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Keeping close to the river, shore and surface: the first marine migration of brown trout (*Salmo trutta*) and Arctic charr (*Salvelinus alpinus*) post-smolts

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Abstract

Acoustic telemetry was utilized to track 49 brown trout (*Salmo trutta*) and 37 Arctic charr (*Salvelinus alpinus*) first-time migrants of wild origin [post-smolts; mean L_F (fork length): 169 and 172 mm] in a large fjord in northern Norway. The *S. trutta* were registered at sea for more than twice the time of the *S. alpinus* (medians of 54 and 22 days, respectively). Both species were mostly detected near river mouths (>80% of detections) and almost exclusively spent their time (>95%) within the interior 18 km of the fjord. They were surface oriented, with most detections at <1 m depth and *S. trutta* deeper on average (median mean depths of 0.7 and 0.5 m, respectively). This study concludes that post-smolts of both species stay closer to the surface and to river mouths than larger veteran migrants. This study emphasizes the importance of river mouths and upper water layers for the survival of both species during their first marine migration.

KEYWORDS
anadromous, charr, fjord, marine, migration, post-smolt, salmonid, trout

1 | INTRODUCTION

Anadromy is a life-history strategy that allows individuals from freshwater ecosystems to exploit the relatively productive foraging areas of the sea, experiencing fitness benefits through increased growth and fecundity (Gross *et al.*, 1988). For salmonids, anadromy comes at a high cost as the smolt and early marine life stages are often associated with mortality rates of more than 60% (Jensen *et al.*, 2018a; Kristensen *et al.*, 2018a; Thorstad *et al.*, 2007). Anadromous salmonid abundance has declined significantly over the past 60 years, with many populations collapsing in the 1990s and early 2000s (ICES, 2017, 2020). Human industry contributed to these declines, as salmonid smolts and post-smolts are particularly vulnerable to negative effects from freshwater acidification (Kroglund *et al.*, 2007),

hydropower production (Johnsen *et al.*, 2010) and increased salmon lice abundance linked to aquaculture (Finstad *et al.*, 2010). Many of the threats to salmonid populations will persist or even increase in the future, especially anthropogenic climate change (Blanchet *et al.*, 2019; Forseth *et al.*, 2017). For the best management of anadromous fish species, it is therefore important to understand the behaviour and ecology of salmonids in their early marine life stages. Nonetheless, there is still relatively little known about the post-smolt life stage of salmonids and, thus, how human actions and management may affect these species.

Brown trout *Salmo trutta* L. are native to fresh waters in the eastern North Atlantic but have a near-global distribution due to introductions by humans (Klemetsen *et al.*, 2003). Arctic charr *Salvelinus alpinus* (L.) have a circumpolar distribution and are the northernmost

freshwater fish in the world (Klemetsen, 2013). *S. trutta* exhibit a wide range of life histories, varying from non-migratory freshwater residents to highly migratory anadromous individuals (Klemetsen *et al.*, 2003). *S. alpinus* also have variable life histories but are anadromous only in the northern part of their range (Klemetsen, 2013; Klemetsen *et al.*, 2003). Anadromous *S. trutta* and *S. alpinus* typically spend 1–8 years in fresh water before migrating to the sea as smolts and spend from a few months to multiple years at sea before returning to fresh water (Klemetsen *et al.*, 2003). Both species are iteroparous, with individuals able to spawn and undergo multiple sea migrations during their life span. First-time migrants are termed "post-smolt" upon entering the marine environment and referred to as a "veteran migrant" during any successive marine migrations (Allan & Ritter, 1977; Klemetsen *et al.*, 2003). The post-smolt migration of *S. trutta* and *S. alpinus* is particularly important, as survival and growth during this period influence subsequent spawning success and survival (Jensen *et al.*, 2018a, 2018b; Rikardsen & Elliott, 2000).

S. trutta and *S. alpinus* primarily utilize near-coastal areas as feeding grounds, experiencing high growth rates at sea (Grønvik & Klemetsen, 1987; Klemetsen *et al.*, 2003; Thorstad *et al.*, 2016). *S. trutta* have been found to spend more time at sea and experience more growth than sympatric *S. alpinus* (Jensen *et al.*, 2018a). Previous studies have shown that *S. trutta* behaviour varies greatly among individuals and populations, as *S. trutta* in Norwegian fjords often resided near their source river (Eldøy *et al.*, 2015; Flaten *et al.*, 2016; Jensen *et al.*, 2014), whereas *S. trutta* in Danish fjords typically migrated through the fjord to the open sea (del Villar-Guerra *et al.*, 2014; Kristensen *et al.*, 2018a). Studies of veteran migrant *S. alpinus* in a Norwegian fjord have suggested that *S. alpinus* may use the outer fjord areas more often than *S. trutta* and that the higher use of the outer fjord could be related to a preference for colder waters (Jensen *et al.*, 2014; Rikardsen *et al.*, 2007a), whereas studies from the Canadian Arctic have demonstrated that even large *S. alpinus* mainly reside in estuaries (Moore *et al.*, 2016; Spares *et al.*, 2015). For both species, marine depth use studies have mostly been limited to larger veteran migrants, with results suggesting that both species are surface oriented with occasional deeper dives to depths of more than over 5 m (Eldøy *et al.*, 2017; Kristensen *et al.*, 2018b; Mulder *et al.*, 2020; Rikardsen *et al.*, 2007a).

Most studies of *S. trutta* and *S. alpinus* in the marine environment have not focused on the post-smolt life stage, instead focusing on veteran migrants (*e.g.*, Eldøy *et al.*, 2015, 2017; Harris *et al.*, 2020; Spares *et al.*, 2012). This has resulted in limited specific knowledge of the migratory behaviour of *S. trutta* and *S. alpinus* post-smolts. This knowledge gap is particularly evident in the limited information available on *S. alpinus* post-smolt migrations and lack of information available on the depth use of *S. trutta* and *S. alpinus* post-smolts.

The present study examined and compared the fjord migrations of sympatric *S. trutta* and *S. alpinus* post-smolts in the Alta Fjord system of Arctic Norway. Utilizing acoustic telemetry transmitters and a series of acoustic receiver arrays, this study was designed to provide a representative sample of salmonid migration during the summer and covered the fjord system from the inner estuaries to the outer fjord

straits. The aim was to expand upon current knowledge of salmonid post-smolt behaviour. It was hypothesized that (a) *S. trutta* would be detected in the study area for a longer period than *S. alpinus*; (b) both species would primarily utilize nearshore habitats, but *S. alpinus* would utilize the outer fjord areas more than *S. Trutta*; and (c) both species would utilize the upper 3 m of the water column almost exclusively, with no interspecific differences in depth use.

2 | MATERIALS AND METHODS

2.1 | Study area

The study was conducted from June to October 2017 in the Alta Fjord system of Troms and Finnmark County, northern Norway (70° N, 23° E). The Alta Fjord is 38 km long and 4–14 km wide and has a maximum depth of 488 m. The shortest migration distances from the Hals River to the Norwegian Sea were 43 km through the straits Stjernsund and Rognsund, whereas the distance through the Vargsund Strait was longer at 50 km (Figure 1). The inner Alta Fjord is protected as a National Salmon Fjord (NSF; Figure 1). The Alta River is the largest river draining into the Alta Fjord and affects the salinity, temperature and currents of the inner fjord (Mankettikkara, 2013).The Hals River drains into the fjord near the village of Talvik and creates a small estuary near its river mouth.

2.2 | Ethical statement

The care and use of fish in this study complied with Norwegian animal welfare laws, guidelines and policies approved by the Norwegian Food Safety Authority (17/63184-1).

2.3 | Fish capture and tagging

As part of this study, 54 wild-origin *S. trutta* and 45 wild-origin *S. alpinus* post-smolts were captured and surgically implanted with acoustic transmitters from 28 June to 14 July 2017. All fish were captured using a bag-style fjord net in a bay 3 km south of Talvik and released near the mouth of Hals River, at receiver array 3 (Figure 1).

Before tagging, fish were anaesthetized with a solution of 0.5 ml 2-phenoxy-ethanol per litre water (Sigma Chemical Co., St. Louis, MO, USA) and placed ventral side up with the head and gills submerged in a v-shaped surgical tray. A 1 cm long incision was made on the body surface, asymmetric to the *linea alba*, between the pelvic and pectoral fins. The transmitter was pushed into the body cavity, and the incision was closed using a braided silk suture (5-0 Ethicon Inc., Somerville, NJ, USA). Fork length (L_F, mm), total length (mm) and mass (g) were recorded after tagging (Table 1). Tagged fish were then placed in a large holding tub for recovery and transported to the release site, with at least 15 min of recovery time between tagging and release. All fish were released on the same day as capture and tagging.

FIGURE 1 Map of the Alta Fjord system in northern Norway with fish trap location (✴), acoustic receivers (○) and the protected National Salmon Fjord area (shaded light blue). Receiver arrays are numbered and correspond to the area number. Place names and the division of the fjord into zones are shown. Inset map shows the study area's position in Fennoscandia
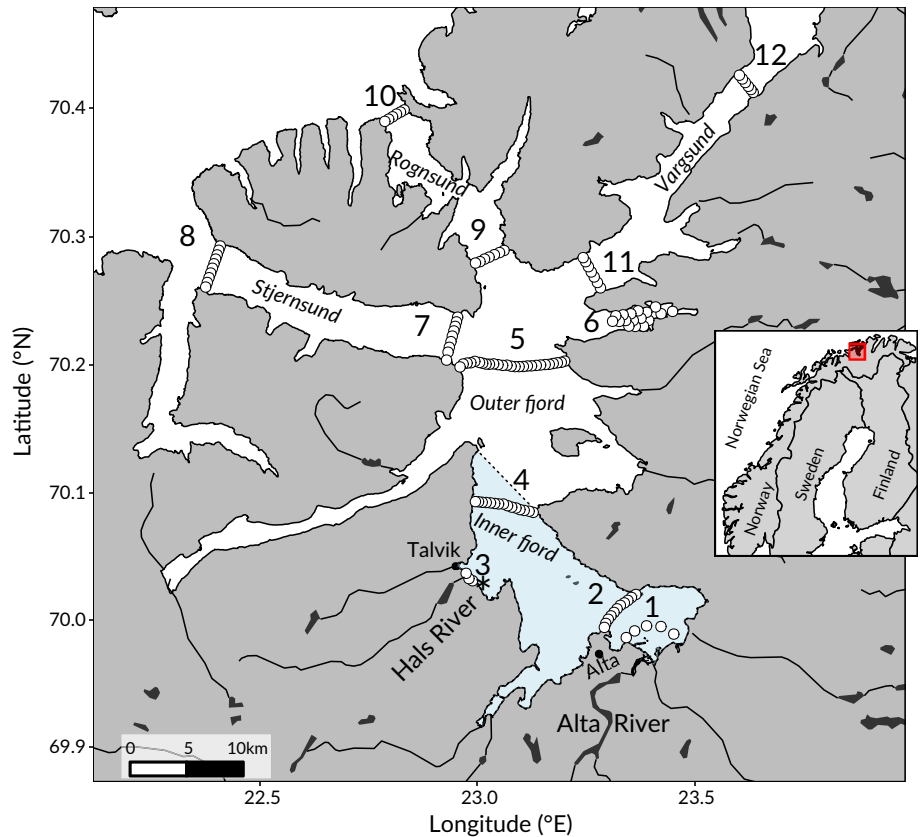
TABLE 1 Numbers (*n*) and morphological characteristics of tagged *Salmo trutta* and *Salvelinus alpinus*

Species	*n* total (*n* ID tag, *n* depth tag)	Mean L_F ± S.D. (mm)	L_F range (mm)	Mean mass ± S.D. (g)	Mass range (g)
S. trutta	54 (19, 35)	169 ± 17	141–204	45 ± 13	26–82
S. alpinus	45 (10, 35)	172 ± 21	136–219	44 ± 17	20–85

Note. L_F: fork length.

Two types of acoustic transmitters from Thelma Biotel AS (Trondheim, Norway) were used: an identification (ID)-type tag that transmitted only the ID number and a depth-type tag that transmitted the depth and ID number (models ID-LP7 and D-LP7, respectively; diameter: 7.3 mm; length: 17 and 21.5 mm, respectively; mass in water: 1.2 g; transmission rate: 30–90 s random interval; life span: 6 and 5 months, respectively). The presence and depth information were recorded when the transmitters were within the range of an acoustic receiver. Transmitter detection range in the Alta Fjord under similar environmental conditions for similar transmitters and receivers has typically been 200–800 m (Jensen *et al.*, 2014).

2.4 | Fish tracking

The movements of tagged fish were recorded by 123 receivers grouped as 12 arrays throughout the study area (Figure 1). Receivers were either the Thelma Biotel TBR-700 or the Vemco VR2-W (Vemco Inc., Bedford, Nova Scotia, Canada). The receivers on the landward

edges of arrays were 200 m from shore, and receivers within the array were positioned 400 m apart to maximize detection probability (after Jensen *et al.*, 2014). Array 4, 18 km from the mouth of Alta River, was used as the boundary between the inner and outer fjord zones, which matched the division of the Alta Fjord by Jensen *et al.* (2014) and placed the inner fjord entirely within the boundaries of the NSF-protected area (Figure 1).

2.5 | Data retrieval and filtering

Data were downloaded from the receivers in October 2017. The depth tags transmitted a raw depth value as a single byte of data, which was the same value whether received by a Thelma or Vemco hydrophone (Thelma Biotel, 2021). Raw depth values were converted to pressure-adjusted depths before analysis by multiplying the tag's "resolution" (*i.e.*, "slope") and then subtracting the "intercept" (Thelma Biotel, 2021). The resolution for the depth tags used was constant (0.2; Thelma Biotel, 2021). The intercept varied with the

atmospheric pressure relative to the tag's calibrated pressure (1000 mBar; Thelma Biotel, 2021) and was calculated for each day using 24 h averages of atmospheric pressure at the Alta Airport (Norsk Klimaservicesenter, 2021).

Data were filtered to remove any detections of shed tags, dead fish or preyed-upon fish from analyses. Shed tags and dead fish could be recognized by depth tags that registered near the sea floor or maximum tag sensor depth (51 m). Preyed-upon fish could be identified by movement after being registered at maximum tag depth or change in swimming depth that resembled that of post-smolt predators (Thorstad et al., 2011, 2012). If there was a period of no detections for a 24 h period before mortality/shedding/predation, the antecedent detections were stored for analyses. Fish with no movement, less than five detections or less than 1 h between their first and last detections were removed from analyses to avoid low sample bias. In addition to records fully removed from analysis (Table 2), one *S. alpinus* record was partially removed due to mortality/shedding, three *S. alpinus* records were partially removed due to predation and one *S. trutta* was partially removed due to predation (Supporting Information I and Supporting Information II).

2.6 | Data analyses

All data and analyses are available from the corresponding author upon request. All data analyses were performed in R Studio (version 1.3.1073, running R version 3.6.3; R core team, 2018). Fish movement distances were calculated as the shortest two-dimensional distance between the receivers of each detection relative to the sea surface using the *gdistance* package ("costDistance" function, using a transition layer with 16 directions, and geocorrection of type "c" with scale set to "FALSE"; version 1.3-6; van Etten, 2018). Movement distances should be considered minimum estimates as they do not account for vertical movements by fish or the fish taking a less-direct route. Each fjord area (1–12) was defined as the area interior to the respective receiver array (Figure 1). Movements between fjord areas were classified as outward or inward (*i.e.*, towards the open sea or towards the interior of the fjord). With outward movement, residence in the outer area started at the time of last detection on the inner array. With inward movement, residence in the outer area ended at the time of first detection on the inner array. Due to concerns over tagging effects, depth detections from the first 24 h after release were removed from depth use analysis. The remaining individuals with less than five depth detections were then removed from depth analysis,

leaving 31 *S. trutta* and 30 *S. alpinus* for depth analysis. The average daily sea-surface temperatures and salinities in the Alta Fjord system were acquired from the Norwegian Institute of Marine Research Nor-Fjords160 model simulations (described in Skarðhamar et al., 2018).

Reported group statistics were derived from the median or mean of individual means. Non-parametric tests were preferred due to non-normal distributions of most data being analysed and chosen following recommendations from Mood (1954) and Zar (1999); data normality was assessed with a Shapiro–Wilk test using "shapiro.test" function, *stats* package (version 3.6.3; R Core Team, 2018). Mann–Whitney U-tests ("Mann–Whitney") were utilized to test for a significant difference between two groups of independent samples (*e.g.*, *S. trutta*–*S. alpinus* total swim distance; "wilcox.test" function, *stats* package). Wilcoxon signed-rank tests ("paired Wilcoxon") were used for comparisons of two groups of dependent samples (*e.g.*, temperature in different fjord zones during the same time period; "wilcox.test" function with "paired = TRUE," *stats* package). χ^2 tests were used for comparisons of proportions among groups (*e.g.*, *S. trutta*–*S. alpinus* proportion of individuals detected in outer fjord; "chisq.test" function, *stats* package).

3 | RESULTS

3.1 | Morphological characteristics

The L_F, mass or release dates did not differ between tagged *S. trutta* and *S. alpinus* (Mann–Whitney U-tests: L_F: $U = 1102$, $P = 0.4$; mass: $U = 1290$, $P = 0.6$; release date: $U = 975$, $P = 0.09$; Table 1). The morphological characteristics of *S. trutta* or *S. alpinus* that were removed from analysis did not differ from those included in analysis (*S. trutta* Mann–Whitney U-tests: n removed = 5, n included = 49; L_F: $U = 144$, $P = 0.8$; mass: $U = 96$, $P = 0.4$; release date: $U = 101$, $P = 0.5$. *S. alpinus* Mann–Whitney U-tests: n removed = 8, n included = 37; L_F: $U = 187$, $P = 0.3$; mass: $U = 200$, $P = 0.1$; release date: $U = 86$, $P = 0.06$).

3.2 | Fjord residence and area use

S. trutta were detected in the study area for more than 50 days, with median dates of first and last detections being 1 July and 27 August (Table 3). *S. trutta* spent over 95% of their time in the interior 18 km of the fjord (Figure 2). Almost half of the *S. trutta* were recorded exclusively by the receiver array near the mouth of Hals River, and

TABLE 2 The number (*n*) of *Salmo trutta* and *Salvelinus alpinus* removed from analysis

Species	n initially detected (% tagged)	n removed due to shedding/ mortality	n removed due to predation	n removed due to low movement, time or detections	n included in analysis (% tagged)
S. trutta	54 (100%)	0	1	4	49 (91%)
S. alpinus	45 (100%)	0	2	6	37 (82%)

TABLE 3 The number of individuals (*n*) of *Salmo trutta* and *Salvelinus alpinus* recorded in the different fjord areas and medians of their fjord migration characteristics

Species	n recorded only near Hals (%)	n detected in outer fjord (%)	n detected in fjord straits (%)	Time detected (quartile range) (days)	Maximum distance from Hals (quartile range) (km)	Total movement distance (quartile range) (km)
S. trutta	22** (45%)	8 (16%)	2 (4%)	53.5*** (26.0–63.0)	7.7* (1.2–16.0)	28.6* (1.5–92.8)
S. alpinus	28** (76%)	4 (11%)	1 (3%)	22.1*** (13.3–32.9)	1.2* (1.2–1.2)	5.9* (2.2–22.8)

Note. Asterisks indicate the level of significance between groups.
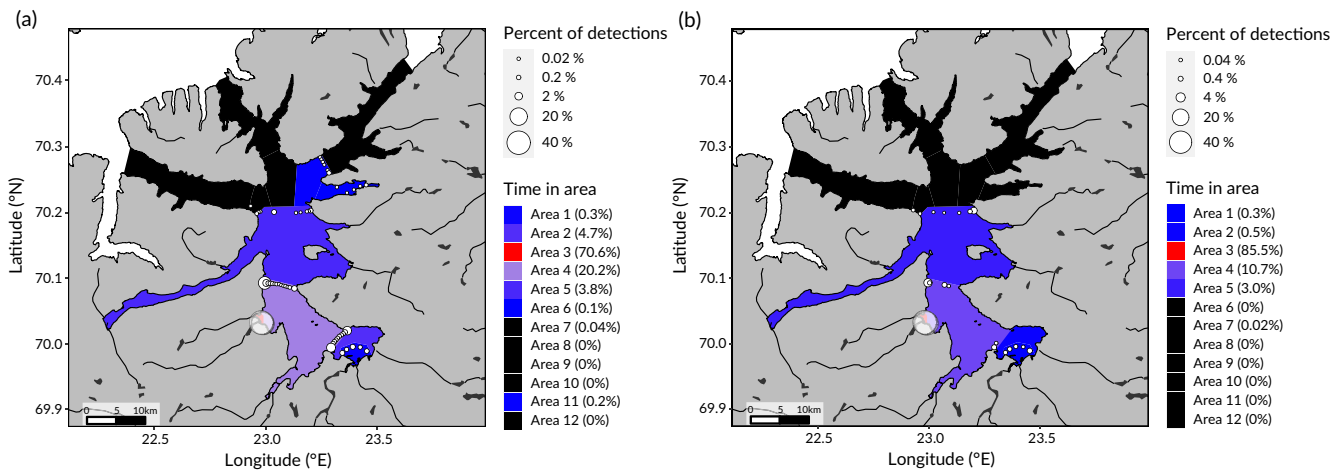
FIGURE 2 The study area with time spent in each area by (a) *Salmo trutta* (b) *Salvelinus alpinus* and receivers where they were detected (white circles). The relative size of the receiver represents the average proportion of detections at that receiver (range: 0.002%–41.9% for *Salmo trutta* and 0.004%–46.9% for *S. alpinus*). The area colour is a gradient representing the average percentage of time spent in the area with a relatively high percentage of time represented by red, relatively low represented by blue and 0% by black

those receivers accounted for a mean 80% of *S. trutta* detections (Table 3; Figure 2). Outside of the Hals River estuary area, a mean 79% of *S. trutta* detections were on the receivers closest to shore (Figure 2). *S. trutta* that visited the outer fjord spent a median 33.3 days in the inner fjord before their first detection in the outer fjord (quartile range: 28.6–44.1 days; maximum: 68.1 days). The maximum distance a *S. trutta* was detected from the mouth of Hals River was 34 km (Table 3; Figure 2), and *S. trutta* that visited the outer fjord had higher total movement distances than trout that stayed in the inner fjord (medians: 13.1 and 136.8 km; Mann–Whitney: $U = 309$, $P < 0.001$; Table 3).

S. alpinus were detected in the study area for about 20 days, with median dates of first and last detections being 2 and 27 July (Table 3). *S. alpinus* spent over 95% of their time in the interior 18 km of the fjord (Figure 2). A mean 93% of *S. alpinus* detections were on receivers in the Hals River estuary area, and over three-quarters of *S. alpinus* were recorded only by those receivers (Figure 2; Table 3). Outside of the Hals River estuary area, a mean 85% of *S. alpinus* detections were on the receivers closest to shore (Figure 2). *S. alpinus* that visited the

outer fjord spent a median 27.5 days in the inner fjord before their first detection in the outer fjord (quartile range: 20.8–45.5 days; maximum: 81.3 days). The maximum distance a *S. alpinus* was detected from the mouth of Hals River was 22 km (Table 3; Figure 2), and *S. alpinus* that visited the outer fjord had higher total movement distances than those that stayed in the inner fjord (medians: 4.8 and 43.3 km, respectively; Mann–Whitney: $U = 119$, $P = 0.01$; Table 3).

S. trutta were detected in the study area for a longer period (Mann–Whitney: $U = 1380$, $P < 0.001$; Table 3), were detected further from the mouth of Hals River (Mann–Whitney: $U = 1160$, $P = 0.01$; Table 3) and had higher total movement distances than *S. alpinus* (Mann–Whitney: $U = 1142$, $P = 0.04$; Table 3). A higher proportion of *S. alpinus* were exclusively detected by receivers at the mouth of Hals River (χ^2: $x^2 = 7$, $P = 0.008$; Table 3). There was no difference in the proportion of *S. trutta* and *S. alpinus* that visited the outer fjord (χ^2: $x^2 = 0.2$, $P = 0.7$; Table 3). The amount of time *S. trutta* and *S. alpinus* spent in the inner fjord before progressing to the outer fjord did not differ (Mann–Whitney: $U = 18$, $P = 0.8$), whereas outside of the Hals River estuary, *S. trutta* and *S. alpinus* were detected on the receivers

closest to shore at similar rates (Mann–Whitney: $U = 84$, $P = 0.7$; Figure 2).

3.3 | Depth use

S. trutta and *S. alpinus* post-smolts predominantly utilized the upper 3 m of the water column and had mean depths of about 1 m (Figure 3). *S. trutta* were recorded at deeper mean depths than *S. alpinus* (median mean depth: 0.7 and 0.5 m, respectively; quartile range: 0.6–0.9 and 0.4–0.7 m, respectively; Mann–Whitney: $U = 668$, $P = 0.003$; Figure 3). *S. trutta* were recorded diving to deeper depths than *S. alpinus*, with maximum depth for individuals ranging from 1.5 to 23.9 m for *S. trutta* and from 1.7 to 7.1 m for *S. alpinus* (median maximum depth: 5.1 and 3.4 m, respectively; quartile range: 3.5–8.8 and 2.1–4.3 m, respectively; Mann–Whitney: $U = 707$, $P < 0.001$).
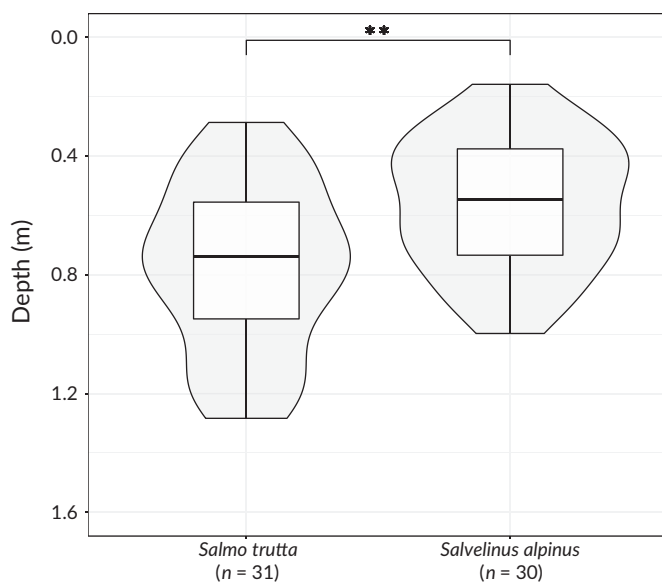
FIGURE 3 Box, whisker and violin plot of mean depths by *Salmo trutta* and *Salvelinus alpinus* (*n* is number of individuals). The width of grey shaded regions represents the relative distribution of mean depths. The horizontal line inside each box represents the group median, the lower- and upper box boundaries are the first and third quartiles, and the whiskers extend to 1.5 times the interquartile range (but do not extend beyond the minimum or maximum values in the group). The level of significance between *S. trutta* and *S. alpinus* depths is represented by asterisks

Overall, both species had a very low proportion of their depth detections at 3 m depth or deeper (*S. trutta*: 1%; *S. alpinus*: 0.4%).

3.4 | Environmental conditions

During the period of most fish detections, July and August, daily sea-surface temperatures in the Hals River estuary area were warmer than in the fjord straits but did not differ from the outer fjord or the rest of the inner fjord (paired Wilcoxon: $n = 62$; Hals straits: $W = 1781$, $P < 0.001$; Hals outer: $W = 1228$, $P = 0.08$; Hals inner: $W = 935$, $P = 0.9$; Table 4). The sea-surface temperatures where *S. trutta* and *S. alpinus* were detected did not differ (Mann–Whitney, through July: $n = 49$ and 37, respectively, $U = 856$, $P = 0.7$; Mann–Whitney, August: $n = 39$ and 14, respectively, $U = 331$, $P = 0.2$; Table 4).

In July and August, sea-surface salinity in the study area was generally a gradient from brackish water in the inner fjord to near-full strength sea water in the fjord straits, with the salinity of the inner fjord significantly lower than that of the outer fjord and fjord straits [mean daily salinity ± s.d.: 21.9 ± 2.6 (inner), 27.7 ± 2.5 (outer), 29.6 + 2.0 (straits); paired Wilcoxon: n pairs = 62; inner–outer: $W = 0$, $P < 0.001$; inner straits: $W = 0$, $P < 0.001$]. The sea-surface salinity where *S. trutta* and *S. alpinus* were detected did not differ [July mean salinity ± s.d.: 22.2 ± 1.5 (*S. trutta*), 22.1 ± 1.4 (*S. alpinus*); Mann–Whitney, through July: $n = 49$ and 37, respectively, $U = 1027$, $P = 0.3$; August mean salinity ± s.d.: 26.4 ± 2.1 (*S. trutta*), 26.4 ± 2.5 (*S. alpinus*); Mann–Whitney, August: $n = 39$ and 14, respectively, $U = 265$, $P = 0.9$].

4 | DISCUSSION

Salmonidae is one of the most researched fish families in the world (Birnie-Gauvin et al., 2019). This study built upon previous studies (e. g., Eldøy et al., 2015, 2017; Flaten et al., 2016; Jensen et al., 2014) by addressing information gaps concerning *S. alpinus* post-smolt behaviour, in general, and the depth use of *S. trutta* and *S. alpinus* post-smolts. The fjord migration of *S. trutta* and *S. alpinus* post-smolts differed in their duration and depth use but was generally similar in their area use. The nearshore areas of the inner fjord, especially near river mouths, were highly utilized by both *S. trutta* and *S. alpinus* post-smolts. Post-smolts of both species were surface oriented, with mean depths near 1 m, Nonetheless, *S. trutta* were on average deeper in the

TABLE 4 The sea-surface temperature in July and August for each fjord zone and where *Salmo trutta* and *Salvelinus alpinus* were detected

Fjord zone (area numbers)	July mean ± s.d. (°C)	*S. trutta* July mean ± s.d. (°C)	*S. alpinus* July mean ± s.d. (°C)	August mean ± s.d. (°C)	*S. trutta* August mean ± s.d. (°C)	*S. alpinus* August mean ± s.d. (°C)
Hals estuary (3)	11.5 ± 0.6	11.5 ± 0.4	11.4 ± 0.3	10.8 ± 0.8	10.8 ± 0.5	10.9 ± 0.7
Inner fjord (1, 2, 4)	11.3 ± 0.6			10.9 ± 0.6		
Outer fjord (5, 6)	11.2 ± 0.8			10.8 ± 1.0		
Fjord straits (7–12)	10.7 ± 1.0			10.3 ± 0.8		

water column than *S. alpinus*. These results represent some of the first information regarding *S. alpinus* post-smolt behaviour in fjords and indicate that *S. alpinus* migrations may change throughout their life.

4.1 | Fjord residence and area use

S. trutta post-smolts were recorded in the study area for a longer period than *S. alpinus*, as hypothesized. The median time *S. trutta* were detected in the study area, 54 days, was near the long-term mean residence time of *S. trutta* post-smolts in the Alta Fjord system (55 days; Jensen *et al*., 2018a, 2018b). Also, the median date of last detection for *S. trutta*, 27 August, was similar to the median freshwater return date for first-time migrants from long-term studies of the Hals River population (28 August; Jensen *et al*., 2012, 2018b).

The median time *S. alpinus* were detected in the study area, 22 days, was much lower than earlier estimates of *S. alpinus* post-smolt marine residence within the Alta Fjord system (33 and 34 days; Jensen *et al*., 2018a, 2018b). The median date of last detection for *S. alpinus*, 27 July, was near the median freshwater return date for first-time migrants from long-term studies on the Hals River population (29 July; Jensen *et al*., 2012, 2018b).

Due to capture at sea, it is unknown how long post-smolts from the present study were in the marine environment before being captured. Whereas *S. trutta* were captured before or near their long-term median outmigration date from the Hals River (4 July; Jensen *et al*., 2012), all *S. alpinus* were captured after their median date of outmigration (25 June; Jensen *et al*., 2012). Therefore, the results suggest that the majority of the *S. trutta* fjord migration in this study was recorded but, while capturing the intermediate and final phases of the *S. alpinus* fjord migration, the initial phase of sea residency by *S. alpinus* post-smolts was not captured. Despite this possible bias, this study is in agreement with long-term studies in the Alta Fjord that the post-smolt migrations of *S. trutta* are relatively of a longer duration, typically near 50 days, and the post-smolt migrations of *S. alpinus* are of a shorter duration, typically a month or less.

S. trutta spent the vast majority of their time in the inner fjord, and they indicated a strong preference for nearshore areas, as hypothesized. High detection rates in nearshore areas and in estuaries by *S. trutta* post-smolts were also characteristic of the fjord migrations by post-smolt and veteran migrants from central Norway (Eldøy *et al*., 2015; Flaten *et al*., 2016). Nonetheless, *S. trutta* post-smolts in the present study spent more time and were detected at higher proportions in the inner fjord than veteran migrants from the same fjord system (Jensen *et al*., 2014). It also appears that no *S. trutta* post-smolts migrated out of the fjord, which is common with *S. trutta* populations from Denmark (del Villar-Guerra *et al*., 2014; Kristensen *et al*., 2018a). Differences between findings could be due to variations among years and across geographic areas with a north–south gradient of behaviour possible, as shown by the contrast in behaviour to the Danish populations.

S. alpinus exhibited a strong preference for nearshore areas, as hypothesized. *S. alpinus* also spent most (>95%) of their time in the inner fjord, were mostly detected near their presumed source river and had shorter total movement distances than *S. trutta*. The low use of outer fjord areas by *S. alpinus* post-smolts is in contrast to authors' own hypothesis of area use and earlier findings of veteran migrants in the same study area (Jensen *et al*., 2014; Rikardsen *et al*., 2007a). Nonetheless, studies of *S. alpinus* in the Canadian Arctic show a range of behaviours, with *S. alpinus* generally preferring marine areas near river mouths (Harris *et al*., 2020; Moore *et al*., 2016; Spares *et al*., 2015). In addition, Davidsen *et al*. (2019) found a significant proportion of freshwater-origin prey in the stomachs of Norwegian *S. alpinus*, likely foraged in estuary areas. Moore (1975) found that younger *S. alpinus* did not migrate as far as older individuals. Mulder *et al*. (2020) concluded that older and larger *S. alpinus* showed ontogenetic changes in their behaviour based on their size-dependent temperature preferences and depth use and suggested that this was related to the purposes of maximizing growth. Rikardsen *et al*. (2007b) found that smaller *S. alpinus* had different diets than larger individuals in the Alta Fjord. Therefore, authors' hypothesis regarding area use by post-smolt *S. alpinus* is partially rejected, and there is likely a shift in behaviour between the post-smolt and veteran migrant life stages of anadromous *S. alpinus*.

High levels of foraging in the inner fjord are a possible explanation for the observed behaviours of *S. trutta* and *S. alpinus* post-smolts and could indicate good foraging conditions in the inner fjord (Grønvik & Klemetsen, 1987; Rikardsen *et al*., 2007b). Nonetheless, sampling bias may have amplified the high use of the inner fjord. Jensen *et al*. (2014) found that veteran migrant *S. alpinus* progressed to the outer Alta Fjord within their first 2 weeks at sea. By capturing post-smolts in the inner fjord, individuals that migrated quickly to the outer fjord could simply have been missed. Sampling bias could also be used to dispute the usage rates of nearshore areas, as individuals caught in the nearshore habitat of the fjord may be predisposed to residing in nearshore areas. Despite possible sampling bias, the results demonstrated that areas near the shore in the inner fjord were important to *S. trutta* and *S. alpinus* post-smolts, with the caveat that the usage rates for the entire population may be lower than those found here.

4.2 | Depth use

S. trutta and *S. alpinus* were surface oriented with mean depths near 1 m and over 95% of their depth detections in the upper 3 m of the water column, as hypothesized. Nonetheless, *S. trutta* had significantly deeper mean depths than *S. alpinus* – a rejection of the null hypothesis that depth use would not differ between the two species. Rikardsen *et al*. (2007a), in a study of veteran migrants of Alta Fjord, had previously observed deeper mean depths by *S. trutta* relative to *S. alpinus*. The dives to deeper depths observed in larger veteran migrant *S. trutta* and *S. alpinus* by several studies (Harris *et al*., 2020; Mulder *et al*., 2020; Rikardsen *et al*., 2007a; Spares *et al*., 2012) were not as prominent a feature of the depth use by the smaller post-smolts in the present study. Also, the mean depths of *S. trutta* and *S. alpinus*

post-smolts were shallower those than in previous studies of veteran migrants (Eldøy *et al*., 2017; Kristensen *et al*., 2018b; Rikardsen *et al*., 2007a), perhaps as a result of differing diets between life stages (Rikardsen *et al*., 2007b).

In coastal areas there is overlap in the diets of *S. trutta* and *S. alpinus* (Davidsen *et al*., 2019; Grønvik & Klemetsen, 1987; Rikardsen *et al*., 2007b). Common foraging techniques are a possible explanation for the similarities in depth and area use by *S. trutta* and *S. alpinus* post-smolts. Nonetheless, there was a distinction in behaviour by *S. alpinus*, which eat more prey of freshwater origin, surface insects and planktonic crustaceans, than *S. trutta* (Davidsen *et al*., 2019; Grønvik & Klemetsen, 1987; Rikardsen *et al*., 2007b). Planktonic prey may maintain a diel diving behaviour even in the midnight sun (Falkenhaug *et al*., 1997). Thus, the shallower mean depths of *S. alpinus* could be related to a diet consisting of more surface and diel-migrating prey relative to *S. trutta*.

4.3 | Environmental conditions

The sea-surface temperatures of the inner and outer Alta Fjord during the period of most fish detections, July–August, were near their long-term averages (Mankettikkara, 2013) but did not differ as in previous studies (Jensen *et al*., 2014; Rikardsen *et al*., 2007a). Sea-surface salinities in the inner and outer fjord were lower than long-term averages due to the relatively high discharge from the Alta River (Mankettikkara, 2013; Ugedal *et al*., 2018). *S. trutta* and *S. alpinus* area use overlapped extensively in space and time, so it is logical that the environmental conditions in which they were detected did not differ. Previous studies have suggested that temperature was a factor in the behaviour of *S. alpinus* in marine areas (Jensen *et al*., 2014; Rikardsen *et al*., 2007a; Spares *et al*., 2012). Although sea-surface temperatures during the present study were relatively uniform, results showed that the inner fjord and estuary areas are highly utilized by post-smolt *S. alpinus* – a behaviour that differed from the veteran migrants in the same area (Jensen *et al*., 2014; Rikardsen *et al*., 2007a). As discussed earlier, *S. alpinus* may exhibit an ontogenetic shift in temperature preference (Larsson, 2005; Mulder *et al*., 2020), and this may influence their habitat choices. Nonetheless, environmental conditions experienced by fish will vary at a much finer scale than those measured in this study. Future research should further examine the possible interaction between temperature, migratory behaviour and ontogeny in *S. alpinus*.

Environmental conditions are only a few dimensions of the many that make up a post-smolt's niche (Magnuson *et al*., 1979). The behavioural results observed here are from individuals responding to a complex web of ecological factors working in concert (*e.g*., environmental conditions, prey location, prey availability, avoidance of parasites and other predators). The environmental conditions of the upper water column may have thermodynamic and ecological advantages for salmonid post-smolts. Water temperatures near the water surface were close to *S. trutta*'s temperature of maximum growth efficiency (Elliott & Elliott, 2010) and near the experimentally preferred

freshwater temperatures of *S. alpinus* from the Hals River (Mortensen *et al*., 2007). Moreover, residing in the brackish waters of the upper water column may reduce exposure to salmon lice *Lepeophtheirus salmonis* (Krøyer 1837), a potentially deadly ectoparasite of salmonids that has a low tolerance for brackish waters (Bricknell *et al*., 2006; Finstad *et al*., 2010; Wright *et al*., 2016). *S. trutta* and *S. alpinus* can tolerate a wide range of environmental conditions (Elliott & Elliott, 2010; Finstad *et al*., 1989; Klemetsen *et al*., 2003), yet they almost exclusively utilized the upper water column of estuary and nearshore inner fjord areas. Thus, it is a logical conclusion that the use of the upper water column by *S. trutta* and *S. alpinus* post-smolts was partly due to the advantageous environmental conditions found there.

4.4 | Conclusion

In conclusion, the results from this study showed that *S. trutta* and *S. alpinus* post-smolts utilized areas close to rivers, shore and surface at very high rates, and thus, these areas are important in the development and survival of both species. The observed behaviour of *S. alpinus* post-smolts was different from veteran migrants in previous studies, which may be due to differences in diet and temperature preference between life stages. The observed behaviour of the *S. trutta* post-smolts resembled the behaviour of veteran migrants in previous studies to a large degree, suggesting less behavioural differences across their life stages.

Coastal areas and fjords in the Arctic are generally in good condition, though global climate change and continued development of Arctic resources are expected to degrade some areas. This study has highlighted the importance of nearshore areas to anadromous *S. trutta* and *S. alpinus*, and it is recommended that resource managers protect near-coastal and inner fjord areas, especially estuary areas near the river mouths of salmonid-bearing streams. The present study represents some of the first detailed information on the behaviour and depth use of *S. alpinus* and *S. trutta* post-smolts. Future research should focus on testing the generalizations and alternative hypotheses raised by these results for multiple years and across the geographic ranges of these species.

AUTHOR CONTRIBUTIONS
B.J.A. aided in fieldwork and majority of writing, performed the main analysis and created figures and tables.

E.B.T. advised on several drafts, suggested analysis techniques, performed major edits and contributed to writing the manuscript.

A.H.R. suggested analysis techniques, performed minor edits and contributed to writing the manuscript.

J.L.A.J. secured the main project funding and fish handling and tagging permits, led fieldwork, advised on several drafts, helped with analysis, performed major edits and contributed to writing the manuscript.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of this article.

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