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Brown trout (*Salmo trutta* L. 1758) and Arctic charr [*Salvelinus alpinus* (L. 1758)] display different marine behaviour and feeding strategies in sympatry

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Abstract

Brown trout (*Salmo trutta* L. 1758) and Arctic charr [*Salvelinus alpinus* (L. 1758)] tagged with acoustic transmitters migrated from fresh water to the sea mainly in May and June, but with large individual variation in migration timing. For *S. trutta*, large individuals (42–86 cm total length) migrated earlier in the season than small individuals (18–27 cm). For *S. alpinus*, no such pattern was found, likely because of the small size range of tagged fish (28–41 cm). *S. trutta* stayed longer at sea than *S. alpinus* (average 2 *vs.* 1 month). Early migrants of *S. trutta* stayed for a shorter period at sea than late migrants, whereas no such pattern was observed for *S. alpinus*. Large *S. trutta* moved quickly away from the river and spent average 3 days to reach a receiver line 20 km from the river mouth, whereas small *S. trutta* and *S. alpinus* migrating that far spent 2–3 weeks on the same distance. *S. trutta* utilized the entire fjord system and had a greater proportion of long-distance migrants (>20 km, 78% and 59% of large and small *S. trutta*, respectively) than *S. alpinus* (29%). *S. alpinus* mostly stayed in the inner fjord areas, and none were recorded in the outermost part of the fjord. The difference in the use of marine areas may be caused by variation in prey choice and spatial distribution of the preferred prey groups. Stable isotope analysis showed that *S. trutta* had been feeding at a higher trophic level than *S. alpinus*. *S. trutta* had mainly fed on marine fish and shrimps, whereas *S. alpinus* had large proportions of freshwater invertebrates in the diet, suggesting that the estuary with benthos and amphipods drifting from the river was an important feeding habitat for *S. alpinus*. In conclusion, major differences in habitat use, migration patterns and feeding strategies were found between sympatric anadromous *S. trutta* and *S. alpinus* while at sea.

KEYWORDS
acoustic telemetry, diet analyses, marine migrations, sea run Arctic charr, sea trout, stable isotopes

1 | INTRODUCTION

Animals in many taxa use migration between habitats as a strategy to increase individual growth, survival and lifetime reproductive success (Chapman *et al*., 2011; Dingle, 1996; Shaw, 2016). Some migratory fish move between salt- and fresh water during different parts of the life cycle, including many of the salmonids, such as brown trout (*Salmo trutta* L. 1758) and Arctic charr [*Salvelinus alpinus* (L. 1758)]. *S. trutta* and *S. alpinus* spawn in fresh water and may remain in fresh water during their entire life. Nonetheless, in populations having free access to the sea, it is common that some or all individuals undertake marine feeding migrations, followed by a return migration to the watercourse for spawning and/or overwintering (Klemetsen *et al*., 2003).

Migration to better feeding grounds at sea is associated with increased growth (Gross *et al*., 1988; Jonsson & Jonsson, 1997; Solomon, 2006) and thereby increased fecundity because the number of eggs increases with body size, and larger males become more successful when competing for mates on the spawning grounds (Fleming, 1996; Hendry *et al*., 2004). Nonetheless, migration may be costly by, for example, increased mortality rates and delayed maturation (Gross, 1987; Jensen *et al*., 2019; Jonsson & Jonsson, 1993). Migrating is also energy demanding in terms of distance travelled, osmoregulation and physiological processes that prepare the fish for life at sea (Hendry *et al*., 2004; Jonsson & Jonsson, 1993; McDowall, 1988).

In previous studies, it has been observed that *S. trutta* typically migrate further than *S. alpinus* (Jonsson, 1989; Klemetsen *et al*., 2003) and stay longer at sea during the marine feeding migration (Berg & Berg, 1989a; Bordeleau *et al*., 2018; Davidsen, Eldøy, *et al*., 2018; Jensen *et al*., 2014). Both species are opportunistic generalist feeders, and their diet is expected to reflect changes in food availability, habitat, season, age and size (Bridcut & Giller, 1995; Klemetsen *et al*., 2003). Also within the species, there is large variation among individuals and populations in the duration and distance of the marine migration (Eldøy *et al*., 2021; Klemetsen *et al*., 2003; McDowall, 1988). Individuals typically migrate to sea in spring or early summer and return to the watercourse in late summer or fall, but there are many exceptions to this pattern.

S. alpinus are usually slow-growing and late-maturing and may spend many years in fresh water before their first migration to sea (Johnson, 1980; Klemetsen *et al*., 2003; McDowall, 1988). They usually overwinter in freshwater habitats. After their first marine migration, most *S. alpinus* migrate annually until they reach the first maturity, after which they may continue to migrate annually or skip migrations for several years before migrating again (Johnson, 1980; McDowall, 1988). In *S. trutta*, some individuals live most of the life at sea, and some migrate to sea and remain there for 2 or more years before returning, whereas others migrate to sea for only a few weeks or months at a time (Klemetsen *et al*., 2003; McDowall, 1988; Thorstad *et al*., 2016).

The biology of both *S. trutta* and *S. alpinus* has been extensively studied, but most studies focus on the freshwater part of the life cycle (ICES, 2013). The marine life of these species is less studied, particularly in *S. alpinus*, despite the ecological, economic and cultural importance anadromous forms of these species represent. In recent decades, population declines in both species have been observed across Europe, and deteriorating conditions in both marine and freshwater environments have contributed to this (Anon., 2022; ICES, 2013; Svenning *et al*., 2012). In northern Norway, anadromous populations of *S. alpinus*, *S. trutta* and Atlantic salmon (*Salmo salar* L.1758) coexist, but in recent years, recreational catches of *S. alpinus* have decreased (Svenning *et al*., 2016; Svenning *et al*., 2022). Svenning *et al*. (2016) suggested that juvenile Atlantic salmon may benefit from a warmer climate at the expense of the more cold-water-adapted *S. alpinus*. In addition, these salmonid species are impacted negatively by a range of human activities in coastal areas, in particular by Atlantic salmon farming and the spread of salmon lice (*Lepeophtheirus salmonis* Krøyer 1837) (Thorstad *et al*., 2015) and other pathogens from these farms. The construction of harbours, roads and other installations; dredging; flood control; boat traffic and other activities may also impact these species in the estuaries and near-coastal areas. To be able to assess impacts and implement mitigation measures, it is necessary to know the timing of migrations and habitat use of the affected species. To preserve these species and their anadromous forms for the future, it is, therefore, crucial to understand their behaviour at sea.

In this study, the aim was to compare marine migration patterns and feeding behaviour of anadromous *S. trutta* and *S. alpinus* through studies of sympatric populations in northern Norway. The hypothesis was that *S. alpinus* had migrations of shorter distance from the home river and shorter duration of marine stays and were feeding at a lower trophic level than *S. trutta*. Acoustic telemetry was used to document migration timing, duration, distance travelled and space use of the fjord system, whereas stable isotope analysis was used to estimate important prey groups for each species during the marine migration. The combined use of acoustic telemetry and stable isotope analyses made it possible to link the behaviour observed during the marine feeding migration with the general feeding habits of the two species.

2 | MATERIALS AND METHODS

2.1 | Study area

The study was conducted during 2016–2018 in a 51-km-long north-Norwegian fjord system (67° N 15° E; Figure 1), which consists of Saltdalsfjorden and Skjerstadfjorden. Eight Atlantic salmon farms are located in the area (Figure 1). The Botnvassdraget watercourse is connected to Saltdalsfjorden *via* the River Botnelva.

Water temperature and depth in the River Botnelva (Figure 2) and temperature and salinity at several receiver locations in the fjord (Supporting Information Figure S1 in Appendix S1) were recorded every 4 h using depth-, temperature- and salinity data loggers (Star-Oddi, Reykjkavik, Iceland, model DST milli-TD, DST milli-CT).

2.2 | Fish capture, tagging and tracking

In total, 21 *S. alpinus* (5 females and 16 males) and 49 *S. trutta* (24 females, 18 males and 7 unknown gender) were captured for tagging in Lake Botnvatnet and the River Knallerdalselva. Groups of large *S. trutta* were captured during spring and fall 2016 and *S. alpinus* during fall 2016 and 2017, using fishing rods, gillnets (35–45 mm mesh-size), dip nets and flashlights for capture at night. Small *S. trutta* were captured during spring 2018 using fyke nets dedicated to the capture of down-migrating smolts. The fish were kept in holding nets until tagging (<4 h). Mean total length (L_T) was 332 mm (range 280–410) for

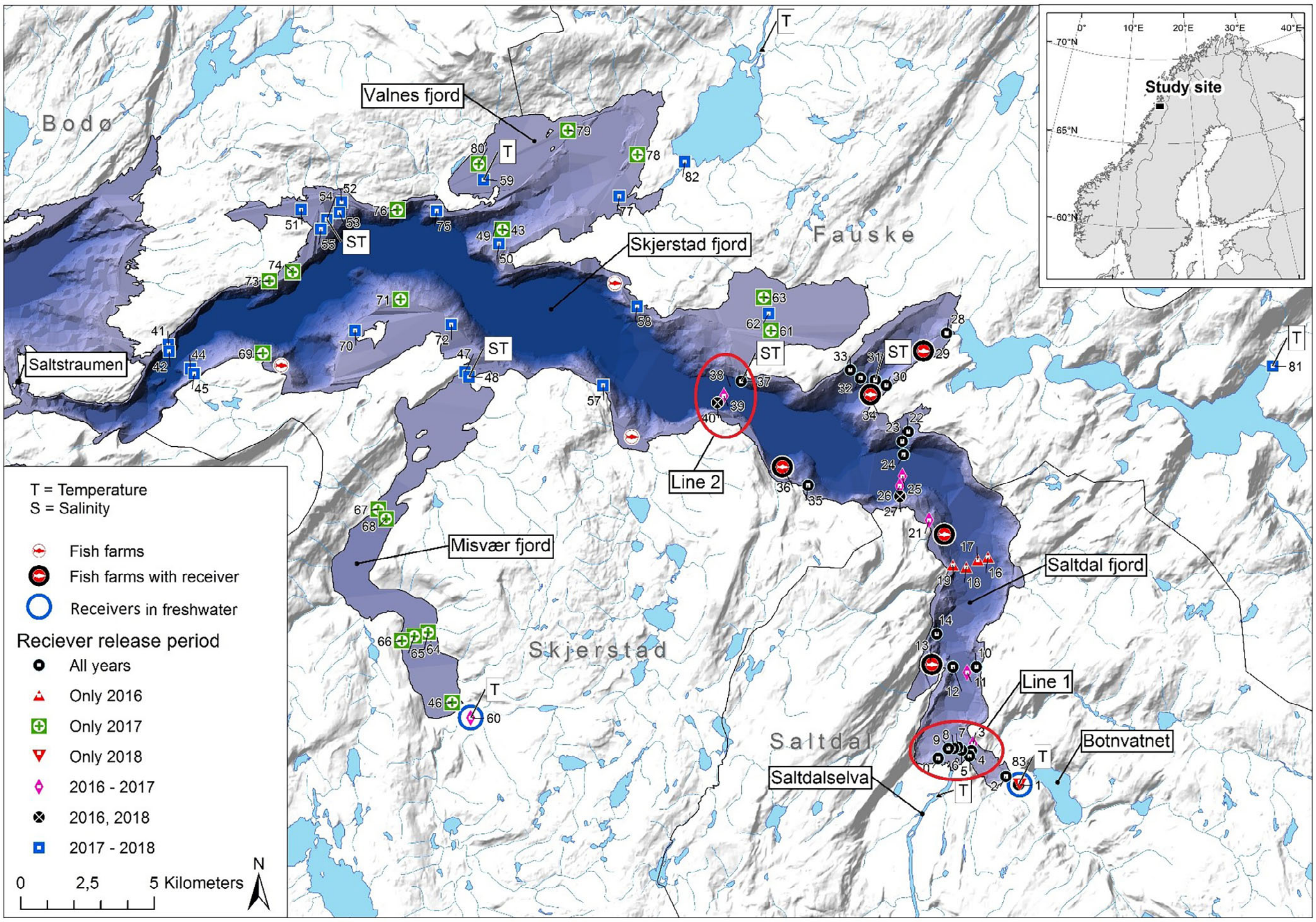


FIGURE 1 The study area showing the positions of acoustic receivers used for tracking tagged fish and the time period they were in operation. The location of temperature and salinity loggers and fish farms with and without acoustic receivers are shown. Red circles indicate lines of acoustic receivers used in the analyses. The locations of Botnvassdraget (Lake Botnvatnet and the River Knallerdalselva) and the neighbouring rivers Saltdalselva and Saltstraumen are also shown

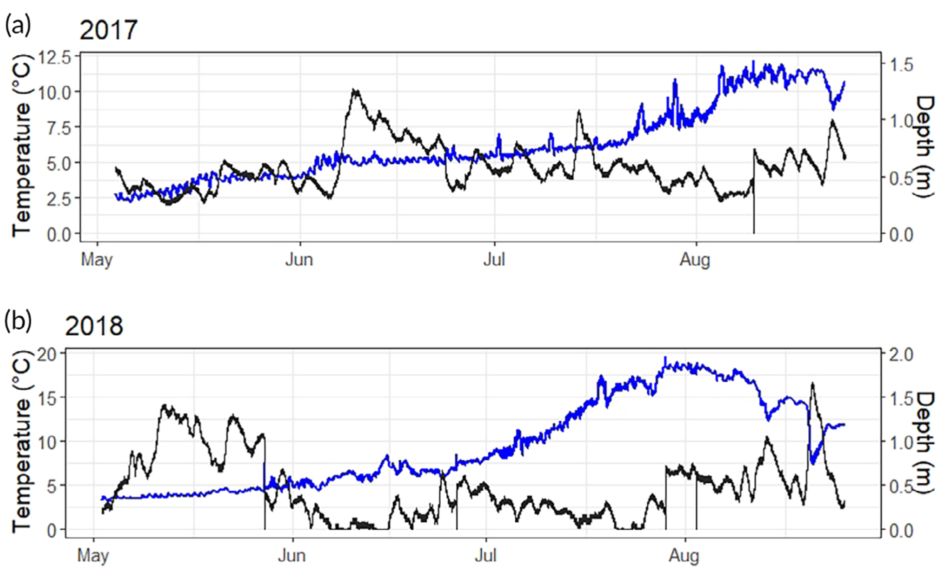


FIGURE 2 Water temperature (blue line) and water depth (black line) as an indication of water discharge in the River Botnelva during May–September (a) 2017 and (b) 2018

S. alpinus, 204 mm (range 178–268) for small *S. trutta* and 649 mm (range 420–860) for large *S. trutta* (Figure 3).

The fish were anaesthetized in a solution of phenoxy-ethanol (EEC No 204 589-7, 0.5 ml per litre of water). L_T and mass of the fish were measured. The tag was inserted into the body cavity through a 1.5–2.0-cm-long incision on the ventral surface of the fish, anterior to the pelvic girdle. The incision was closed by two to three sutures (Resolon 3/0). Six tags of different sizes were used (Supporting Information Table A in Appendix S1), and the tag chosen for any individual fish was based on the L_T of the fish. A Carlin tag (Carlin, 1955) was attached below the dorsal fin of fish >270 mm to inform fishers that the fish was tagged. The fish were released once normal swimming behaviour was regained at the capture site. The care and use of field-sampled animals complied with the Government of Norway animal welfare laws, guidelines and policies as approved by the Norwegian Food Safety Authority (permit 18/67706). All methods are reported in accordance with ARRIVE guidelines (Animal Research: Reporting of *In Vivo* Experiments).

In total, 85 acoustic receivers (Vemco Inc., Halifax, Canada, models VR2, VR2W and VR2W-AR) were used to track the tagged fish: 81 in the fjord and 4 in the watercourses Botnvassdraget, Misvær, Laksså and Sulitjelma (Figure 1). The receivers were deployed at 0.5–3.0 m depth in fresh water and 5 m depth in the fjord, except a few at 50–150 m depth. In 2018, twenty-two of the receivers had built-in pinger tags (Vemco model VR2-W-AR). Recordings of signals from these tags by neighbouring receivers indicated a detection range for receivers of 200–400 m. The detection efficiency of the second outermost receiver line was 100%, based on all 10 *S. trutta* recorded at the outermost receiver line being recorded also at this line (Figure 1). All telemetry data were uploaded to the Ocean Tracking Network (https://members.oceantrack.org/OTN/projects) and European Tracking Network data warehouses (https://www.lifewatch.be/etn/).

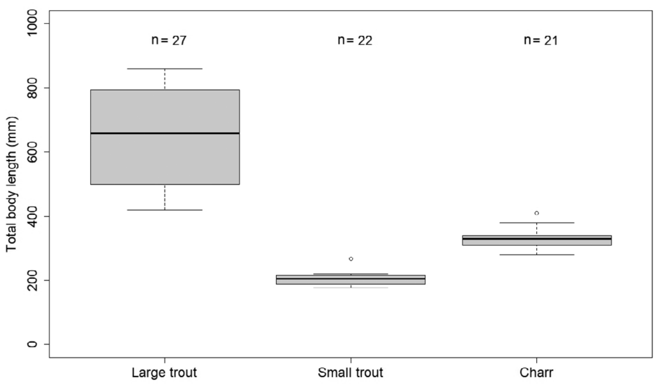


FIGURE 3 Total body length (L_T) of tagged fish. Trout: brown trout (*Salmo trutta*). Charr: Arctic charr (*Salvelinus alpinus*). The box-and-whisker plots show the median values (bold lines), the interquartile ranges (boxes), the 5th and 95th percentiles (whiskers) and the outliers (dots). Numbers above each plot indicate sample size of each group

2.3 | Isotope analyses

A trap was installed in the outlet of Lake Botnvatnet (Figure 1) to record the return of tagged and untagged fish between 26.06-19.08.2017. A total of 26 *S. alpinus* (9 males, 11 females, 6 unknown sex; 17 immature, 6 mature, 3 unknown maturity) and 110 *S. trutta* (51 males, 47 females, 12 unknown sex; 103 immature, 6 mature, 1 unknown maturity) sampled from the trap were stored at −18°C for 6 months prior to further analyses. After thawing in the lab, *c.* 1 cm^3 of muscle tissue from the area behind the dorsal fin and above the lateral line was extracted and used for stable isotope analysis.

L_T was smaller for *S. alpinus* (mean 276 mm, range 204–390, S.D. = 35.93; n = 26) than *S. trutta* (mean 336 mm, range 185–720, S.D. = 98.51; n = 110) (Wilcoxon rank sum test, W = 1021; $P < 0.01$). Mean body mass was 209 g (range 66–599, S.D. = 101.58; n = 25) for *S. alpinus* and 479 g (range 27–2292, S.D. = 455.81; n = 117) for *S. trutta*. Mean age was 5.4 years (range 4–8, S.D. = 0.91) for *S. alpinus* and 4.3 years (range 3–10, S.D. = 1.17) for *S. trutta* (see Supporting Information Figure B in Appendix S1).

To determine the marine diet of *S. alpinus* and *S. trutta* based on stable isotope levels in sampled fish, potential prey species (see Supporting Information Table B in Appendix S1) were collected for stable isotope analyses in Skjerstadfjorden during 5–8 June and 21–23 August 2018. In June, hauls with a fine mesh seine net were conducted from the beach near the outlet of Botnvassdraget. Captured prey species included three-spined stickleback (*Gasterosteus aculeatus* L. 1758), sand gobies [*Pomatoschistus minutus* (Pallas 1770)], sand shrimps (*Crangon* sp.), amphipods (Amphipoda), European plaice (*Pleuronectes platessa* L. 1758) and common dab [*Limanda limanda* (L. 1758)]. In August, bottom gillnets (6–25 mm mesh-size) in near-shore areas were used to capture prey species. These included saithe [*Pollachius virens* (L. 1758)], Atlantic herring (*Clupea harengus* L. 1758), Atlantic mackerel (*Scomber scombrus* L. 1758), Atlantic cod (*Gadus morhua* L. 1758), haddock [*Melanogrammus aeglefinus* (L. 1758)] and lesser sand eel (*Ammodytes tobianus* L. 1758). Larger fish were captured in the fjord using rods to sample additional prey species from their stomachs. Krill (Euphausiacea) and crabs (*Hyas* sp.) were sampled from stomachs of Atlantic cod, whereas krill and flying insects were found in the stomachs of *S. alpinus* and *S. trutta*. The prey items collected were identified to the lowest taxonomic group possible. Up to about 1 cm^3 of tissue was collected from each specimen, but due to small prey sizes, samples were often smaller. For larger crustaceans, the exoskeleton was removed, and the tissue inside was used as the sample. For smaller specimens, the whole body was included in the analysis.

Each sample was dried in aluminium foil in a drying oven for 48 h and subsequently crushed to a fine powder using a mortar. Approximately 1 mg of sample was weighed up for analysis and placed in 5 × 9 mm tin containers. Each container was placed in a "Thermo Scientific FLASH 2000 HT Elemental Analyzer" with columns set up for "NC with Flash IRMS." The samples were burned with O_2 in a carrier gas of He, at 1020°C. NO_x was reduced to N_2 with Cu at 680°C. The products were then separated in a glass column and transferred to a "Thermo Electron DELTA V Advantage IRMS" *via* a "Thermo Fisher Scientific Confo IV

Universal Interface" for analysis of carbon and nitrogen isotope ratios, as described by Davidsen, Sjursen, *et al.* (2018). Carbon and nitrogen stable isotope compositions were measured as the ratio of the heavier isotope to the lighter isotope ($^{13}C/^{12}C$ and $^{15}N/^{14}N$) and reported in standard delta (δ) notation as parts per thousand (per mil, ‰) relative to internationally defined standards for carbon (Vienna Pee Dee Belemnite; Craig, 1953) and nitrogen (Ambient Inhalable Reservoir; Mariotti, 1983). Every third sample run was a gelatine fish mix with already known variables (G7041 GelatineFish), and the first and last samples in a series of 32 were empty control samples.

Scales were used for age determination of individual *S. trutta* (Dahl, 1910; Lea, 1910). For *S. alpinus*, age was estimated from sagittal annuli counts following Grainger (1953).

All scales and otoliths were analysed independently by two people. If there was disagreement in the age determination, the lowest age estimate was used in the analyses.

2.4 | Data analyses

Detections of tagged fish from April 2016 to October 2018 were analysed. Data from the receiver in Botnvassdraget were filtered to reduce the risk of recording false IDs resulting from several fish residing within the range of the receiver at the same time, by excluding detections that were not followed by a second detection of the same tag ID within 10 min. Transmitters consistently detected at the same receiver for more than a week, indicating tag expulsion or fish mortality, were excluded. Eleven *S. trutta* that disappeared within 3 days of fjord entry were excluded from analyses, because they either returned to fresh water without being recorded or died or tags were expelled or malfunctioning.

Duration of the marine migration was estimated from the first detection of the fish by a receiver in the fjord to the last detection by the receiver closest to the watercourse (or first detection in fresh water if not recorded there). If a fish had its last detection outside another watercourse, it was assumed to have travelled up that watercourse, and that detection was used as the last detection in the fjord. If a fish returned to a watercourse several times during the season, the time spent in the watercourse was subtracted from the overall duration of the marine migration.

Each fish was classified as either a short-, medium- or long-distance migrant. Short-distance migrants were fish recorded at, but never beyond, the closest receiver line to the watercourse (line 1, Figure 1), *i.e.*, fish that travelled about 2–5 km from the river. Medium-distance migrants were fish recorded beyond line 1, but never at or past line 2, *i.e.*, fish that travelled about 5–20 km. Long-distance migrants were fish recorded at or past receiver line 2, which was the last line that crossed the main body of the fjord system, *i.e.*, fish that travelled more than 20 km.

Statistical analyses were conducted in RStudio (RStudio Team, 2016). When comparing mean values between *S. alpinus* and *S. trutta*, the Welch two-sample *t*-test was used when the assumption of normality was met and the Wilcoxon rank sum test when not. Correlations were examined using Pearson's product–moment correlation (normality) and Spearman's correlation test (non-normality). Normality was tested using functions ggqqplot(), ggdensity(), plotNormalHistogram() and shapiro. test() in packages dplyr (Wickham *et al.*, 2018), ggpubr (Kassambara, 2018) and rcompanion (Mangiafico, 2019). To test if there was a difference in the proportions of short-, medium- and long-distance migrants between the two species, a χ^2-contingency test was used.

The stable isotope data were analysed using the simmr-package in RStudio (Parnell, 2016; RStudio Team, 2016). simmr is a stable isotope mixing model based on the siar-package (Parnell & Jackson, 2013). Stable isotope mixing models are often used to quantify source contributions to a mixture (Phillips *et al.*, 2005). Prey $\delta^{15}N$- and $\delta^{13}C$-values were corrected for trophic enrichment using fractionation factors of 3.23 and 1.03 for *S. trutta* (Jensen *et al.*, 2012) and 3.80 and 0.66 for *S. alpinus* (Linnebjerg *et al.*, 2016; Søreide *et al.*, 2006). In addition to the 14 groups of marine prey collected in the study area, isotopic values from five groups of freshwater prey were extracted from existing literature (Eloranta *et al.*, 2010; Hayden *et al.*, 2013). The 19 groups of prey were further assembled into 10 groups used in the analyses, which were flying insects, freshwater zooplankton, freshwater profundal benthos, freshwater littoral benthos, freshwater amphipods, marine amphipods, marine shrimp, marine crabs, marine krill and marine fish.

3 | RESULTS

3.1 | Migration timing and duration of the marine migration

All tagged fish (21 *S. alpinus* and 49 *S. trutta*) were at some point recorded in the fjord (Table 1). Of these, 20 *S. trutta* and 9 *S. alpinus* were recorded to return to the watercourse after the marine migration.

Median date of sea entry was 28 May (range 1 May–6 July) for large *S. trutta*, 17 June (range 30 May–12 July) for small *S. trutta* and 5 June (range 8 May–1 June) for *S. alpinus*, all years combined (Table 1). Median date of return to fresh water was 5 August (range 18 July–29 September) for large *S. trutta*, 29 August (range 4 July–8 September) for small *S. trutta* and 29 July (range 12 June–27 September) for *S. alpinus*, all years combined (Table 1).

When including individuals with last recording in other places than in Lake Botnvassdraget, large *S. trutta* spent median average of 65 days in the fjord (2016 and 2017 combined; $n = 27$; range = 6–121; S.D. = 31), whereas small *S. trutta* spent median average of 56 days ($n = 22$; range = 11–116; S.D. = 29). *S. alpinus* spent median average of 31 days (2017 and 2018 combined; $n = 21$; range = 4–112; S.D. = 31). Large and small *S. trutta* spent significantly longer time in the fjord than *S. alpinus* (Welch *t*-test, $P < 0.01$ and $P < 0.05$; Figure 4), whereas there was no difference between large and small *S. trutta* ($P > 0.05$).

TABLE 1 Timing (date and distribution) of seaward and return migration of brown trout (*Salmo trutta*) and Arctic charr (*Salvelinus alpinus*) in Lake Botnvassdraget and the proportion of short/medium/long-distance migrants

	Large *S. trutta* 2016	Large *S. trutta* 2017	Small *S. trutta* 2018	Large *S. trutta* 2016 and 2017	*S. alpinus* 2017 and 2018
Date outward migration	*n* = 14 Median = 29 May Range = 1 May–6 July IQR = 27	*n* = 13 Median = 28 May Range = 20 May–8 June IQR = 12	*n* = 22 Median = 17 June 2018 Range = 30 May–12 July IQR = 6	*n* = 27 Median = 28 May Range = 1 May–6 July IQR = 10	*n* = 21 Median = 5 June Range = 8 May–16 June IQR = 2
Distribution outward migration (percentage of individuals per month)	57% May 36% June 7% July	69% May 31% June	5% May 82% June 14% July	63% May 33% June 4% July	19% May 81% June
Date return migration	*n* = 6, Median = 11 August Range = 18 July–29 September IQR = 45	*n* = 6, Median = 7 August Range = 20 July–20 September IQR = 24	*n* = 8, Median = 29 August Range = 4 July–8 September IQR = 12	*n* = 12, Median = 5 August Range = 18 July–29 September IQR = 39	*n* = 9, median = 29 July Range = 12 June – 27 September IQR = 33
Distribution return migration (percentage of individuals per month)	50% July 17% August 33% September	33% July 50% August 17% September	13% July 50% August 38% September	42% July 33% August 25% September	22% June 44% July 22% August 11% September
Proportion short/medium/long-distance migrants	14% short 29% medium 57% long	0% short 0% medium 100% long	14% short 27% medium 59% long	7% short 15% medium 78% long	29% short 43% medium 29% long

Abbreviation: IQR, interquartile range.

The timing of sea entry was not correlated with fish L_T for large *S. trutta* (Spearman's rank correlation; rho = −0.31; P > 0.05), small *S. trutta* (rho = −0.29; P > 0.05) or *S. alpinus* (rho = −0.21; P > 0.05), but large *S. trutta* entered the sea earlier than small *S. trutta* (Welch *t*-test, P < 0.01). There was no difference in time of sea entry between large trout and *S. alpinus* (Welch *t*-test, P > 0.05). Migration duration was negatively correlated with the timing of outward migration for small *S. trutta* (rho = −0.57; P < 0.01) but not for large *S. trutta* (rho = −0.25; P > 0.05) nor *S. alpinus* (rho = −0.22; P > 0.05).

3.2 | Migration distance and use of the fjord system

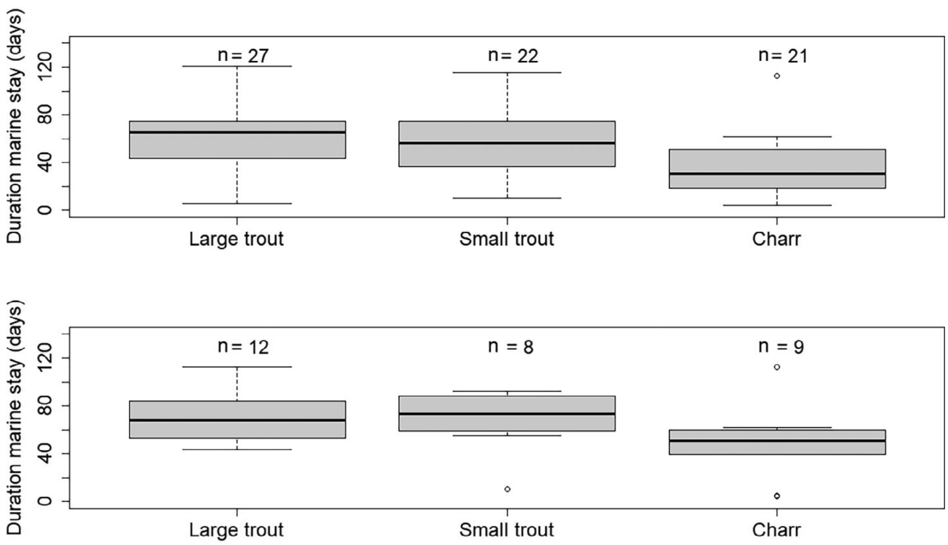
Among the large *S. trutta*, 21 (78%) were long-distance migrants, 4 (15%) medium-distance migrants and 2 (7%) short-distance migrants (Table 1). Among the small *S. trutta*, 13 (59%) were long-distance migrants, 6 (27%) medium-distance migrants and 3 (14%) short-distance migrants. Among the *S. alpinus*, six (29%) were long-distance migrants, nine medium-distance migrants (43%) and six short-distance migrants (29%). A larger proportion of *S. trutta* (large and small combined) than of *S. alpinus* undertook long-distance migrations (χ^2 contingency test, χ^2 = 9.4; *df* = 2; P < 0.01). Large *S. trutta* defined as long-distance migrants spent on average 2.9 (± 2.9) days to reach the defined boundary qualifying them for long-distance migration (20 km), whereas small *S. trutta* spent on average 18.5 (± 8.3) days and *S. alpinus* on average 13.3 days (± 8.7) on the same stretch. In general, *S. trutta* utilized the entire fjord system and was frequently recorded by receivers in the outer regions, whereas *S. alpinus* mostly utilized the inner areas and were never registered at the outermost receiver lines.

3.3 | Stable isotope analysis

S. alpinus and *S. trutta* had significantly different isotope signatures (Wilcoxon rank sum test δ^{15}N; W = 112; P < 0.001 and δ^{13}C; W = 136; P < 0.001), although with some overlap between individuals (Figure 5). *S. alpinus* had a mean δ^{15}N isotopic value of 9.1‰ (range 6.6‰–11.9‰) and a mean δ^{13}C of −23.2‰ (range − 27.1‰ to −20.7‰). *S. trutta* had mean δ^{15}N of 12.3‰ (range 6.9‰–15.0‰) and mean δ^{13}C of −20.2‰ (range − 26.2‰ to −19.2‰; Figure 5). *S. alpinus* had a diet dominated by freshwater littoral benthos and freshwater amphipods, whereas *S. trutta* had a diet dominated by marine shrimps and fish (Figure 6).

There was a positive correlation between δ^{15}N-values and L_T (Spearman's correlation; rho = 0.67; P < 0.001, Figure 7). When separating the species, the correlation was still significant for *S. trutta* (rho = 0.75; P < 0.001) but not for *S. alpinus* (rho = −0.32; P > 0.05). If looking only at low-δ^{15}N individuals (those with δ^{15}N < 12‰, which includes all *S. alpinus*), there was no difference between the two species in terms of body length (L_T) (Wilcoxon rank sum test; W = 563; P > 0.05), but even within this comparable size group, *S. trutta* had more enriched δ^{15}N-values than *S. alpinus* (W = 112; P < 0.001).

FIGURE 4 Duration of the marine migration for large and small brown trout (*Salmo trutta*), and Arctic charr (*Salvelinus alpinus*) during 2016–2018. Upper panel: based on individuals returning to the water course where they were tagged and fish with last recording other places. Lower panel: based on individuals returning to the watercourse where they were tagged only. The box-and-whisker plots show the median values (bold lines), the interquartile ranges (boxes), the 5th and 95th percentiles and the outliers (dots). *n*, sample size



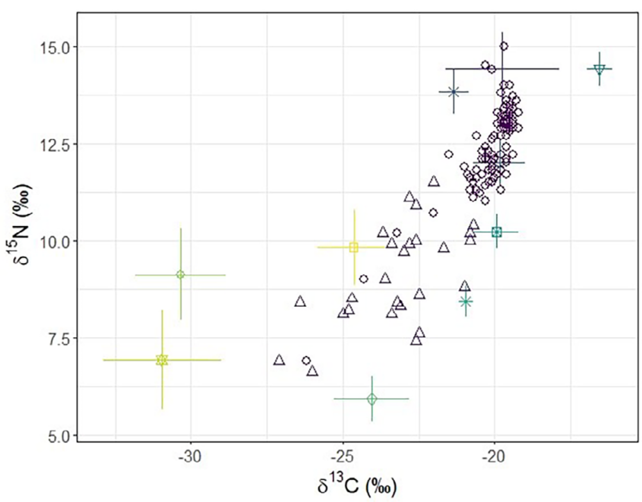


FIGURE 5 Isospace plot for brown trout (*Salmo trutta*; Consumer grp 1 – circles), Arctic charr (*Salvelinus alpinus*; Consumer group 2 – triangles) and 10 prey groups based on carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) isotope values. Symbols represent the average mean isotopic value of each group, whereas lines represent S.D. Values were corrected for trophic enrichment. ◇, Consumer grp 1; △, Consumer grp 2; +, Marine fish; +, Marine krill; +, Marine crab; +, Marine shrimp; +, Marine amphipods; +, Freshwater amphipods; +, Freshwater littoral benthos; +, Freshwater profundal benthos; +, Freshwater zooplankton; +, Flying insects

3.4 | Discussion

This study of sympatric *S. trutta* and *S. alpinus* showed differences in habitat use, migration patterns and feeding strategies between the species during their marine migration. *S. alpinus* generally stayed in the estuary and fjord areas close to the river mouth and had a diet dominated by freshwater invertebrates and amphipods drifting from the river, whereas *S. trutta* utilized the entire fjord system and were to a large extent recorded in the outer part of the fjord and had a piscivorous and marine diet. Nonetheless, there was large individual variation in migration patterns and diet for both species, demonstrating the large flexibility in behaviour of both *S. trutta* and *S. alpinus*. Individuals of both species migrated from the river to the fjord in May and June and returned to the watershed in late summer or autumn, which is a typical behaviour of *S. trutta* and *S. alpinus* in northern Norway (Berg & Berg, 1989a; Jensen *et al.*, 2020). Some *S. trutta* are known to overwinter in sea water but do so more commonly further south in the distributional range (*e.g.*, Knutsen *et al.*, 2004). Osmoregulation efficiency may be poor in cold water for many salmonids (Berg & Berg, 1989b; Finstad *et al.*, 1989), and *S. alpinus* have been observed to overwinter in estuaries only if they do not have access to a lake (Jensen & Rikardsen, 2008).

S. alpinus generally spent a shorter time at sea than *S. trutta*, although both species showed large individual variation in date of sea entry and freshwater return. The duration of the marine migration of *c*. 2 months for *S. trutta* was in accordance with the results from other studies in northern Norway, and also these other studies found that *S. alpinus* stayed for a shorter time period in the sea than *S. trutta* (Berg & Berg, 1989a; Bordeleau *et al.*, 2018; Davidsen, Eldøy, *et al.*, 2018; Jensen *et al.*, 2014). Nonetheless, the duration of the marine migration for *S. alpinus* in this study of *c*. 1 month was shorter than that observed in some of the previous studies (Berg & Berg, 1989b; Jensen *et al.*, 2014), which may be due to differences among watersheds, size groups of fish and environmental conditions in the sea, which may also vary between years.

There was a larger proportion of long-distance migrants among *S. trutta* than *S. alpinus*, independent of individual body size, and *S. trutta* were frequently recorded by the outermost receivers in the fjord system, 20–40 km from the river mouth. Large *S. trutta* spent on average 3 days reaching the receiver line 20 km from the river mouth, whereas *S. alpinus* and small *S. trutta* migrating that far spent 2–3 weeks reaching the same distance. It might be that large *S. trutta* aimed directly for a more pelagic piscivorous lifestyle in the outer fjord system than the smaller *S. trutta* and *S. alpinus*. The stable isotope analysis indicated that *S. trutta* were generally more piscivorous

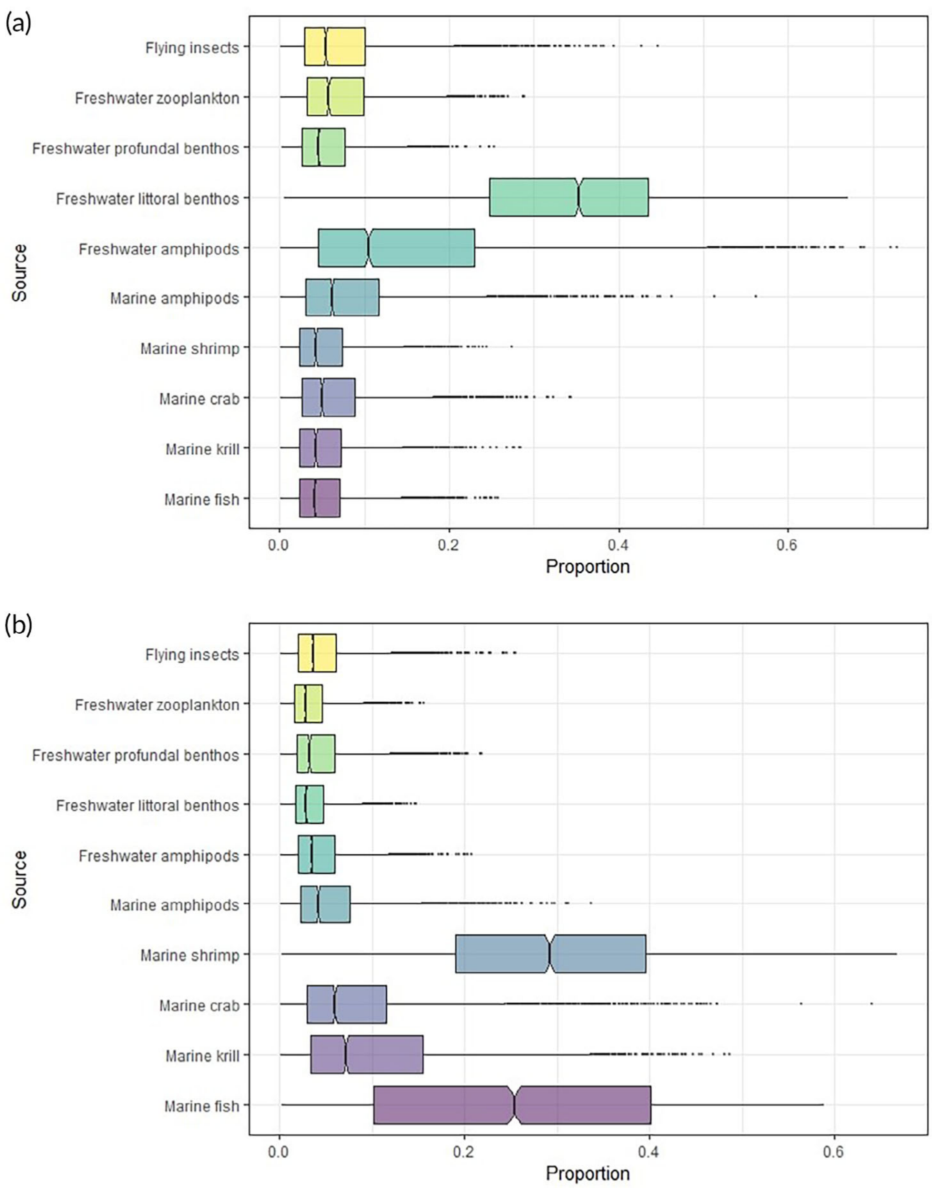


FIGURE 6 The proportion of estimated prey groups of Arctic charr (*Salvelinus alpinus*; upper panel) and brown trout (*Salmo trutta*; lower panel), based on simmr-analyses

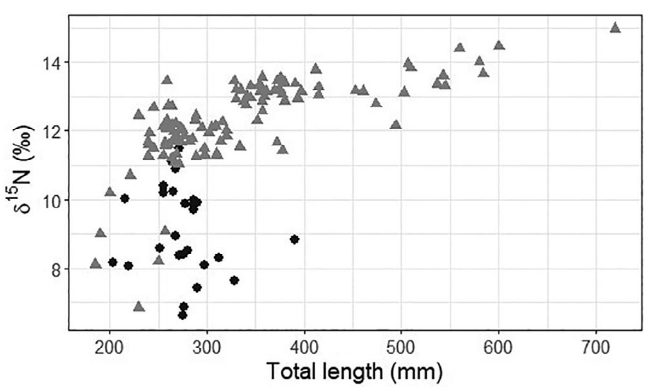


FIGURE 7 Total body length (L_T, in mm) plotted against δ^{15}N-values for Arctic charr (*Salvelinus alpinus*, black circles) and brown trout (*Salmo trutta*, grey triangles). δ^{15}N-value increased with body size for *S. trutta* but not for *S. alpinus*. Species: ●, Arctic char; ▲, Brown trout

than *S. alpinus*, independent of body size. Feeding opportunities might therefore be important in determining distance travelled in the fjord by *S. trutta*, because they are likely to seek out areas with a high occurrence of fish to prey on.

S. trutta had higher δ^{15}N- and δ^{13}C-values than *S. alpinus*, according to the isotope analysis. A higher δ^{15}N-value indicates feeding at a higher trophic level, whereas a higher δ^{13}C-value indicates marine as opposed to freshwater feeding (Fuller *et al*., 2012; Hobson, 1999; Van der Zanden & Rasmussen, 1999). The results suggest that *S. trutta* had a marine diet consisting mainly of fish and shrimps, whereas *S. alpinus* had a freshwater diet consisting of littoral benthos and amphipods. Stomach contents additionally showed that both *S. trutta* and *S. alpinus* had been feeding on surface insects, fish and crustaceans prior to capture (Halvorsen, 2019).

The diet of *S. trutta* as shown in this study is in accordance with other studies that have found fish, crustaceans, polychaetas and surface insects to be important prey groups for this species at sea

(Davidsen *et al*., 2017; Knutsen *et al*., 2001; Lyse *et al*., 1998). More surprising is the finding that *S. alpinus* had been feeding on freshwater species. All individuals examined were presumed to be anadromous individuals returning from a marine feeding migration. Muscle tissue is a metabolically active tissue that will equilibrate to diet within the order of a few months in rapidly growing salmonids (Perga & Gerdeaux, 2005; Tieszen *et al*., 1983; Trueman *et al*., 2005). For anadromous individuals of *S. trutta* and *S. alpinus*, this would typically reflect the summer period of somatic growth, which is the period when most of the growth occurs (Perga & Gerdeaux, 2005). Although the telemetry data showed that some individuals of *S. alpinus* performed long-distance migrations, the majority of the *S. alpinus* remained in the inner parts of the fjord system, near the estuary of the home river or neighbouring rivers, as also found in a study by Atencio *et al*. (2021). In addition to containing both marine and estuarine species, estuaries often contain freshwater species having drifted down with the currents from the river (*e.g*., Roper *et al*., 1983). It is therefore possible that *S. alpinus* feed on freshwater species when they are in the estuary. The *S. alpinus* sampled for stable isotopes may have moved to the estuary for a short time period before returning, which is sometimes observed for immature *S. alpinus* (Johnson, 1980).

Both *S. trutta* and *S. alpinus* are opportunistic generalist feeders whose diets are expected to reflect changes in food availability, habitat, season, age and size (Bridcut & Giller, 1995; Klemetsen *et al*., 2003; Knutsen *et al*., 2001). *S. alpinus* sampled for stable isotopes were significantly smaller than the *S. trutta*. Moreover, both *S. trutta* and *S. alpinus* sampled for stable isotopes were smaller than *S. trutta* and *S. alpinus* tagged for telemetry (60 mm shorter on average for *S. alpinus*). Feeding is typically size-dependent for fish, and fish in particular is known to become an increasingly important food item as individuals grow larger (Amundsen, 1994; Damsgård, 1993; Davidsen *et al*., 2017). Observed differences in isotopic values might therefore be a reflection of a difference in size.

It is common for δ^{15}N-values to increase with size, as larger individuals usually feed higher up in the food chain than do smaller ones (an increase of *c*. 3‰ per trophic level is commonly observed; *e.g*., Fuller *et al*., 2012; Schoeninger & DeNiro, 1984). Nonetheless, no pattern of increased δ^{15}N-values with size was observed for *S. alpinus* in this study, possibly due to the small size range of fish caught. All *S. alpinus* were smaller than 400 mm and had a δ^{15}N-value less than 12. When comparing *S. alpinus* with *S. trutta* of equal body length (L_T < 400 mm), eliminating body size as a factor explaining the observed differences between the species, *S. trutta* had still a higher δ^{15}N-value than *S. alpinus*. A difference in feeding behaviour between the two species, even when comparing fish of similar body length, is therefore apparent, with *S. trutta* feeding higher up in the food chain than *S. alpinus*. When found in sympatry in fresh water, it is commonly observed that *S. trutta* are more piscivorous and typically begin to feed on fish at a smaller size than *S. alpinus* (*e.g*., 130 mm contra 160 mm in fresh water in Björnsson, 2001; L'Abée-Lund *et al*., 1992). Stomach content analysis did, however, show that some *S. alpinus* had been feeding on fish prior to capture (Halvorsen, 2019), even though this was not apparent in the stable isotope analysis. *S. trutta* movement patterns in the fjord system indicated that piscivorous food conditions might be poor in the innermost, near-estuarine parts of the fjord. *S. alpinus* can exploit lower trophic levels if abundance of suitable prey fish is low, including plankton and littoral hyperbenthos (Grønvik & Klemetsen, 1987).

Only isotopes of carbon and nitrogen were used for analysis in this study, and ideally the simmr model should have been run with only three food groups (Phillips *et al*., 2014). Nonetheless, both *S. trutta* and *S. alpinus* are generalist feeders, and the final count of food groups ended up at 10 in the present study. This makes the analysis less accurate when it comes to the individual food groups, and the emphasis should be on the separation of a more marine *S. trutta* diet at a higher tropic level as opposed to a more freshwater *S. alpinus* diet at a lower tropic level. In addition, some food groups may have been important parts of the diet but not included in this study's samples, like freshwater sticklebacks and marine zooplankton and benthos.

S. alpinus had an overall return rate to the watershed after the marine migration of 43% and *S. trutta* of 41%. Berg and Jonsson (1990) found higher minimum annual survival rates of large *S. alpinus* and *S. trutta* in the Vardnes River (57% and 50%, respectively). Nonetheless, survival may vary greatly between watercourses, and return rates between 15% and 86% have been reported for large *S. trutta* in different studies (Bordeleau *et al*., 2018; Jonsson & Jonsson, 2009; Kristensen *et al*., 2019). Mortality at sea is typically highest soon after the fish enter the marine environment as smolts (Jensen *et al*., 2017; Klemetsen *et al*., 2003; Thorstad *et al*., 2016) and subsequently decrease as the fish become larger (Jensen *et al*., 2022). This was also shown in the present study, and the return rate of the small *S. trutta* (36%) was similar to first-time migrants of *S. trutta* from the Vardnes River (37%, Berg & Jonsson, 1990).

When combined, the telemetry results and the feeding analyses in the present study suggest that species-specific differences in prey choice may have influenced the observed habitat use and marine migratory strategies of *S. trutta* and *S. alpinus*. For *S. trutta*, size-specific differences in habitat use and migration patterns were also found. Such differences in prey choice and area use of the marine coastal habitat may cause human activities, which are known to vary in both time and space, to influence the species and size groups differently. This should be taken into consideration when working towards the conservation of these species.

AUTHOR CONTRIBUTIONS

J.G.D. designed the study. J.G.D., A.E.H., S.H.E., E.B.T. and L.A.V. conceived the idea for the manuscript. J.G.D., A.E.H. and S.H.E. conducted the field work and analysed the data and E.B.T. and L.A.V interpreted the results. J.G.D. and A.E.H. wrote the manuscript with input from S.H.E., E.B.T. and L.A.V. All authors reviewed and approved the manuscript.

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SUPPORTING INFORMATION

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

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