



Behaviour and habitat use of first-time migrant Arctic charr: novel insights from a subarctic marine area

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ABSTRACT: Anadromous Arctic charr *Salvelinus alpinus* is a cold-adapted salmonid that is vulnerable to climate warming and anthropogenic activities including salmon farming, hydropower regulation, and pollution, which poses a multiple-stressor scenario that influences or threatens populations. We studied the horizontal and vertical behaviour of Arctic charr tagged with acoustic transmitters (n = 45, mean fish length: 22 cm) in a pristine, subarctic marine area to provide insights into the behaviour of first-time migrants. Tagged fish spent up to 78 d at sea, with high marine survival (82% returned to their native watercourse). While at sea, they utilized mostly near-shore areas, up to 45 km away from their native river. Arctic charr showed large variation in migration distance (mean ± SD: 222 ± 174 km), and the migration distance increased with body size. Although the fish displayed a strong fidelity to surface waters (0–3 m), spatiotemporal variation in depth use was evident, with fish utilizing deeper depths during the day and in late July. These results represent baseline data on Arctic charr's marine behaviour in a pristine fjord system and highlight the importance of near-shore surface water as feeding areas for first-time migrants. Furthermore, the observed dependency on coastal areas implies a vulnerability to increasing human-induced perturbations, on top of impacts by large-scale climate change in marine and freshwater habitats.

KEY WORDS: Anadromous salmonids · Acoustic telemetry · *Salvelinus alpinus* L. · Depth use · Marine migration · Swimming behaviour

1. INTRODUCTION

Coastal marine ecosystems are highly productive environments, providing habitat for many fish species, marine mammals, sea birds, and other animals. The coastal zone is also an important area for human activities, such as recreational and commercial fisheries, tourism, aquaculture, and transport, and offers great economic and social value for people living near or travelling to the coast, a variety of economic sectors, and other stakeholders; but such anthropogenic activities may put biodiversity in coastal

areas under pressure (He & Silliman 2019). Northern marine fjords are highly productive coastal ecosystems (Gross et al. 1988) where there are still large areas with relatively modest human impact. However, these areas are experiencing increased anthropogenic pressure due to development that includes aquaculture, hydropower regulation, and mining, in addition to the stress exerted by rapid climate change (Halpern et al. 2019).

Many animals migrate between different habitats to maximize overall fitness. Among fishes, diadromy is a common migration pattern where individuals

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move between freshwater and saltwater habitats to feed and spawn (Gross 1987, McDowall 1997). Diadromous fishes either migrate through the coastal zone as they move between freshwater and open ocean habitats or spend the entire marine phase within the coastal zone. At high latitudes, ocean productivity exceeds freshwater productivity (Gross et al. 1988), and the most common form of diadromy in these regions is anadromy, which involves reproduction in freshwater and feeding in the marine environment (Myers 1949, Jørgensen & Johnsen 2014). For anadromous salmonids, the marine feeding migration represents a 'high-risk, high-reward' life-history strategy, which may result in higher fitness by increased growth and fecundity, despite an increased mortality risk at sea (Jørgensen & Johnsen 2014, Kendall et al. 2015, Ferguson et al. 2019).

Arctic charr *Salvelinus alpinus* L. is a cold-water-adapted salmonid with a circumpolar distribution. In Europe, Arctic charr range from high-altitude lakes in the Alps in the south to Svalbard in the north, with anadromous populations present in subarctic and Arctic regions of Norway and Russia (Klemetsen et al. 2003, Jørgensen & Johnsen 2014). In contrast to Atlantic salmon *Salmo salar* L., which perform obligate long-distant feeding migrations to open ocean areas, anadromous Arctic charr are partial migrants, with a marine migration restricted to fjords and other near-coastal areas lasting between 30 and 60 d (Klemetsen et al. 2003, Jørgensen & Johnsen 2014).

For anadromous salmonids with partial migration, changes in the marine environment may shift the balance between the costs and benefits of anadromy (Ferguson et al. 2019). Due to its adaptation to low temperatures, Arctic charr seems particularly vulnerable to climate change, and currently, numerous populations are declining in large parts of the distribution area (Kelly et al. 2020, Svenning et al. 2021). In northern Norway, the rise in air and water temperatures since the early 1990s correlate with a reduction in the proportion of Arctic charr compared to other anadromous salmonids (Svenning et al. 2021). The projected increase in freshwater primary production and water temperatures is expected to decrease the overall prevalence of anadromy in Arctic charr populations (Finstad & Hein 2012). Furthermore, large areas of near-unused coastline, as well as warmer conditions due to climate change, are expected to facilitate industrialization of high-latitude regions. In Norway, the projected northward shift of the salmon farming industry is particularly concerning for the northernmost anadromous salmonids, as more aquaculture facilities could reduce

suitable marine feeding areas, in addition to increasing their exposure to diseases and parasites, including salmon lice *Lepeophtheirus salmonis* (Vollset et al. 2021). Increasing water temperatures are expected to increase the production of salmon lice larvae, decrease their development time, and lead to a significant increase in the infestation pressure of salmon lice from farmed to wild salmonids in northern areas (Sandvik et al. 2021). Arctic charr first-time migrants are likely especially vulnerable to increased infestation pressure because high infestation levels could result in growth loss caused by a premature return to freshwater (Strøm et al. 2022) and a physiological burden causing increased mortality (Fjellidal et al. 2019).

To be able to understand, predict and mitigate impacts of human activities in coastal areas on anadromous salmonids such as Arctic charr, and for planning of marine reserves and other protected areas, it is crucial to have basic knowledge on their migration timing and area use. For aquaculture planning, including predicting and mitigating the impacts of salmon lice, it is important to have data and a basic understanding of the horizontal movements and depth use of the fish, due to the strong horizontal and vertical stratification of the salmon lice (Johnsen et al. 2014, Sandvik et al. 2020). With the recent advances in electronic tagging methods, several studies have provided information on the habitat use of adult Arctic charr in coastal areas (Spares et al. 2012, Jensen et al. 2014, 2016, Harris et al. 2020). However, information of the species' marine migration is limited compared to brown trout *Salmo trutta* L. and Atlantic salmon *Salmo salar* L. (e.g. Thorstad et al. 2007, Flaten et al. 2016, Halttunen et al. 2018, Strøm et al. 2021). Particularly little is known of the movement and behaviour of first-time migrating Arctic charr (life stage termed post-smolt), which is a critical life stage due to their small body size when they enter the sea. We know of only 2 previous studies of Arctic charr at this life stage (Atencio et al. 2021, Strøm et al. 2022), and our aim is to expand the knowledge by providing baseline data on their behaviour for future reference.

In this study, we investigate the spatiotemporal behaviour of Arctic charr first-time migrants using acoustic telemetry. The study was conducted in a relatively pristine subarctic fjord in northern Norway, with low industrial activity and no aquaculture facilities. We specifically aimed to investigate the post-smolts' horizontal and vertical migration patterns, as well as their probability and timing of returning to freshwater.

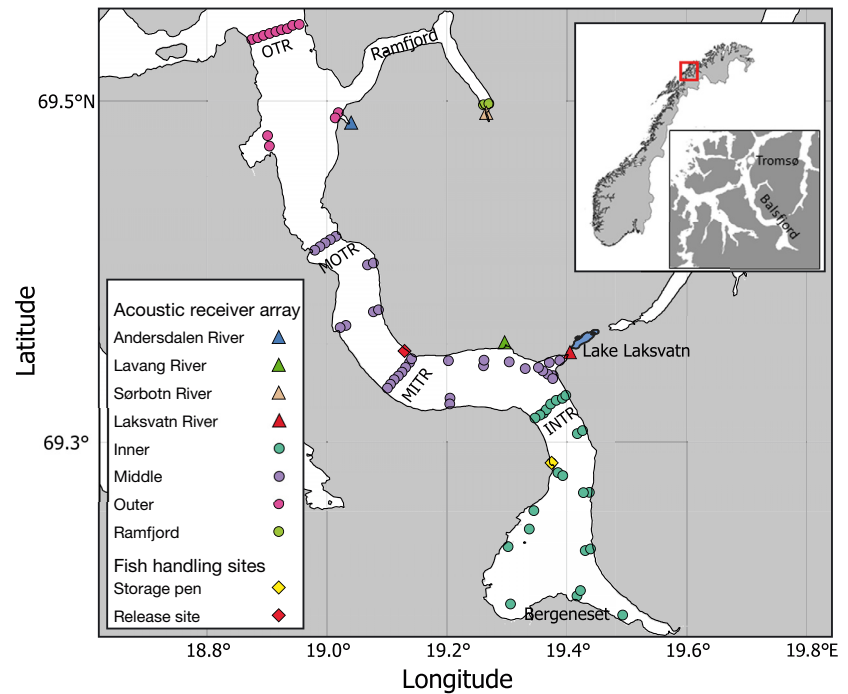


Fig. 1. The Balsfjord study area in northern Norway (inset: the position of Balsfjord in Norway). Acoustic receivers colour-coded by fjord section, and in either freshwater (filled triangles) or at sea (filled circles). Cross-fjord transects denoted by: OTR: outer transect; MOTR: middle outer transect; MITR: middle inner transect; and INTR: inner transect

2. MATERIALS AND METHODS

2.1. Study area

The study was conducted from June to October 2018 in the subarctic Balsfjord in northern Norway (Fig. 1). The Balsfjord is 57 km long, 2–7 km wide with the dynamics influenced by freshwater runoff, wind, tide, and the stratified Norwegian coastal current (Wassmann et al. 2000, Eilertsen & Skardhamar 2006). The fjord is relatively pristine with little industrial activity and no aquaculture facilities. The fjord has a maximum depth of 195 m and is separated from the outer coast by 3 straits (8–30 m depth). The average tidal difference is 1.3–1.5 m in central Balsfjord, and minor variations in high tide timing (± 30 min) could be observed within a few kilometres (Wassmann et al. 2000). Seasonal variations in salinity in the upper metres of the water column normally range between 23.2 and 33.5 ppt, with the lowest salinity observed in August (Wassmann et al. 2000). In June 2018, the water masses in the fjord were stratified, with a surface water temperature of approximately 8°C, compared to 5°C at 20 m depth (Barth-Jensen et al. 2020). The thermocline persisted through August, when water temperatures were approximately 10°C at the surface and 7°C at 50 m depth (Barth-Jensen et al. 2020).

The Laksvatn watercourse (69.23° N, 19.23° E) empties into the central part of the Balsfjord and is one of several rivers draining the fjord system that are inhabited by populations of anadromous Arctic charr or anadromous brown trout (Fig. 1). The watercourse has a catchment area of 13.3 km² and includes Lake Laksvatn (0.8 km²), which is situated 6 m above sea level, 0.6 km from the sea. The lake is normally ice-covered from November to May.

2.2. Capture and tagging of fish

Arctic charr were captured within the Laksvatn River between 2 and 19 June 2018. The fish were caught in a small fyke net (mesh size: 10 mm) in the Laksvatn River, 560 m downstream from Lake Laksvatn and 215 m upstream from the sea. Due to the distance from the lake and time of the year, all descending fish were assumed to be migrating towards the sea. The fyke net had 2 side arms (length: 2.5 m, mesh size: 16 mm) directed diagonally across the river, efficiently closing three-quarters of the river's width. The fyke net was connected to a storage tank from which fish were collected using a fine-meshed dip net. The trap was emptied once a day and captured fish were relocated to a tank in the river for temporary storage. Fish were tagged in 2 events on 14 and 19 June. Prior to tagging, fish were

transported to Bergeneset (Fig. 1) approximately 30 km away by car. During transport, oxygen levels were monitored and kept at saturation level. Fish were reloaded to a tank with circulating water on board a boat. Within a few minutes after transport, all fish showed normal swimming behaviour and were assessed as recovered and ready for surgery. Fish were tagged on deck and transported to a storage pen (diameter 4 m, depth 2 m) at sea for recovery (Fig. 1). The trap was operated until 26 June in an effort to increase the sample size, and fish were therefore held for 9 and 14 d in the pen at sea prior to the release on 28 June. Fish were not fed during the captive phase before the release.

Only Arctic charr with no evidence of infections by the marine parasite *Cryptocotyle lingua* (black spot disease) (Kristoffersen 1991) were tagged. Fish were anaesthetized by a 3 min immersion in an aqueous solution of benzocaine (0.1–0.2 ml Benzoak® l⁻¹) and thereafter placed ventral side up onto a V-shaped surgical table. Fish length (as fork length, FL) and weight were recorded. A 1.5–2 cm surgical incision was made on the ventral side between the pelvic and pectoral fins. An acoustic transmitter (model V7P; 19 × 7 mm, 1.2 g in water, estimated battery life of 167 d, 30–90 s random pulse interval; Vemco) was inserted into the body cavity. Fish swimming depth was estimated from a pressure sensor in each tag (resolution: 0.15 cm, maximum depth: 34 m). The incision was closed by 1 or 2 independent silk sutures (Ethicon 4/0). After tagging, the fish were transported to a marine net pen where they were kept until release in the sea on 28 June (Fig. 1). In total, 48 Arctic charr were tagged and released. The experiment was approved by the Norwegian Animal Research Authority (NARA FOTS ID 15473).

2.3. Tracking of tagged fish

In total, 76 acoustic receivers (Vemco VR2Tx and VR2AR) were deployed in the study area, 72 of them at sea and 4 in freshwater. The receivers were arranged in 4 across-fjord transects (approximately 400 m between each receiver) distributed along the length of the Balsfjord: outer transect (OTR), middle-outer transect (MOTR), middle-inner transect (MITR), and inner transect (INTR) (Fig. 1). For analyses, the marine study area was grouped into 4 main sections: Inner fjord section, Mid-fjord section, Outer fjord section, and Ramfjord section (Fig. 1). In addition, 1 receiver was deployed in each of 4 rivers draining into the Balsfjord: Laksvatn River, Lavangsdal River,

Andersdal River, and Sørbotn River (Fig. 1). Six (8%) of the deployed acoustic receivers were lost at sea. Of the remaining 70 receivers, 56 (80%) contained detections from tagged fish. No range test was performed *in situ*, but the detection range was assumed to be 200 m based on a recent study with similar tags and receivers in a smaller fjord in southern Norway (Serra-Llinares et al. 2020). Tagged fish were monitored between 28 June and 8 October.

2.4. Filtering of data

Detections from tags in our study were filtered out and exported using the VUE (Vemco User Environment) software. Analyses were performed in R version 3.6.2 (R Core Team 2019), where false detections (Simpfendorfer et al. 2015) were identified and removed by using the GLATOS package (Holbrook et al. 2018). In total, 789 false detections (0.7%) were removed from the dataset.

2.5. Survival, freshwater return, and marine residence time

Individual fish fates were assessed by examination of individual detection plots. Based on their vertical profile and horizontal movements, the fish were classified as:

(i) **Dead**, when the vertical profile indicated that a tag became stationary at the sea bottom. If a diving pattern inconsistent with expected Arctic charr vertical swimming behaviour was observed prior to the tag becoming stationary (Serra-Llinares et al. 2020), the fish was considered as eaten by a predator. The final individual Arctic charr record was defined as the last transmitter detection before the tag became stationary or before the fish was considered to have been consumed by a predator. Transmitter detections after this time were removed before further analyses.

(ii) **Returned**, for fish having their last detection in the Laksvatn watercourse.

(iii) **Unknown**, for fish that disappeared (i.e. sudden cessation of detections for no apparent reason) inside the study area before the end of the study.

Only 1 fish was classified as dead and further survival analysis was not performed. Return to freshwater was investigated using Cox proportional hazards models fitted with the *survival* package in R (Therneau 2022). Fate/status was set to 1 for fish that returned to the watercourse and to 0 otherwise.

Fate time t of returned fish was set to the number of days between release and fate date. Fate time t for fish that did not return to freshwater was defined by the last observation and specified as right-censored data. The following was used to model the probability of freshwater return at time t , as a function of FL (in mm):

$$h(t) = h_0(t) \times e^{(\beta_1 \cdot FL)} \quad (1)$$

The term $h(t)$ denotes the probability of returning to freshwater at time t , and $h_0(t)$ is the baseline probability. The marine residence time of Arctic charr was calculated as the number of days between the release date and the freshwater return date for fish re-entering the Laksvatn watercourse.

2.5.1. Marine area use

The marine area use of the tagged fish was investigated by exploring (1) the time spent in different fjord sections, (2) the approximate minimum travelled distance at sea, and (3) the preference for near-shore versus pelagic habitats.

2.5.2. Time spent in different fjord sections

The time individuals spent in the different fjord sections was calculated by using the *residency* function in the *actel* package (Flávio & Baktoft 2021). When a tagged fish was detected in multiple fjord sections within a single day, it was assigned to the section where it spent most of its time.

2.6. Approximate minimum distance travelled

For each fish, the shortest paths between consecutive detections were calculated using the *runRSP* function in the *RSP* package (Niella et al. 2020). This function interpolates in-water positions and associated errors between consecutive detections based on a given detection range (200 m) and the *residency* output from the *actel* package. The shortest paths were subsequently used to estimate the minimum travelled distance of each fish using the *getDistances* function in the *RSP* package, which calculates the minimum accumulated movement distance for each fish during the study period. The approximate minimum travelled distance indicates the minimum migration distance for individuals, because no data exists on where fish resided between detections. To

investigate the effect of fish size on migration distance, approximate minimum travelled distance (Y) was modelled as a function of FL and marine residence time in days using multiple regression:

$$Y = \beta_0 + \beta_1 FL + \beta_2 \text{Marine residence time} \quad (2)$$

Prior to modelling, the explanatory variables were examined for multi-collinearity using Pearson's product moment correlation. Only fish that returned to Laksvatn ($n = 37$) were used in this analysis, as they represent the full migration.

2.7. Near-shore versus pelagic habitat

Detections at the 4 cross-fjord receiver transects were classified as either near-shore or pelagic, based on the receiver position. Detections at receivers deployed <200 m from mid-tide shoreline (closest to land in both ends) were defined as near-shore (Eldøy et al. 2017), while detections at all other receivers were classified as pelagic. The percentage of detections in near-shore versus pelagic habitat was calculated for each transect. The proportion of near-shore and pelagic receivers in a transect was set as the expected ratio of detections between the 2 habitats, given equal detection range for all receivers. Differences in habitat use were tested using a χ^2 test. One near-shore and one pelagic receiver at the middle-inner transect were lost during the summer but the remaining receivers were included in the analysis.

2.8. Depth use

Detection positions and depth values were averaged on a 30 min basis to reduce a possibly biased sampling distribution if fish reside close to the receivers. To account for the potential influence of atmospheric pressure on depth (i.e. pressure) values (Veilleux et al. 2016), depth observations were corrected using recorded atmospheric pressure from the meteorological station Langnes, Tromsø, situated approximately 40 km from Laksvatn. Detections with negative depth values after this correction were set to 0.01 m. To investigate which factors influenced depth use, a set of generalized additive mixed-effect models (GAMMs) was used. The most complex model included FL in mm as a continuous fixed effect, diel period and section as factorial fixed effects, a non-linear smooth function of day of year (YD), and fish ID as a random effect on the model's intercept:

$$Y_{(j,k)} = \beta_0 + \beta_1 \text{FL} + \text{Diel period}_{(j)} + \text{Section}_{(k)} + s(\text{YD}) + \text{ID} \quad (3)$$

where $Y_{(j,k)}$ is the averaged depth during diel period j in section k . To achieve normality of residuals, a square-root transformation was applied to the response variable. Due to the 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 h were set as day and detections between 22:00 and 03:00 h as night. These diel periods were fixed for all dates, despite decreasing daylengths from the end of July to the end of the tracking period. To verify the diel period depth use, we used the *sunalc* package (Thieurmél & Elmarhraoui 2019) in R to calculate night duration when the midnight sun was absent and compared to the depth use of the fixed night duration. All GAMMs were fitted using the *bam* command from the *mgcv* package and were corrected for temporal autocorrelation by using a first-order autoregressive process (Wood 2011).

2.9. Model selection

For the Cox proportional hazards model and the linear regression models, model selection was performed using the *dredge* function in the MuMIn package in R (Bartón 2019), with models producing the lowest conditional AIC value (AICc) considered the most parsimonious. In the GAMM, model terms were selected based on their significance.

3. RESULTS

3.1. Survival, freshwater return, and marine residence time

Of the 48 fish that were tagged and released, 45 fish (FL, mean \pm SD: 221.7 \pm 16.9 mm, range: 190–260 mm; mass, mean \pm SD: 89.9 \pm 22.6 g, range: 50–38 g) were detected during the study period and produced a total of 112 033 detections. The tags omitted from the data set failed to report ($n = 3$). One fish (2%) was classified as eaten by a predator. Seven fish disappeared at sea (Inner fjord = 1, Mid-fjord = 5, Outer fjord = 1) for unknown reasons and the remaining 37 Arctic charr returned to Laksvatn between 29 June and 14 September, after spending 0–78 d (mean \pm SD: 31.0 \pm 25.7 d) at sea. There was no effect of FL on the probability of return to freshwater (Coxph, 0.002 \pm 0.010 SE; hazard ratio: 1.002, 95% CI: 0.982–1.02, $z = 0.205$, $p = 0.84$). However, the fish formed 2 distinct groups based on the duration of the marine residency. Of the 37 fish that returned, 13 (35%) re-entered Laksvatn River less than 7 d after release (residence time, mean \pm SD: 2.6 \pm 1.6 d, range: 0–6 d; Fig. 2). The remaining 24 fish (65%) returned to Laksvatn River after spending on average 50 d (SD: 15.3 d, range: 19–78 d) in the marine environment. No difference in FL was found between these 2 groups (Welch 2-sample *t*-test, $p = 0.387$). All fish returning to Laksvatn River resided in freshwater for the remaining part of the summer. Of the receivers positioned in rivers adjacent to the Laksvatn watercourse, 9 individuals were detected in the Sørbotn River while none were detected in the other rivers.

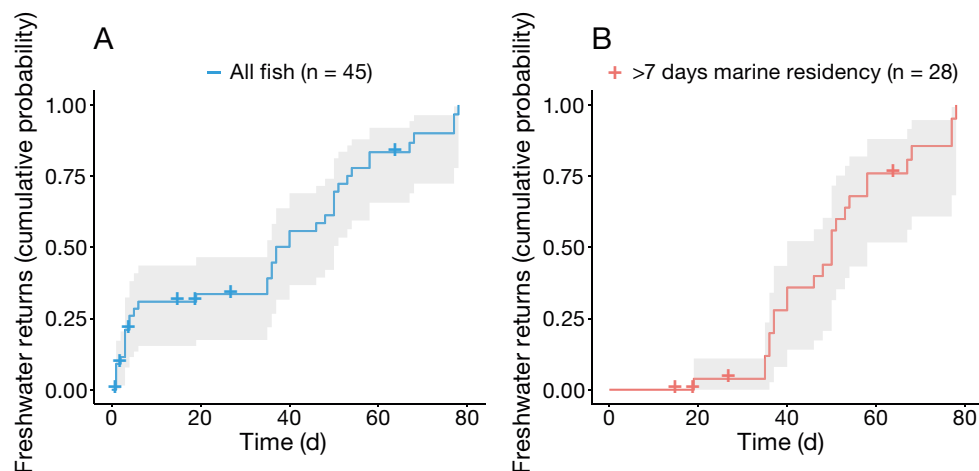


Fig. 2. Cumulative probability of freshwater returns to Laksvatn River for (A) all fish, and (B) fish residing >7 d at sea. Fish disappearing at sea were right-censored by their last detection date and are indicated by crosses (+). Shaded area: 95% confidence intervals based on Cox proportional hazards model

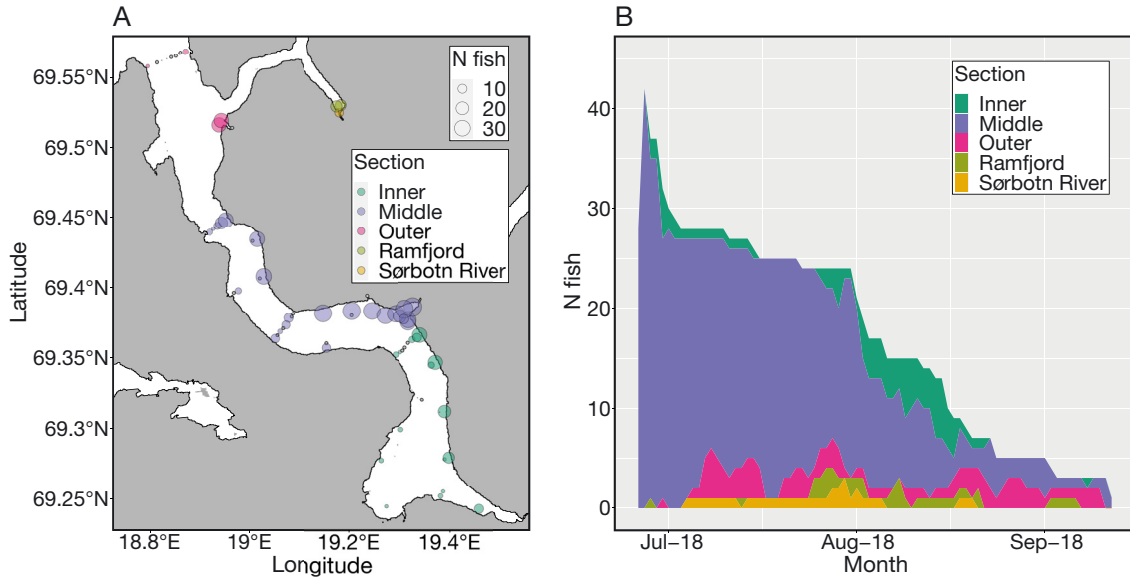


Fig. 3. Spatial marine use of Arctic charr in Balsfjord. (A) The number of fish detected at each acoustic receiver in the different sections, coded by size and colour. Open dots: empty receivers. (B) Spatial and temporal distribution of post-smolts, grouped by sections and stacked on individuals. Laksvatn River is included in the Middle section. The number of fish declining towards August is indicative of fish either ascending the Laksvatn River or disappearing at sea

3.1.1. Marine area use

Arctic charr were detected in all fjord sections, with the middle section as the most utilized area (Fig. 3). Twenty-five of the 45 fish were observed in the inner and the outer section, while 15 individuals were detected within the Ramfjord section. All 45 fish were detected in the middle section, which included loggers near the release site.

The approximate minimum travelled distance by Arctic charr post-smolts ranged from 0.85 to 588 km (mean ± SD: 222 ± 174 km). The top model (Table 1) included a positive effect (m d⁻¹) of marine residence time ($\beta = 5596$, SE: 507, 95 % CI: 4566–6625, $p < 0.001$) and FL (m mm⁻¹) ($\beta = 2717$, SE: 738, 95 % CI: 1217–4216, $p < 0.001$) and explained a high proportion (80 %) of the variance ($R^2 = 0.80$, $F_{2,34} = 71.48$, $p < 0.001$).

During the first days after release (Week 26), the space use of the Arctic charr was limited to the east-

ern side of the middle and the outer sections in Balsfjord and the Ramfjord section (Fig. 4). As the summer progressed, the space use expanded, and in Week 30, fish were observed throughout the entire fjord both at the eastern and western side (Fig. 4). While the utilization of all fjord sections persisted throughout the study period, fish were mostly observed on eastern side of the fjord system from Week 34 onwards (Fig. 4).

3.1.2. Near-shore versus pelagic habitat use

During their marine migration, Arctic charr post-smolts were detected predominantly in the near-shore areas rather than in the pelagic habitat. The 4 cross-fjord receiver transects received in total 4991 detections, of which 96 % were in the near-shore habitat and 4 % in the pelagic habitat. At the 4 transects, a total of 30 fish were observed in the near-

Table 1. Model selection table of models describing the approximate minimum travelled distance. R^2 gives the adjusted r^2 . Model candidates with weight = 0.00 were omitted from the table

Model	Log likelihood	AICc	Δ AICc	Akaike weight	R^2
Approximate minimum travelled distance (Linear model)					
~ Fork length + Marine residence time	-467.959	945.2	0.00	0.997	0.796
~ Marine residence time	-474.171	955.1	9.90	0.007	0.724

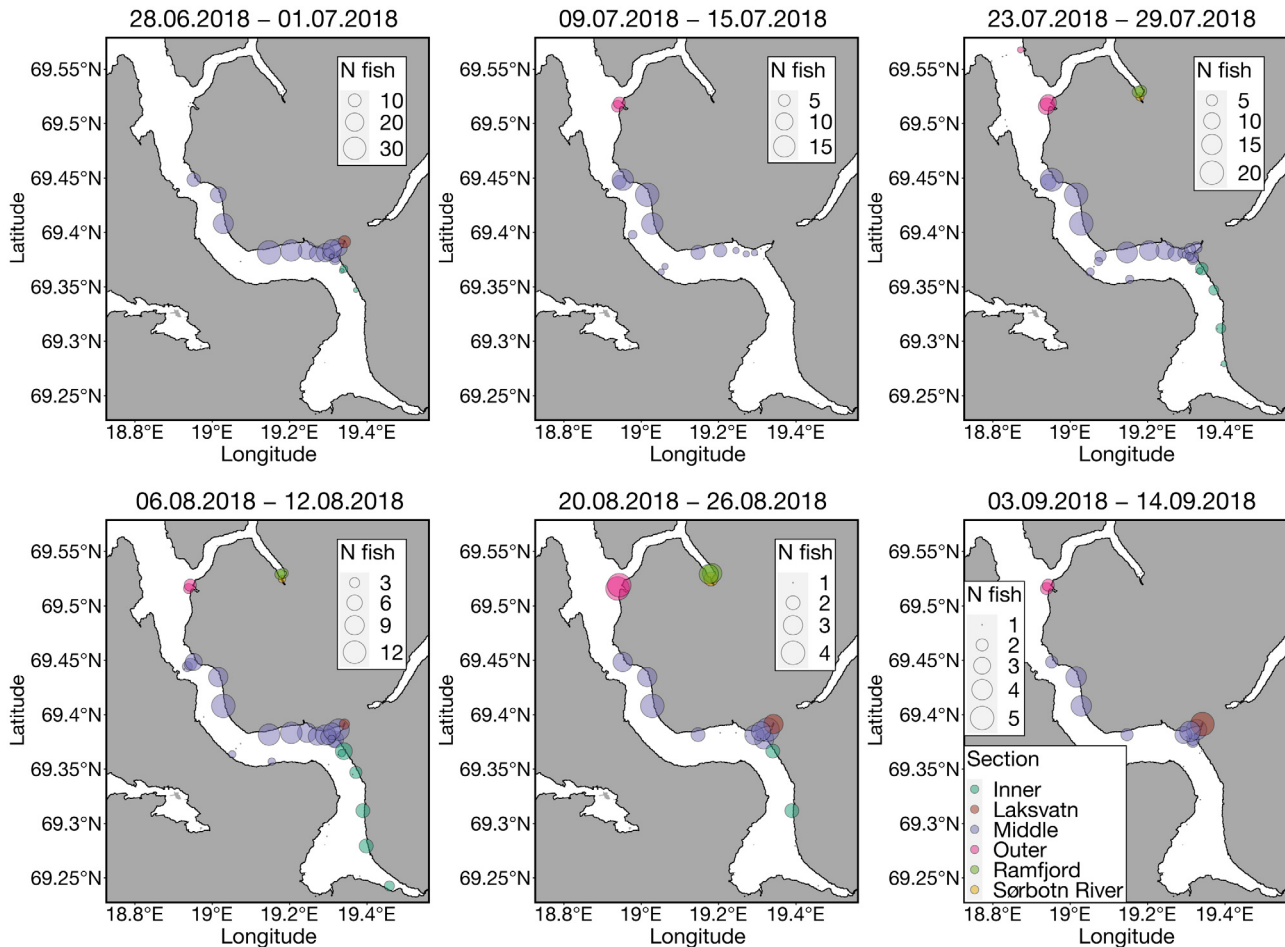


Fig. 4. Weekly spatial distributions of Arctic charr post-smolts in Balsfjord. Selected marine area use from Week 26 (28.06–01.07), Week 28 (09.07–15.07), Week 30 (23.07–29.07), Week 32 (06.08–12.08), Week 34 (20.08–26.08), and combined Weeks 36 and 37 (03.09–14.09) in 2018. Note the different scales in bubble sizes which indicates number of fish detected during the week. Dates are dd.mm or dd.mm.yyyy

shore while 25 of these were observed in the pelagic zone. All 4 transects had more detections in the near-shore than the pelagic habitat (OTR: $\chi^2_1 = 95.935$, $p < 0.001$, $n = 41$; MOTR: $\chi^2_1 = 21316$, $p < 0.001$, $n = 4064$; MITR: $\chi^2_1 = 219.9$, $p < 0.001$, $n = 421$; INTR: $\chi^2_1 = 1389.7$, $p < 0.001$, $n = 577$). We examined the pelagic habitat use by period and transect and found no significant trends. The furthest offshore detection was at a receiver 1755 m from shore in late July.

3.2. Depth use

The Arctic charr displayed a strong surface-orientation behaviour, with >95% of detections in the uppermost 0–3 m of the water column (Fig. 5). The overall marine depth use ranged between 0.0 and 20.9 m (overall mean \pm SD: 0.98 ± 1.00 m). Detections

at depths >5 m contributed marginally (0.6%) to the data set, and 98% of these detections occurred during daytime.

The most parsimonious GAMM for explaining depth use included diel period and section as fixed effects, no effect of FL, and fish ID as random effects ($p < 0.001$). The fish swam slightly deeper in daytime than at night ($\beta = -0.047$, SE: 0.008, 95% CI: -0.062 to -0.031 , $p < 0.001$; Fig. 5), with a mean depth of 1.04 m (SD: 0.91 m) in the day and 0.88 m (SD: 0.81 m) at night. Fish utilized significantly shallower depths in the Outer section (mean: 0.958 m, $\beta = -0.061$, SE: 0.029, 95% CI: -0.118 to 0.004, $p = 0.037$) and Ramfjord section (mean: 0.504 m, $\beta = -0.131$, SE: 0.038, 95% CI: -0.206 to -0.056 , $p = 0.001$) compared to the Inner section (mean: 1.126 m). Furthermore, a significant seasonal trend was present in the data (day of the year smoother: estimated degrees of free-

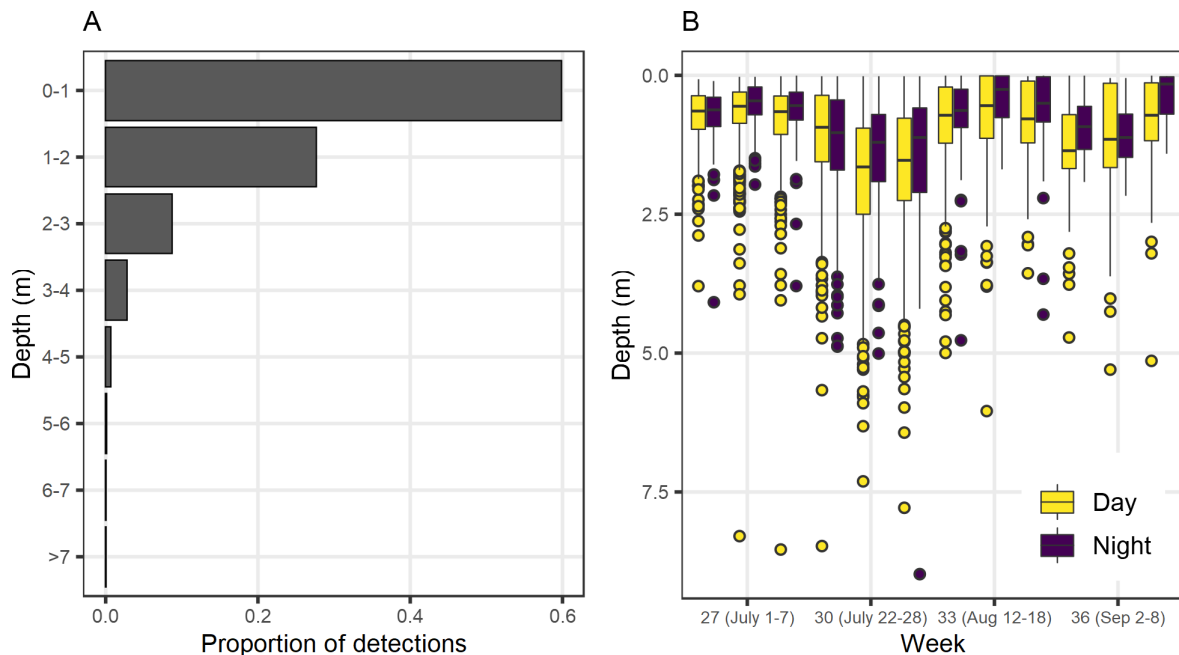


Fig. 5. Depth use of anadromous Arctic charr in Balsfjord ($n = 44$). (A) Proportion of observed time at depth. (B) Seasonal and daily variation in depth use (boxes: 25th and 75th percentiles; bars: medians; whiskers: observation $\pm 1.5 \times$ interquartile range)

dom = 8.855, $p < 0.001$), with fish utilizing the deepest depths in late July (Fig. 5).

4. DISCUSSION

4.1. Survival, freshwater returns, and marine residence time

For Arctic charr, annual marine survival is lowest for first-time migrants, and the proportion that survives increases for each repeated sea migration (Jensen et al. 2019). The observed post-smolt survival (return rate) of 82% in this study was substantially higher than for Carlin-tagged first-time migrants from the nearby watercourse Hals River (16–58%) in the Altafjord (Jensen et al. 2018). In our study, Arctic charr post-smolts were on average 5 cm larger (mean: 22 cm, $n = 45$) compared to post-smolts from the Hals River (mean: 17 cm, $n = 1626$). We suggest that the differences in survival between the studies may be explained by body-size related predation (Scharf et al. 2000), and perhaps influenced by better osmoregulatory capacity in larger fish (McCormick 1994, Jensen et al. 2012).

The Arctic charr post-smolts in this study showed 2 distinct patterns in marine residence times, with a group of fish returning to their home river within the

first week at sea. The short marine residence time of these fish was unexpected, and there could be several reasons for this behaviour. Physiological complications caused by osmoregulatory stress imposed by salmon lice infestations could result in fish returning prematurely to freshwater (Strøm et al. 2022). However, this was considered unlikely given the low salmon louse infestation pressure within Balsfjord. Alternatively, the premature returns may be related to the handling procedure either directly through stress imposed by tagging (Serra-Llinares et al. 2020, Vollset et al. 2020), or indirectly through the extended holding time at sea (9–14 d) before release. Given that only experienced personnel performed the tagging, in combination with the normal behaviour observed prior to release, we argue that the most likely cause for the premature returns was the extended holding period and that the absence of natural foraging conditions upon exposure to marine waters caused these premature returns. Notably, the rapid returns were directed to the Laksvatn watercourse, with fish ignoring rivers between their native watercourse and the release site. This, in combination with the observation that no fish entered other rivers to overwinter, suggests a strong homing behaviour, consistent with previous findings on between-watercourse movements in Arctic charr (Jensen et al. 2015). Of the watercourses draining

into the Balsfjord basin, the Laksvatn watercourse may be the best suited site for overwintering, as it contains a relatively large lake only 600 m from the sea and 6 m above sea level.

The fish in this study that did not return within the first week at sea resided longer at sea compared to previous observations of first-time migrants (Berg & Berg 1993, Jensen et al. 2019, Strøm et al. 2022) but displayed similar marine residence times as adults (Jensen et al. 2014, 2016). The drivers behind variation in the marine residence time for Arctic charr are likely complex and dependent on both physical and biological conditions. Between-year differences in marine residence time were not correlated with river temperature for post-smolts in the Vardnes river (Berg & Berg 1993). Berg & Berg (1993) observed that Arctic charr maintained their typical marine residence time in cold summers, in contrast to sympatric sea trout, indicating lower influence of sea temperatures on Arctic charr migration duration compared to sea trout. Photoperiod may be the main driver for the timing of the smolt run for Arctic charr, possibly modified by river temperature and waterflow. This contrasts with other anadromous salmonids for which water temperatures and water flow are considered the most important triggers (Jensen et al. 2012). The result of a light-induced smolt run is a more fixed timing for the smolt run between years. Biological and physical conditions at sea may therefore cause the variation in marine residence time. Physical conditions such as sea temperature and salinity may affect the choice of marine area use (Jensen et al. 2014, 2016, Harris et al. 2020). Between-year variation in prey availability within and between fjords may occur (Rikardsen & Amundsen 2005, Rikardsen et al. 2006, 2007a), and these events may influence the duration of the marine migration.

Despite Arctic charr's relatively short average marine residency of 50 d, 33% of the fish travelled distances beyond 300 km inside the fjord system. It is important to note that the actual swimming distances are likely substantially farther. The approximate minimum travelled distance varied among individuals and was, as expected, positively correlated to marine residence time and fish size, which enhance swimming capacity and swimming efficiency (Peake et al. 1997, Nøttestad et al. 1999).

4.2. Marine area use

While at sea, the Arctic charr resided within 45 km from their native watercourse, with a tendency

to utilize the eastern side of the fjord to a greater extent than the western side. In general, the fish showed seasonal variation in marine area use. The mid-fjord section was the most used area during the first weeks after release, then the use of the inner, outer, and Ramfjord sections increased in August. Arctic charr in our study performed longer migrations and used larger parts of the fjord system than Arctic charr in a recent study from the neighbouring Altafjord, where first-time migrants resided within 18 km from their watercourse during most of their marine residency (Atencio et al. 2021). For anadromous salmonids, the marine area use is related to food availability, and it is likely that the differences in dispersion observed between Arctic charr post-smolt from Balsfjord and Altafjord is shaped by the spatial distribution of prey and predators, based on physical and ecological differences between the 2 fjord systems (Rikardsen et al. 2006, 2007a). The Altafjord is a more complex fjord system compared to Balsfjord and is deep, slightly warmer, and more connected to the coast through 3 deep sounds. The large Alta River empties into the Altafjord and causes seasonal variation in surface salinities. Balsfjord is cold, long, and narrow and has shallow sills (9–30 m), resulting in less water exchange compared with the Altafjord (Eilertsen & Skardhamar 2006). These physical differences between the fjords will most likely result in differences in local prey availability.

The near-shore habitat was clearly preferred by the Arctic charr, despite most individuals also visiting pelagic areas at some point during their marine migration. Arctic charr have previously been observed 5 km from the shore (Rikardsen & Amundsen 2005); however, the observed fidelity towards the near-shore habitat coincides with most previous studies on the marine habitat use of both first-time migrants (Atencio et al. 2021) and adults (Jensen et al. 2014, 2016). As Arctic charr migrate to the sea to feed, they move through the aquatic environment to habitats where prey availability is high and environmental conditions are favourable. Consequently, the strong fidelity towards near-shore habitats observed here is likely indicative of superior ecological conditions compared to more pelagic habitats. Although the diet of Arctic charr has not been studied in Balsfjord, a dietary study on sea trout from the same area documented that crustaceans, fish, and Polychaeta were the dominating prey items (Rikardsen et al. 2006). In northern Norway, sea trout and Arctic charr have been observed to display overlapping diets while in the marine environ-

ment (Rikardsen et al. 2007a), which may suggest that these prey items are also dominating the diet of Arctic charr in this fjord system.

4.3. Depth use

During their marine migration, Arctic charr post-smolts had a strong preference for surface waters (0–3 m). A diel shift in depth use was found with individuals swimming slightly closer to the surface at night. Diel variation in depth use is common in anadromous salmonids, including Arctic charr adults and post-smolts (Rikardsen et al. 2007b, Davidsen et al. 2009, Atencio et al. 2021), and likely reflects diurnal responses in feeding behaviour and predator avoidance, commonly linked to daily variation in light intensity (Hedger et al. 2017). In northern Norway, the presence of the midnight sun from mid-May to the end of July reduces the variation in diurnal light availability. However, many Arctic charr prey taxa, such as copepods and krill, still exhibit diel vertical migrations during midnight sun conditions (Rabindranath et al. 2011, Pinti et al. 2019), which may explain the diel shift in depth use.

Subarctic fjords surface water is less saline and warmer than deeper water during the summer months. The Arctic charr's positioning in this layer has been linked to increased metabolism and digestion (Mulder et al. 2020), and may aid in osmoregulation (Spares et al. 2012). Both salinity and temperature have been shown to influence the choice of residency areas and depth use in Arctic charr (Harris et al. 2020). In subarctic fjords such as Balsfjord, winds often calm at night during the summer, and waves therefore occur more regularly during daytime. Wave action may prevent fish from using the surface layer, but they can also influence the detection probability of acoustic tags (Gjelland & Hedger 2013), making it difficult to disentangle these 2 factors.

4.4. Future research on Arctic charr and management implementation

Throughout their range, anadromous Arctic charr experience increased temperatures both in freshwater and at sea, and it is possible that ongoing climate change will have strong impacts on various aspects of their life history (Finstad & Hein 2012, Svenning et al. 2021). For instance, it has been suggested that individuals may alter their spatial

distribution in response to increased temperatures (Jensen et al. 2014). An increase in sea temperatures is likely to reduce the marine habitat of Arctic charr, which in combination with the ecological effects expected as marine temperatures rise (Hofmann et al. 2010), may reduce marine growth of individuals. Furthermore, warmer and wetter winters are expected in northern Norway as a consequence of climate change (Vikhamar-Schuler et al. 2016). If precipitation comes as rain during the winter, less snow will accumulate in the mountains, which could lead to lower spring and summer waterflow in rivers (Rolls et al. 2017). This may contribute to reduced freshwater input and higher salinities in the fjords, which could be negative for Arctic charr post-smolts (McCormick 1994, Jensen et al. 2012).

Ongoing climate change may increase the industrialization of high-latitude coastal systems. In Norway, the expected northward shift of the Atlantic salmon farming industry towards the subarctic will likely have negative impacts on anadromous Arctic charr through habitat loss and increased spillover of salmon lice and other pathogens to wild fish (Vollset et al. 2021). The open net-pen farming of Atlantic salmon implies production of large densities of salmon lice larvae, which are dispersed by the water masses (e.g. Sandvik et al. 2020, 2021) to the migration corridors of wild Atlantic salmon (Bøhn et al. 2020) and feeding habitats of wild sea trout and Arctic charr (Bjørn et al. 2001, Bøhn et al. 2022). Salmon lice infestation can cause altered behaviour, such as premature return to freshwater, but also increased mortality of wild sea trout and Arctic charr (Bjørn et al. 2001, Thorstad et al. 2015, Serra-Llinares et al. 2020). Arctic charr have been shown to respond with a premature return to freshwater even at very low densities of salmon lice, i.e. at <0.05 lice g^{-1} fish (Strøm et al. 2022), and may therefore be more vulnerable than Atlantic salmon and sea trout to salmon louse infestations.

In conclusion, a comparative future perspective on Arctic charr needs to include its high-latitude geographical distribution and that the species has a lower density of anadromous populations compared with sea trout and Atlantic salmon in Scandinavia. Moreover, Arctic charr is adapted to a cold climate and will likely meet a multiple-stressor scenario, which includes the effects of climate change. Finally, when new industrial activities are developed in the northern areas, with increasing salmon farming and a subsequent increase in the density of salmon lice in the environment, Arctic charr may get an additional stressor with negative impact on both anadromous

populations and anadromy as a life history strategy. We therefore recommend increased research efforts to expand the knowledge on whether relevant stressors may result in high mortality, behavioural changes, and/or reduced growth and fecundity in anadromous Arctic charr. Such effects may ultimately reduce the diversity of Arctic charr life histories and represent a long-term threat to Arctic charr as a species.

Data availability. The data underlying this article will be shared on reasonable request to the corresponding author.

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