see Binder et al., 2018). The *false_detections()* function, which filters detections with minimum time intervals >1800 seconds, was used to remove these potential false detections. Potential false detections at the Laksvatn River receiver (10 obs.) were not removed because single detections from tags were expected here as fish ascending the river swims fast and the detection range at this station was assumed to be low. In total, 789 detections (0.7% of all detections) were identified as being type B false detections and were removed from the dataset.

In total, 50 fish were released, where three of these reported zero detections and additional two fish were detected only at the bottom at one receiver the whole tracking period and were therefore excluded from analysis. The 45 tagged fish produced 112 033 detections at 56 receivers during the tracking period, after removing false detections.

Survival

Survival analysis was performed using the *survival* package (Therneau, 2020). Fate was set to 1 (dead) for individuals showing abnormal vertical behaviour and 0 (alive) for fish where mortality could not be detected. Fate time was set to be the number of days between release date and the last observation date (fate date). Fate dates were specified as right-censored data, which allowed inclusion of all fish when event = 0 were analysed. Fish were classified as eaten by a predator when an unexpected changed in vertical swimming behaviour was observed following the tag becoming stationary tag at the bottom, and detections after date of predation were removed from analysis.

Marine residency time and freshwater returns

The marine residency time of Arctic charr smolts was defined as the number of days between release date and the freshwater return date for fish re-entering the Laksvatn watercourse. Analysis of return to freshwater was performed using the *survival* package (Therneau, 2020). Fate/status was set to 1 (returned) if their last observation position was at Laksvatn River and 0 (not returned) if the last observation was at sea. Fate time was set to be the number of days between release date and the last observation date (fate date). Fate date were specified as right-censored data for non-returning fish.

Marine area use

The space use of tagged fish was quantified using the *actel* (Flávio & Baktoft, 2021) and *RSP* (Niella et al., 2020) packages in R.

Time spent in fjord and freshwater sections was calculated by using *preload()* and *residency()* functions in the *actel* package (Flávio & Baktoft, 2021). The *preload()* function combines several input files; biometrics of tagged fish, receiver deployments and positions, detections, and a distance matrix with in-water distances between receivers calculated from the *distancesMatrix()* function. The distance matrix uses a rasterized shapefile of land and water masses projected in a metric projection (UTM 33, EPSG:25833) and returns more realistic distances between receivers by only following the sea pathway. Data were explored by using the *residency()*, which return various results, such as the calculated times spent in each receiver section, based on the output of the *preload()* function. Time spent in different sections was extracted from the main output of *residency()* function. Days when an individual

had been detected in more than one receiver section was assigned to the section where it has spent most of the time that day.

Shortest paths between consecutive detections of individuals were calculated using the *runRSP()* function in the *RSP* library (Niella et al., 2020), the supplementary package to *actel*. The *runRSP()* function interpolates in-water positions and associated errors between consecutive detections based on a given detection range and the *residency()* output from the *actel* package. Since range tests were not performed, the default setting of 500 m detection range was used, which given the assumed detection range of 200 m will overestimate the space used by tagged fish. Further, the *runRSP*() function uses least-cost analysis of random walks to estimate shortest paths. Space use were calculated using *dbbmm()* function in the RSP package. This function applies *dynamic Brownian Bridge Movement Models* (dbbmm) to calculate the area utilized (in m^2) by fish within a chosen time slot. A single tag ping could be detected at multiple receivers if the tag was within the detection range of these receivers at the same time. By default, the *dbbmm()* function removes simultaneous detections at multiple receivers, tracks below eight detections or track duration less than 30 minutes. Areas utilized by tagged fish (space use) was calculated using *dbbmm()* function and week of the year was chosen as the timeslot included in the analysis. In total, 721 detections were removed by the *dbbmm()* function. Weekly space use was plotted using the *getAreas()* and *plotAreas()* functions with 25%, 50% and 95% space use contours.

Littoral versus pelagic habitat

Detections from receivers at the four cross-fjord transects were classified as littoral or pelagic based on the receiver position. Receivers deployed <200 meters from mid-tide shoreline (closest to land in both ends) were defined as littoral (Eldøy et al., 2017), while all the other receivers were classified as pelagic. Mid-tide shoreline was chosen because large areas of the tidal zone in Balsfjord are 0−550 m intertidal soft bottom flats and experience draught during low tide.

The habitat use was measured by calculating the percentage of detections at both habitats for each transect. The proportion of littoral and pelagic receivers in a transect was set as the expected ratio of detections and was tested against the observed habitat use using χ^2-test. Possible simultaneous detections at multiple receivers by a single tag ping was manually

screened for by averaging habitats in detections within a 10 min time frame for each tag ID. Possible simultaneous detections (n = 83, < 2 % of all transect detections combined) was assessed not to influence the distribution of habitat detections in large degree and all detections (n = 4991) were therefore used in the habitat analysis. Two receivers (littoral n = 1, pelagic n = 1) at MITR transect were lost during the summer but the remaining receivers was still included in the analysis.

Depth use

Of the 50 tags, 43 transmitted a total of 29 155 pings with negative depth values (unnatural above-surface values) to receivers during the study period. The lowest value was -0.45 m. Prior to analysis, each tag transmitting negative depths was corrected to positive values by adding the tag's most negative depth value to all of its detections (adding 0.15 to all of the tags detections if the most negative value was -0.15 meters). A similar approach has been applied to negative pressure value data previously in Føre et al. (2017).

The main data set was condensed by averaging detection positions and depth values within a 30 minutes time frame for each tag ID to reduce clustered data.

Linear mixed-effects modelling

To investigate which factors influenced depth use, a linear-mixed effect model was formalized. Due to presence of the midnight sun from mid-May to the end of July, the duration of the night could not be calculated by using sunset and sunrise times. Therefore, detections between 03:00 and 22:00 was specified as *day* and detections between 22:00 and 03:00 specified as *night.* The diel period was associated to each of the averaged detections. For simplicity, these diel periods were fixed for all dates despite decreasing daylengths from the end of July. Week number of the year was chosen as the seasonal component. Week of the year was assessed to be linear with the response variable, despite a low linear correlation, to meet linear mixed-effects model assumptions. Depth values (30 mins averaged depth) were square root-transformed for normality of residuals. Depth use was modelled as linear mixed-effect models by using *lme()* function in the *nlme* library (Pinheiro et al., 2021). *Fish ID* was included as random effect (random intercept), *Diel period* and *Section* as factorial fixed effects and *Length (L_F)* and *Week* (week of the year) as continuous fixed effects. Only

receiver sections at sea (11 572 averaged detections) were included in the linear mixed-effect model to explain variations in depth use in the marine environment only.

Total travelled distance

Shortest paths and total travelled distances were calculated using the functions *runRSP()* and *getDistances()* in the *RSP* package, respectively. The total travelled distances are the accumulated movement distances for each fish during their migration calculated by using both distances between receivers and interpolated positions from *runRSP()* combined. The total travelled distance indicates a minimum travelled distance for individuals because no data on where fish reside between detections exists.

Total travelled distance was modelled for fish residing > 7 days at sea and returning to Laksvatn (n = 24) by using a linear model (multiple regression) y = mx1+mx2+b including *Marine residency time* (migration duration in days) and *Length (L_F)* as explanatory variables. Both explanatory variables were assessed to be normally distributed and were tested for parametric correlation (Pearson correlation) prior to modelling.

Model selection

To determine which model have the best fit to the observed data, a model selection was performed by using *dredge()* function in the *MuMIn* library in R (Bartón 2019). Full models were developed for depth use (LMM) and total travelled distance (LM) including their associated explanatory variables and then run in the model selector separately. The top model candidate was chosen from the model candidate set to describe the variance of the respective response variable.

3 Results

3.1 Survival

In total, 1 out of 45 fish (2%) was classified as dead by unnatural vertical behaviour (e.g. eaten by a predator). Additional 7 (16 %) fish disappeared at sea during the study period. However, for these individuals, no indications of fish mortality were evident, and they were consequently categorized as right censored.

3.2 Marine residency time and freshwater return

Freshwater returns of the post-smolts ranged from 29th June to 14th September, after spending 0−78 days at sea. The fish formed two distinct groups based on the duration of the marine residency. Out of the 37 fish that returned, 13 (35%) individuals re-entered Laksvatn River within the first week after release with a median residency time of 3 days (range = 0-6 days) (Figure 2). The remaining 24 (65 %) fish returned to Laksvatn River spending an average of 50 days (SD= 15.28 days, range 19−78 days) in the marine environment. No difference in fish size (L_F) were found between the two freshwater return patterns (Welch Two Sample t-test, p = 0.3873). All fish ascending Laksvatn River did not descend to the sea after returning to fresh water.
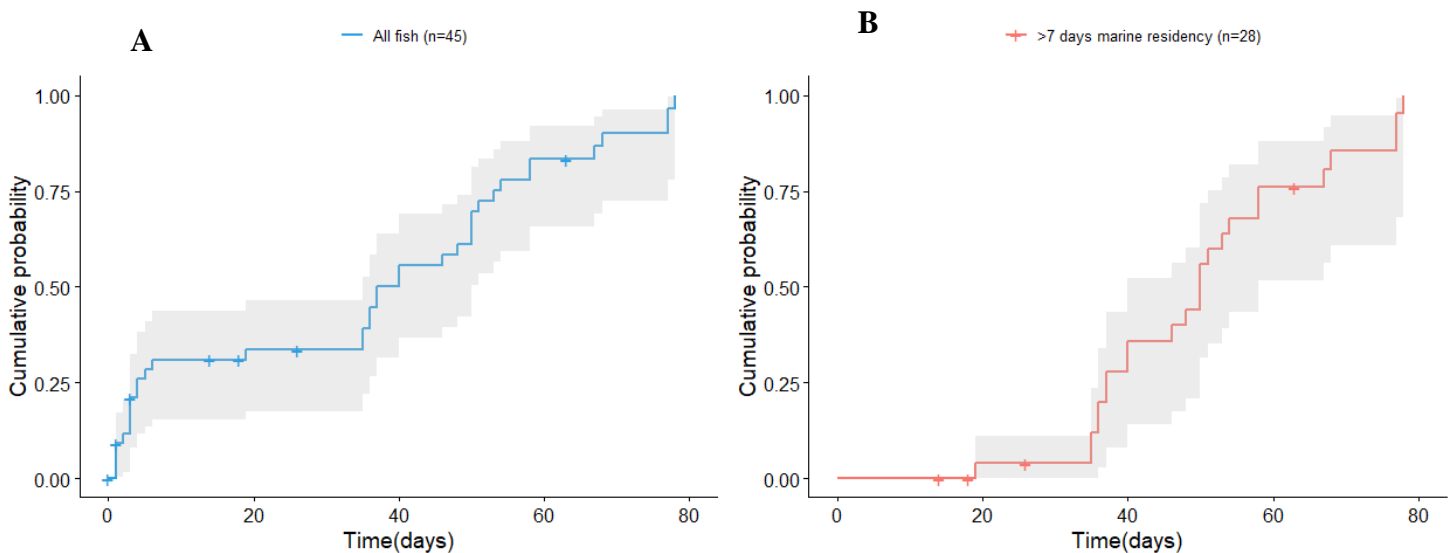

*Figure 2. Cumulative probability of freshwater returns to Laksvatn River for all fish (**A**) and fish residing >7 days at sea (**B**). Fish disappearing at sea were right censored by their last detection date and indicated by crosses (+). Shaded areas show 95% confidence intervals.*

3.3 Marine area use

Arctic charr post-smolts were detected at all fjord sections of the study area during the study period, with Middle section appeared to be the most utilized area (Figure 3b). More Arctic charr were detected at the east side of Balsfjord compared with the west side (Figure 3a). Both receivers at the Inner and the Outer sections detected 25 individuals during the summer while section Ramfjord detected 15 individuals. The Sørbotn River receiver detected a total of 9 fish, where 1 of the individuals resided close to the receiver for several weeks before returning to Laksvatn River (see Appendix 1 for detection distribution). Nevertheless, zero fish disappeared (i.e had last detection) at Sørbotn River despite the high number of detected fish. No fish were detected in the Andersdal River and the Lavangsdal River during the study period.

Utilization distribution in space and time

During the first days after release (week 26), the space use of the post-smolts were limited to the east side of the Middle and Outer sections in Balsfjord and the Ramfjord section (Figure 4). The space use increased to include the Inner section of Balsfjord in week 30 (23th–29th July), when fish were detected in all sections in Balsfjord, both at the eastern and western side. Throughout the summer, Arctic charr were detected in all areas of the Balsfjord, with more fish detected on the eastern side of the fjord (Figure 3a). Ramfjord, including Sørbotn River, was utilized by Arctic charr in most weeks during the study period and peaked in the end of July. In September (week 36−37), fish were residing mostly on the eastern side of the fjord in all fjord sections (Figure 4).
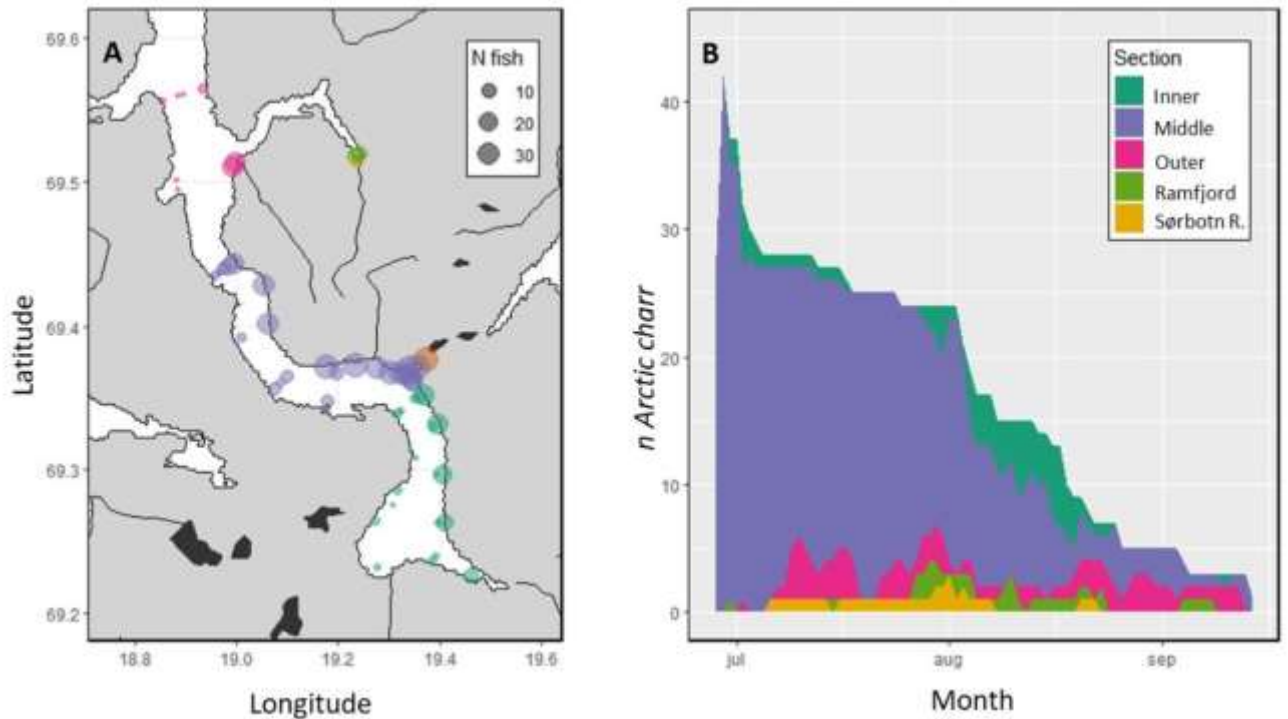
*Figure 3. **A** Marine area use during the study period. Bubble sizes indicate the cumulative number of detected fish at receivers during the study period 28th June–14th September. **B** Spatial and temporal distribution of Arctic charr post-smolts in Balsfjord, grouped on sections and stacked on individuals. The number of fish declined towards the autumn as fish either ascended Laksvatn River (Orange bubble, **A**) or disappeared at sea. In **B,** Laksvatn River was included in the Middle section.*

Littoral versus pelagic habitat use

Overall, Arctic charr post-smolts were detected more in the nearshore littoral zone compared to the pelagic. The four cross-fjord transect receivers produced in total 4991 detections where 96 % were detections in littoral habitats and 4 % in pelagic habitat. In total at the four transects, 30 fish were observed in the littoral while 25 were observed in the pelagic zone. All four transects had significantly more detections in the littoral compared to in the pelagic, OTR: χ^2 (df = 1, N = 41) = 95.935, p < 0.001, MOTR: χ^2 (df = 1, N = 4064) = 21316, p < 0.001, MITR: χ^2 (df = 1, N = 421) = 219.9, p < 0.001, INTR: p < 0.001, χ^2 (df = 1, N = 577) = 1389.7, p < 0.001.
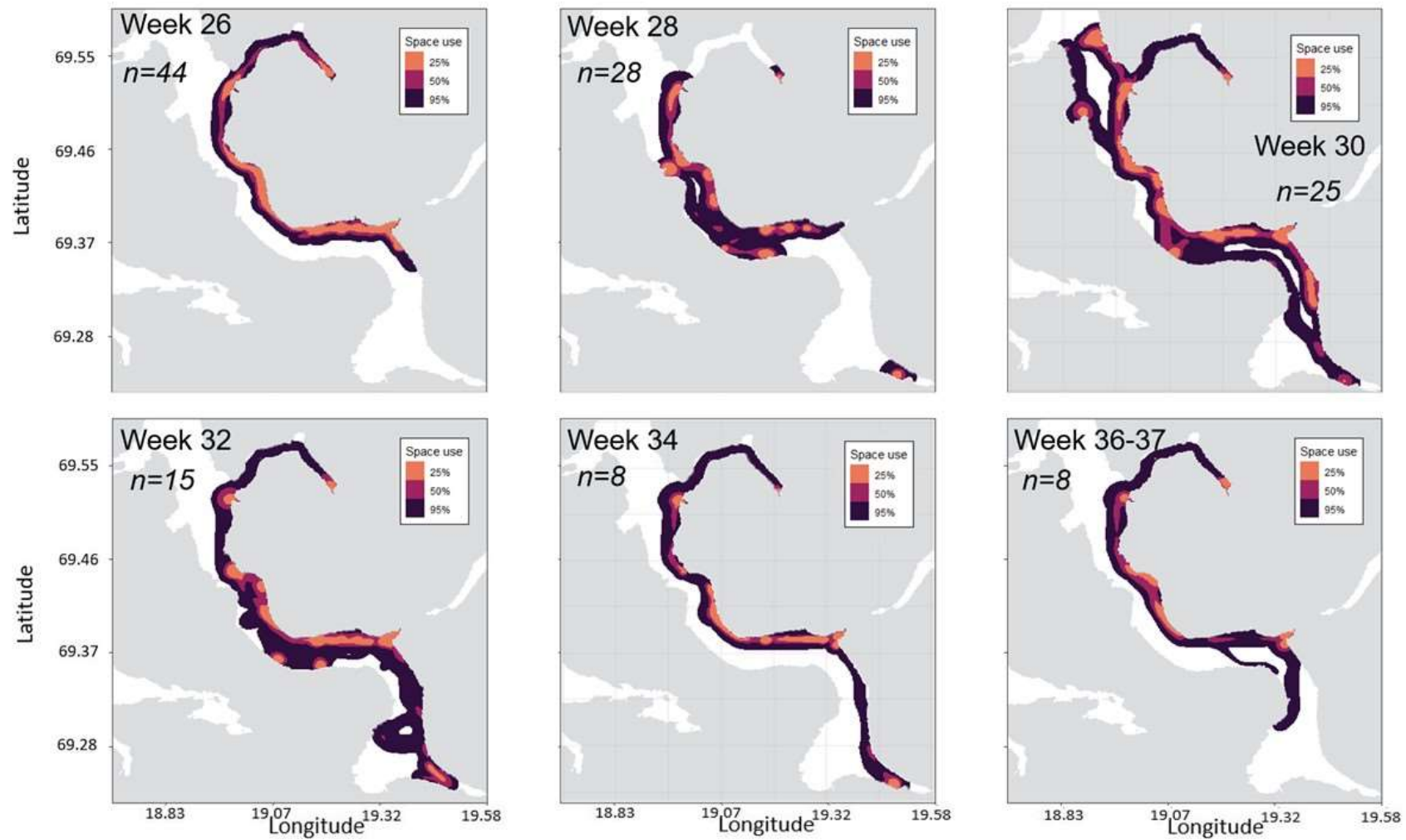
Figure 4. Weekly space use of Arctic charr post-smolts from every other week in the period 28th June – 15th September with 25%, 50% and 95% contours indicating time spent in different areas.

3.4 Depth use

The Arctic charr post-smolts were surface-oriented while at sea with 95 % of detections at sea (Total number of detections at sea = 105 161) in the uppermost 0−3 meters of the water column (Figure 5). The marine depth use ranged between 0.00-20.9 meters (overall mean = 0.98 m ± SD 1.00). Detections at deep water (> 5 m) contributed to 0.6 % (679 detections) of all detections, and 98% of the deep-water detections were detected during daytime.

Diel period, spatial and seasonal variations

The top model ranked by AICc included *Diel period*, *Section* and *Week* but not *Length (L_F)* as fixed effects (Table 2). The fish swam deeper at daytime compared to at night (β = -0.217, SE = 0.009, p < 0.001, Table 2, Figure 5), with mean depth of 1.05 and 0.67 m, respectively. Depth use varied between fjord sections and fish swam closer to the surface in the outer (β = -0.132, SE = 0.023, p < 0.001, Table 2) and Ramfjord sections (β = -0.218, SE = 0.002, p < 0.001, Table 2, Figure 5B) compared to the inner section. A maximum difference of 0.64 meters was found between the mean swimming depth of the sections (Inner = 1.12±0.96 m, Middle = 0.98±0.88 m, Outer = 0.95±0.89 m and Ramfjord = 0.48±0.70 m).

The seasonal variations in depth use between weeks were small (weekly median range: 0.48−1.45 meters, Figure 5C) and a weak positive effect indicating deeper depths in late summer compared to early summer was found by the highest ranked model (β =0.034, SE= 0.002, p < 0.001, Table 2, Figure 5 C and D).

Random effects

The within-group variance (σ^2), the measure of variation in individual fish depth use explained by random effects, was low, but higher than the between-individuals variance (τ) (Table 3). Intraclass Correlation Coefficient (ICC), the proportion of the total variance in depth use explained by individuals, indicated that most of the variance is explained by differences within individual depth use (Table 3) and homogenous depth use samples for individuals.

Table 2. Model selection table of the models ranked by AICc and ΔAICc for Depth use and Total Travelled Distance models. R² (LMM) explains variance in portions for only fixed effects (marginal) and including random effects (conditional). Models with weight = 0.00 were omitted from the table.

Model	*Loglik*	*AICc*	*ΔAICc*	*Weight*	*Marginal*	*Conditional*
Depth use (LMM)						
Diel period + Section + Week	**-5048.9**	**10113.9**	**0.00**	**0.995**	**0.073**	**0.382**
Diel period + Section + Length (L_F) + Week	**-5053.3**	**10124.7**	**10.77**	**0.005**	**0.079**	**0.383**
Total travelled distance (LM)					*Multiple R²*	*Adjusted R²*
Marine residency time + Length (L_F)	**-302.861**	**615.8**	**0.00**	**0.994**	**0.608**	**0.570**
Length (L_F)	**-309.839**	**626.9**	**11.05**	**0.004**	**0.298**	**0.266**
Marine residency time	**-310.781**	**628.8**	**12.93**	**0.002**	**0.241**	**0.206**
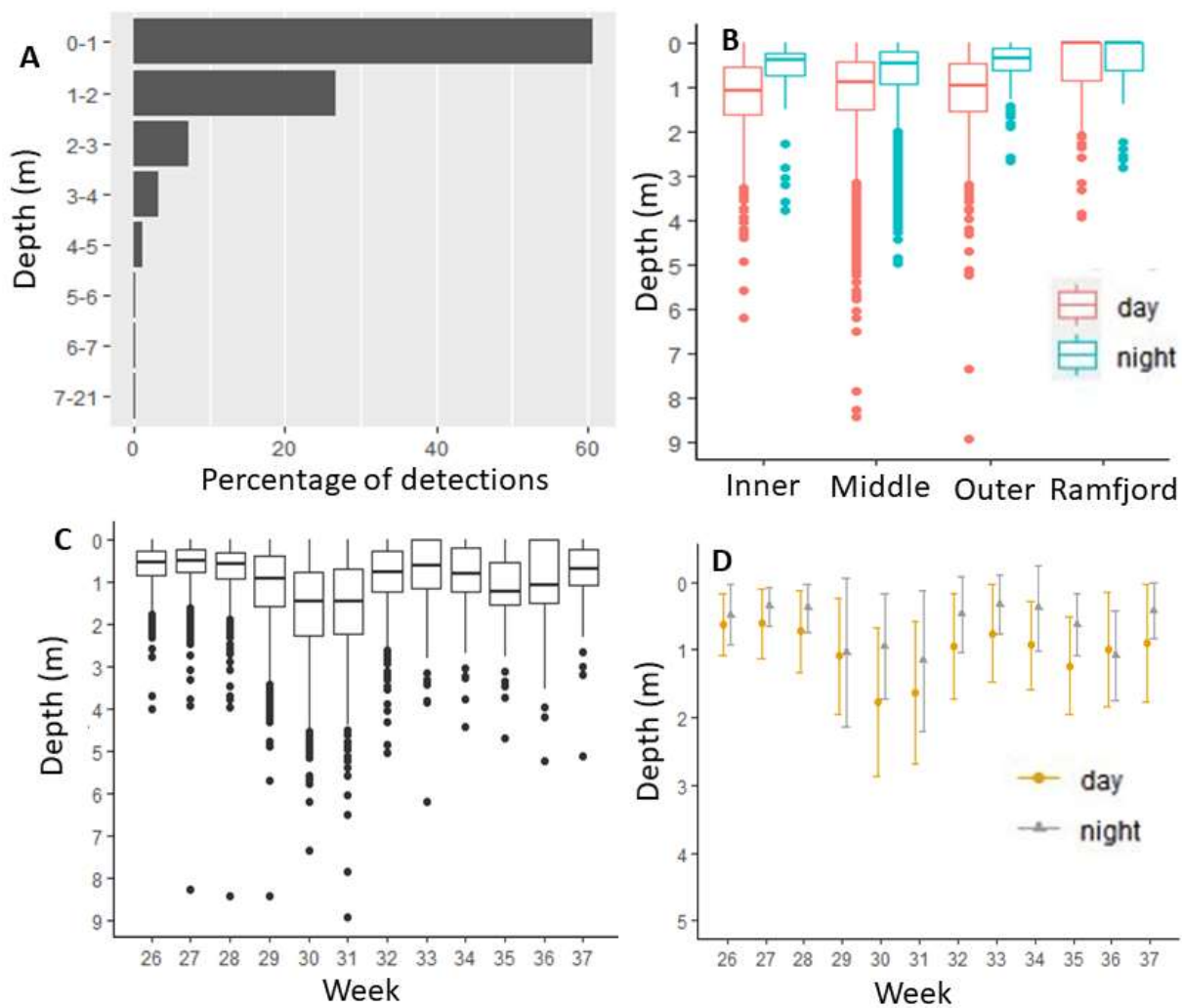
*Figure 5. Distribution of depth use in percentage of all sea detections (**A**), day and night depth use at the four fjord sections (**B**), seasonal variation in overall depth use (**C**) and seasonal diel depth use variations (dots and triangles = mean, whisker =±SD (**D**). In boxplots, boxes show 25th and 75th precentiles and the bar represents the median. Whiskers represent smaller/greater or equal to respective hinges ± 1.5 * interquartile range, and outliers are denoted by dots. All plots were based on 30 min averaged in-fjord detections (11 572 detections). Note axis scale differences beween plots.*

3.5 Total travelled distance

The total travelled distance by Arctic charr post-smolts showed large variation between individuals and ranged between 63-588 km (mean =326 km ± SD 119). Both *Marine residency time* and *Length (L_F)* were significantly correlated to *Total travelled distance* (Figure 6) and included in the top ranked linear model (Table 2). Multiple regression analysis showed significant increased travelled distances by *Marine residency time* ($\beta = 4371$, p < 0.001) and *Length (L_F)* ($\beta = 4104$, p < 0.001). The regression results indicated the top linear model with the two explanatory variables explained 57% of the variance ($R^2 = 0.57$, F (2,21) =16.26, p < 0.001).
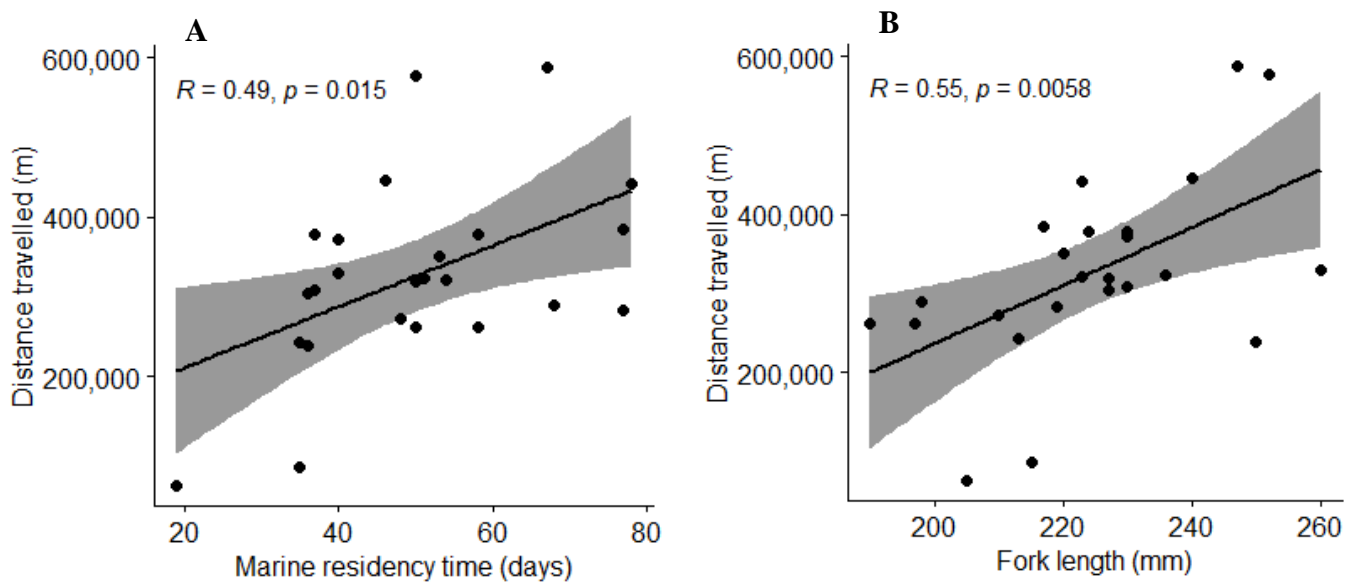

*Figure 6. Regression line and confidence interval (95%) for marine residency time (**A**) and fish size (**B**) with Pearson correlation coefficients and associated p-values.*

Table 3.Parameter estimates, standard error (SE), confidence interval (CI), t-statistic and p-values summary output of the top linear mixed-effect model ranked by AICc. The random effect residual variance (σ^2), between-group variance (τ), intra-class correlation coefficient (ICC) and number of random intercepts (individuals) output of the top model. The response is depth (30 mins average) and reference level in Diel period is "Day" and Section is "Inner". Significant p-values in bold. Based on 11 572 averaged depth observations. Note square-root transformed response variable.

Depth use   Random effects

Parameter	Estimate	SE	95% CI	t	p			σ^2	0.14
(Intercept)	-0.167	0.066	-0.296 – -0.038	-2.531	0.011			τ	0.07
Night	-0.217	0.009	-0.234 – -0.200	-25.398	**<0.001**			ICC	0.33
Section Middle	0.006	0.018	-0.029 – 0.041	0.356	0.722			N	45
Section Outer	-0.132	0.023	-0.176 – -0.087	-5.805	**<0.001**			R^2	
Section Ramfjord	-0.218	0.028	-0.273 – -0.163	-7.799	**<0.001**			*Marginal*	*Conditional*
Week	0.034	0.002	0.030 – 0.037	20.542	**<0.001**			0.073	0.382

4 Discussion

Arctic charr post-smolts were found to reside 50 days on average at sea and experienced high survival during their first migration to the sea. Post-smolts showed a fidelity to surface waters and littoral habitats and showed seasonal variation in the marine area use. The total migration distance of post-smolts varied greatly with a mean of 326 km and a few individuals swam >500 km during their first summer at sea.

The Arctic and subarctic regions experience large variations in seasonal solar radiation during a calendar year, with almost no available light during the polar night and continuous sunlight (midnight sun) during the summer season. The high amount of available light makes subarctic marine areas very productive during summer (Yool et al., 2015) and highly suitable for anadromous fish (Gross et al., 1988). The cold-water adapted Arctic charr's distribution range is expected to contract as temperatures in aquatic habitats increase this century (Finstad & Hein, 2012; Hein et al., 2012). Additional stressors for the Arctic charr is the presence of anthropogenic activity as aquaculture, fishery, and other industries (Halpern et al., 2015; Vollset et al., 2021). In contrast to many areas along the Norwegian coast, the location of this study, Balsfjord, is relatively pristine with limited anthropogenic impacts. Studying the behaviour of anadromous Arctic charr in its natural environment is highly valuable in both scientific and conservation context. In the current study, this telemetry method has revealed fine-resolution details on the marine migration of Arctic charr post-smolts and thus filled a knowledge gap on the behaviour of Arctic charr at sea.

4.1 Survival

For Arctic charr, survival increases for each repeated sea migration and is therefore lowest for first-time migrants (Jensen et al., 2019). The survival of post-smolts observed in the current study was substantially higher compared to first-time migrants' survival from the nearby watercourse Hals River in the Altafjord (Jensen et al., 2012, 2019). In Balsfjord, post-smolts were of larger size, approximately five cm on average, compared to Jensen et al. (2012). The observed difference in survival could be related to body size, as saltwater tolerance increases with size for most anadromous salmonids (Jensen et al., 2012; McCormick, 1994). None of the returning fish were detected at sea after re-entering the Laksvatn River and this could

indicate that early returners resided in fresh water for the remaining part of the summer or that they died after ascending the river.

4.2 Marine residency time and freshwater returns

The Arctic charr post-smolts (n = 24) showed a marine residency time ranging between 19–78 days at sea. The fish resided on average longer at sea compared to previous observations of first-time migrants (Berg & Berg, 1993; Jensen et al., 2019), but similar to marine residency time of adults (Jensen et al., 2014, 2016). Both Jensen et al. (2019) and Berg & Berg (1993) included long-term data on residency times and differences of 20 days in mean marine residency time between-years were observed (Berg & Berg 1993). This indicates that the marine residency time varies from year to year within a population. For Artic charr, it is suggested that photoperiod is the main driver for the timing of the smolt run, which contrasts other anadromous salmonids where water temperatures and waterflow are considered the most important triggers (Jensen et al., 2012). The result of light-induced smolt run is a more fixed smolt run timing between years, especially for populations with access to lakes where juveniles reside in the in habitats less influenced by temperature changes and water level (Jensen et al., 2012). Therefore, other environmental factors such as sea temperature may be the main driver in explaining the variations in marine residency time of Arctic charr (Berg & Berg 1993).

Two distinct duration patterns in marine residency times were present. The short marine residency time group of 17 post-smolts could be a result of handling, as stressed fish show altered behaviour and premature return to freshwater (Serra-Llinares et al., 2020; Vollset et al., 2020). However, the rapid returns of these post-smolts were not just to freshwater habitats but to their home river, ignoring the Lavangsdal River, which empties between the release site and the Laksvatn watercourse. This, in combination with the observation that no fish entered other rivers than the Laksvatn watercourse to overwinter, suggests a strong homing behaviour. The Lake Laksvatn appear to be the best suited site for overwintering in the fjord system, as it is an easily accessible watercourse exhibiting a relatively large lake only 600 meters from the sea and 6 meters above the sea level. Strong homing was found in the long-term study in Hals River in the nearby subarctic Altafjord (Jensen et al., 2015). Jensen et al. (2015) found that immature Arctic charr preferred within-lake overwintering in its native watercourse. In contrast, immature brown trout were found to overwinter in the large Alta

River, but such pattern has not been observed for Arctic charr. However, the same study found a few Arctic charr to be recaptured in other watercourses and being absent from its native river for a year, then returning the following year. Riverine populations of anadromous Arctic charr have been found overwintering in the native river estuary assumingly caused by poor overwintering conditions in the river (Jensen & Rikardsen, 2012). The choice of overwintering site is probably related to availability of suitable habitats (Jensen et al., 2015), which likely varies between populations, rivers and fjord systems. The results from the current study supports our hypothesis that Arctic charr post-smolt return to their native river to overwinter after their first migration to sea.

4.3 Marine area use

The Arctic charr post-smolts resided in the fjord system < 45 km from their native watercourse during their migration to sea. In general, post-smolts utilized the eastern side of Balsfjord more than the western side and had more detections in littoral habitats compared to in pelagic. The fish showed seasonal variation in marine area use. The Middle fjord section was the most utilized area throughout the summer, but the utilization of the Inner, Outer and Ramfjord fjord sections increased in August. These results partly support the hypothesis that Arctic charr reside close to their native river. A recent study was the first to describe Arctic charr post-smolts migratory behaviour at sea (Atencio et al., 2021), where Arctic charr post-smolts resided very to close (< 18 km) their assumed watercourse compared to previous findings on adults (Jensen et al., 2014). Atencio et al. (2021) suggested it could be related to dietary differences between post-smolts and adult Arctic charr in the Altafjord which mostly prey on herring (*Clupea harengus*) (Rikardsen et al., 2007b). In contrast, in the present study in Balsfjord, the tagged post-smolts utilized areas over twice as far away. Fish were almost 5 cm longer on average compared to Atencio et al. (2021) and therefore likely more piscivorous. Dietary differences between sea trout in Balsfjord (Rikardsen et al., 2006) and Altafjord (Rikardsen et al., 2007b) indicate that prey availability in fjords likely varies within and between fjord systems, and between years. It is likely that Arctic charr marine area use is related to prey availability, and this could be a driver behind the observed marine area use differences between Altafjord and Balsfjord.

Littoral versus pelagic habitat use

The littoral habitat was the habitat with most fish detections at all cross-fjord transects, despite that most of the fish were detected pelagic areas at some point during their marine residency. Variations in detection ranges for receivers can vary with environmental conditions (Thorstad et al., 2013). It is, therefore, a possibility for individual detections to be interpreted as one habitat even if it is sent from the other habitat. But the present result indicates that the littoral zone is by far the most utilized habitat by post-smolts and thus supports the hypothesis that the Arctic charr post-smolts utilize the littoral zone over the pelagic zone. This coincides with previous observations of the habitat use while at sea for adults (Jensen et al., 2014, 2016) and first-time migrants (Atencio et al., 2021).

As Arctic charr migrates to the sea to feed, they may move through the aquatic landscape to habitats where prey availability is high and environmental conditions are favorable. Rikardsen and Amundsen (2005) found Arctic charr feeding in the pelagic up to 5 km from the shore in another subarctic fjord (Altafjord), feeding mainly on pelagic fish. The pelagic behaviour could therefore be related to pelagic prey availability, which varies between fjords and seasons (Rikardsen & Amundsen, 2005). In this study in Balsfjord, Arctic charr post-smolts resided almost exclusively in the littoral zone which may indicate higher prey availability in this habitat. Rikardsen et al. (2007b) examined the littoral diet of Arctic charr and sea trout in the Altafjord and found overlapping diets between the two species. They also found all sizes of Arctic charr to prey on fish, but larger charr (>400mm) were strictly piscivorous and fed on herring. Rikardsen et al. (2006) studied the diet of sea trout caught in the littoral zone in Balsfjord. Diets consisted of crustaceans, fish and polychaeta, and the dominating prey item varied with season (Rikardsen et al., 2006). Arctic charr reside in the same habitat in overlapping time periods in Balsfjord, and these prey items are probably the dominating prey items for Arctic charr in Balsfjord as well, as high dietary overlap were found in Altafjord (Rikardsen et al., 2007b).

4.4 Depth use

Arctic charr post-smolts preferred the surface waters and utilized 0-3 meters depth (95% of all detections at sea), which supports the hypothesis post-smolts utilize the uppermost parts of the water column. A diel shift in depth use were found where individual charr swam

approximately 40 cm closer to surface at night on average. There were minor differences in depth use between different areas of the fjord, but fish were found closer to the surface in the outer and Ramfjord sections compared to the Inner section. There was a tendency for deeper depth use in late season compared to early, but only minor differences were found.

Diel period, between-site differences, and seasonal variations

Diel variation in depth use is common amongst salmonids, including Arctic charr adults and post-smolts (Atencio et al., 2021; Rikardsen et al., 2007a), and may reflects responses to light availability on feeding behaviour and predator avoidance (Hedger et al., 2017). In the present study in Balsfjord, diel patterns in depth use for Arctic charr post-smolts were found which coincides with recent reports on post-smolts from the Altafjord (Atencio et al., 2021). In northern Norway, the presence of the midnight sun in mid-May to end of July reduces the variation in diurnal light availability. Many Arctic charr prey taxa, such as copepods and krill, exhibit diel vertical migrations and are found near the surface during night (Pinti et al., 2019), including in midnight sun conditions (Rabindranath et al., 2011), which may explain the Arctic charr's diel shift in depth use. Alternative, diel vertical movements could be a tactic to avoid predation, with post-smolts utilizing deeper areas at daytime when light conditions strengthen predatory success, and closer to surface at night when visibility is reduced (Johnsen & Sosik, 2003). Environmental conditions, for example wave activity, may also influence the Arctic charr's depth use. Surface waves influence water layers down to depths of one half of the wavelength and are strongest at surface and decreases with depth (Toffoli & Bitner-Gregersen, 2017). Furthermore, in subarctic fjords such as Balsfjord during summer, winds often diminish at night and calm surface waters appears (personal observation). This may re-open the uppermost water layer for fish residency. Other environmental factors as temperature and salinity influence the choice of the residency areas and depth use for Arctic charr (Harris et al., 2020; Spares et al., 2012). Higher water temperature is found closest to the surface, and it has been suggested that night-time warm-water residency of Arctic charr could be to increase metabolism for higher growth (Mulder et al., 2020). Salinity is lowest in the uppermost water layer and residency in this layer has been suggested to aid osmoregulation for Arctic charr (Spares et al., 2012). The use of deeper depths at daytime, including waters >5 m depth, indicate foraging behaviour during day and the preference of

near-surface (warmer) water at night, possibly for more rapid digestion. However, it is difficult to disentangle the drivers behind the observed diel depth use differences.

Depth use of post-smolts between the four fjord sections showed small variations. The highest ranked linear mixed-effect model indicated a significantly deeper depth use at the Outer and Ramfjord fjord sections compared to the depth use at the Inner section. The difference between the mean depths of Inner section and Ramfjord section was 0.64 meters, which is relatively large for fish residing mostly in the upper 0−3 meters of the water column. The two acoustic receivers in Ramfjord were placed in the fjord end and relatively close to Sørbotn River. The station may therefore be influenced by freshwater outputs in the surface layer, and the fish could have used this layer for olfactory orientation (Rikardsen et al., 2007a), osmotic regulation or delousing (Thorstad et al., 2015) which in part may explain the surface residency of this fjord section.

The highest ranked linear mixed-effects model showed a statistically significant preference for deeper water late in the season compared to early. However, the seasonal depth use pattern appeared cyclic throughout the summer which could result in a poor fit for a linear mixed-effect model. The random effects contributed to most of the top model's explained variance (conditional R^2) in depth use. This means that variations in individual depth use explained a major part of the explained variation by the model. The low intraclass correlation coefficient (ICC) indicated that the individual variation in depth use explained more of the total random effect variation than between-individual variation, indicating homogenous samples of individuals. Less fish was detected in the late season as many fish had returned to freshwater. Thus, individual variation in depth use in the late season may influence the overall trend in this period. In addition, fish returned to fresh water in different weeks which influence individual fish's trend in seasonal depth use. Despite the statistically significance of deeper depths in the late season, the minor difference in depth use may be of limited biological significance. The cyclic variation in depth use cannot be related to increasing diel light variations in the study period and must therefore be related to other unknown factors.

4.5 Total travelled distance

Despite Arctic charr post-smolt's relatively low marine residency time (mean = 50 days), 33% of the fish travelled distances beyond 300 km while at sea inside the fjord system. It is

important to note that the measurements are minimum distances due to incomplete receiver coverage, and the actual distance are likely higher. The migratory distance of Arctic charr during their sea migration has previously revealed within-fjord residency (<30 km from native river) but also contrasting long migrations to rivers beyond 100 km away outside their native fjord has been observed (Jensen & Berg, 1977; Rikardsen et al., 2007a). Here, Arctic charr post-smolts resided within the fjord < 45 km from their native river. The total travelled distance varied among individuals and was, as expected, dependent on the marine residency time, but also fish size. The top ranked linear model indicated longer migratory distance for larger post-smolts, which could be explained by higher swimming capacity for larger fish (Peake et al., 1997). The outer fjord areas at the Norwegian coastline hold high abundance of prey items for piscivorous fish as the Arctic charr (Jensen et al., 2014). At sea, all size groups of Arctic charr are piscivorous but the occurrence of fish prey and prey species in the diet increases with fish size (Rikardsen et al., 2007b). The increased piscivory may increase swimming distances by increasing the utilization of these outer areas with high prey fish abundance. Finally, the outer fjord areas have more mammal and bird predators which larger sized fish has better protection against (Jensen et al., 2014). Therefore, smaller post-smolts could be more bound to areas close to the native river with less predation risk (Jensen et al., 2014).

4.6 Future research on Arctic charr and management implementation

The Arctic charr's use of nearshore habitats in local fjords and coastal areas should be considered when planning the use of fjord areas for future fish farming, fisheries, mining, and other anthropogenic activities that may impact coastal ecosystems. The impacts of salmon lice spillover to wild salmonids from salmon farms have been investigated thoroughly the last decades (see reviews Costello, 2009; Thorstad et al., 2015; Torrissen et al., 2013). An increase in sea lice infestations are also found in the feeding areas of anadromous Arctic charr (Bjørn et al., 2001). Laboratory studies on Arctic charr have documented that high infestations of salmon lice could result in altered growth, increased mortality and decreased reproduction investment (Fjelldal et al., 2019; Tveiten et al., 2010). Despite this, no study has documented the ecological effects by salmon lice infestations, such as changed fecundity, growth loss and behavioural changes in wild populations of anadromous Arctic charr. Such

studies may be crucial to conservation and management of anadromous Arctic charr, prior to the expected increase in salmon lice infestation pressure in northern Norway.

The previous ecological and behavioural studies on anadromous Arctic charr in northern Norway has described Arctic charr's growth at sea, migration timing and duration, marine area use, depth use and temperature preference at sea (Berg & Berg 1993; Jensen et al., 2014, 2016; Jensen et al., 2012, Rikardsen et al., 2007a). Nevertheless, population genetics and between-population geneflow and interactions (as overwintering) are yet to be studied in detail. Such studies may reveal the connectivity of meta-populations and important coastal residency areas of Arctic charr.

4.7 Climate change and future anthropogenic impacts on anadromous Arctic charr

Anadromous Arctic charr is likely affected by the ongoing climate change and particularly southern anadromous populations are vulnerable to a warmer climate (Layton et al., 2021). The current increase of water temperature, climate change and the expected future increase in salmon farming with a consecutive increase in salmon louse infestation pressure could change Arctic charr's migration behaviour in both direct and indirect ways. Below, these stressors and their impacts on anadromous Arctic charr are discussed.

Arctic charr's migration to fjords occur during the warmest season and most of their time spent at sea are close to the surface which contains the warmest water layer during the summer. Jensen et al. (2014) found increasing probability for adult Arctic charr to leave inner fjord areas when temperature rose above 8 ˚C in Altafjord. This indicates that Arctic charr seek colder water when temperature gets high and moves horizontally at sea to find optimal temperatures. In a scenario with increasing sea temperatures, it is therefore likely that Arctic charr change their feeding areas to colder coastal areas.

Warmer and wetter winters is the trend in the winter climate in northern Norway (Vikhamar-Schuler et al., 2016) and this influence the ice-cover period and summer river water flow (Rolls et al., 2017) . In northern Norway, most of the increase in water discharge during the spring and summer comes from melting snow. If precipitation comes as rain during the winter, less snow accumulates in the mountains which could lead to lower spring and summer waterflow in rivers (Rolls et al., 2017). This may contribute to altered seasonal salinity

patterns in fjords, and possible higher salinity during summer could be negative for Arctic charr post-smolt (Jensen et al., 2012; McCormick 1994). Shorter ice-cover periods in rivers and lakes induced by warmer winters can increase freshwater temperature and facilitate a shift in phyto- and zooplankton communities resulting in cascading effects and lower water clarity and eutrophication symptoms (Jeppesen et al., 2014). These climate change-induced perturbations may alter the Arctic charr recruitment and growth (Rolls et al., 2017), and thus the degree of anadromy (Finstad & Hein 2012). Competition and population dominance by sympatric brown trout populations, which are better adapted to temperate waters may add more pressure on the Arctic charr in the freshwater habitat (Rolls et al., 2017; Svenning et al., 2021). In addition, ecological changes due to warmer water and acidification must also be expected at sea (Hofmann et al., 2010). Food availability and trophic links may change due to changed seasonal temperature and salinity (Andersson et al., 2015) but how this influence Arctic charr's movements, diets and fitness at sea is poorly understood.

The climate change induced increase in sea temperatures in southwestern Norway makes these coastal areas less suited for farmed salmon locations and opens for more aquaculture activity in the colder northern Norway (Vollset et al., 2021). The expected increase in fish farming activity along the coast of northern Norway is likely to increase densities of the salmon louse (Vollset et al., 2018). The open net-pen farming of Atlantic salmon produces high densities of salmon lice which are transported by water masses to the feeding habitat and may impact native salmonids on their marine migration (Bjørn et al., 2001). High densities of salmon lice infestation have caused altered behaviour, such as premature return to freshwater but also increased mortality of wild sea trout and Arctic charr (Bjørn et al., 2001; Serra-Llinares et al., 2020; Thorstad et al., 2015). Increased salmon farming activity may therefore be an additional stressor for the Arctic charr, on top of several climate change-related stressors in both freshwater and at sea. The Arctic charr's seaward migration to increase overall fitness may then result in higher mortality, as well as lower growth and hence lower fecundity, which lower the fitness and reduce the degree of anadromy.

4.8 Conclusion

This study provides new data that describe migratory behavioural patterns in anadromous Arctic charr. Here, the results supported all the hypotheses. Arctic charr post-smolts resided close to their native river during their first summer at sea. They resided in the fjord system <45 km from the river mouth but swam long distances in the fjord. While at sea, post-smolts showed fidelity to littoral areas but many fish were detected in the pelagic habitat during the summer. Arctic charr were strongly surface oriented at sea and used almost exclusively the upper 0−3 meters of the water column. Diel patterns in depth use were evident where fish swam deeper during day compared to at night. All returning post-smolts returned to their home river for assumed overwintering. These findings of post-smolts marine behavior extend to the current knowledge of anadromous Arctic charr and may act as a reference during the ongoing climate change and is important for conservation and coastal area management.

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6 Appendix 1

Table 1. Fish distribution, number of detections and percentage of detections grouped by study area sections.

Section	*n* fish detected	*n* detections	% detections
Inner	26	4294	3.8
Middle	45	88630	79.1
Outer	25	8857	7.9
Ramfjord	15	3380	3.0
Sørbotn River	9	6749	6.0
Laksvatn River	37	123	0.1