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Sea trout *Salmo trutta* in the subarctic: home-bound but large variation in migratory behaviour between and within populations

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Abstract

Anadromous brown trout (sea trout), *Salmo trutta*, is currently in decline throughout its range, largely due to anthropogenic stressors in freshwater and marine habitats. Acoustic telmetry was utilized to study the marine migration of sea trout post-smolts from three populations in a relatively pristine subarctic fjord system. While at sea, the sea trout spent a substantial part of their time close to their natal river, preferred near shore over pelagic habitats and were strongly surface oriented. Despite a fidelity towards local areas, the sea trout utilized various parts of the fjord system, with maximum dispersion >30 km and total migration distance >300 km. Almost half of the sea trout (44%) migrated between river outlets, indicating that a metapopulation approach may be appropriate when managing neighbouring sea trout populations at high latitudes. Furthermore, the different populations displayed different migratory behaviours in terms of distance migrated, dispersion from origin and the likelihood of leaving their home area. This variation in migratory behaviour is likely influenced by spatiotemporal differences in habitat quality between sites, indicating that local habitat variations may promote population-specific behavioural responses even in relatively confined fjord systems.

KEYWORDS

anadromous salmonids, behavioural variability, depth use, habitat use, high-latitude, migration

1 | INTRODUCTION

Describing migration is challenging for aquatic animals, and for many species improved knowledge of the spatiotemporal distribution and habitat use is of great importance for management and conservation (*e.g.*, Mazor *et al.*, 2016; Walli *et al.*, 2009). This is emphasized for fishes that migrate over large areas and encounter a variety of stressors (Campana *et al.*, 2010; Walli *et al.*, 2009), but is also highly relevant for species with smaller distribution ranges (Aspillaga

et al., 2016; Thorbjørnsen *et al.*, 2019), as they can be more vulnerable to negative impacts at local and regional scales.

Brown trout *Salmo trutta* L. 1758 is a facultative anadromous species indigenous to Europe, North Africa and western Asia, with populations ranging from being completely freshwater resident to consisting only of anadromous individuals (Klemetsen *et al.*, 2003). The distribution of anadromous brown trout, hereafter referred to as sea trout, extends from the Bay of Biscay off northern Spain to the Cheshkaya Bay in the south-eastern Barents Sea (Klemetsen

et al., 2003). Sea trout can perform multiple feeding migrations into the marine environment, with fish re-entering fresh water to either spawn or overwinter (Thorstad et al., 2016). The duration of the marine migration is highly variable, and although many sea trout spend only the summer months in the marine environment (Flaten et al., 2016; Jensen et al., 2020), year-round migrations are frequently observed, occasionally also in the northern populations (Jensen & Rikardsen, 2012; Rikardsen et al., 2006). While at sea, sea trout spend most of their time close to the surface and typically reside within fjords and in coastal areas close to their natal river (Thorstad et al., 2016). Nonetheless, the distance of the marine migration varies extensively both among and within populations (Kallio-Nyberg et al., 2002; Pratten & Shearer, 1983). Examples of sea trout migrating several hundred kilometres from their origin have been documented throughout large parts of their distribution range (Birnie-Gauvin et al., 2019; Thorstad et al., 2016).

Since the 1980s, many sea trout populations have declined due to anthropogenic stressors occurring in fresh water and at sea (ICES, 2013). In the marine environment, habitat loss, overfishing, eco-system changes, and pathogen spill-over from aquaculture have all contributed to the decline (ICES, 2013). The parasitic salmon louse *Lepeophtheirus salmonis* Krøyer 1837 is an example of a stressor that impacts anadromous salmonids on local and regional scales. In areas with open net cage farming of Atlantic salmon *Salmo salar* L. 1758, the density of salmon lice can increase by orders of magnitude, to levels that harm wild salmonids (Bøhn et al., 2020; Krkošek et al., 2011; Thorstad et al., 2015). Although sea trout populations can cope with the parasite at natural levels, infections exceeding a certain threshold level increase mortality and reduce individual growth, either directly though physiological processes or indirectly *via* premature returns to fresh water (Serra-Llinares et al., 2020; Thorstad et al., 2015). In Norway, open net cage farming of salmon occurs along almost the entire coast, with the highest activity in the south-western and central parts where numerous sea trout populations are declining (Anon, 2019). In comparison, subarctic sea trout populations are more pristine, but with the expected northward shift of the Norwegian salmon farming industry, there are growing concerns for these populations (Vollset et al., 2021).

In recent years, there has been an increased effort in quantifying the marine habitat use of sea trout, and several studies using electronic tags have provided detailed documentation of their marine migration (e.g., Eldøy et al., 2015; Kristensen et al., 2019). Although these efforts have increased our knowledge of the marine migration of sea trout, they have also highlighted the extensive behavioural variability that exists within the species. This emphasizes the importance of quantifying the marine migration of sea trout throughout their range, particularly in areas where anthropogenic stressors are expected to increase (Thorstad et al., 2016).

This study describes the marine migratory behaviour of sea trout post-smolts from three populations within a subarctic Norwegian fjord system, using acoustic telemetry. The main aim is to provide a detailed description of the marine migration and habitat use of sea trout from different populations within a relatively pristine fjord system. Specifically, the horizontal distribution and depth use of individuals are quantified, to further the understanding of the behaviour of sea trout post-smolt at high latitudes and to investigate if population-specific migration patterns are present within the same fjord system. Based on a recent observation of the behaviour of sea trout post-smolts from one of the populations included in this study (Atencio et al., 2021), it is expected that fish will spend most of their time close to their natal river, primarily occupying near shore surface waters.

2 | MATERIALS AND METHODS

The handling of experimental animals complied with Norwegian animal welfare laws, guidelines and policies as approved by Norwegian Animal Research Authority (permit reference number 12267).

2.1 | Study area

The study was conducted from June to September in 2018 in the Alta Fjord system in northern Norway (70° N, 23° E, Figure 1). The Alta Fjord system refers to the Alta Fjord and the Stjernsund, Rognsund and Vargsund straits, which all connect the fjord to the Norwegian Sea (Figure 1). The Alta Fjord itself is 38 km long, is 4–14 km wide and has a maximum depth of 488 m. The inner part of the fjord is categorized as a National Salmon Fjord (Figure 1), which is a conservation measure to protect important Atlantic salmon populations by preventing potentially harmful industrial activities, such as aquaculture facilities, to establish nearby (Serra-Llinares et al., 2014). The fjord is considered subarctic despite its Arctic location due to the inflow of Atlantic Ocean waters (Skarðhamar et al., 2018). The summer surface temperature in the Alta Fjord varies between 5 and 16°C with an average temperature of 10°C in August (Skarðhamar et al., 2018). During summer, the upper layer (down to 5–10 m) is brackish, with relatively high salinities below (>33) (Skarðhamar et al., 2018).

2.2 | Study populations

A total of 92 sea trout were tagged at three sites in the Alta Fjord system: (a) in the fjord 2.5 km south of the Hals River outlet between 24 June and 5 July ($n = 35$), (b) in the fjord 0.8 km west of the Skillefjord River outlet between 2 and 9 July ($n = 35$) and (c) 8 km upstream the Alta River either in late April ($n = 1$) or between 13 and 16 July ($n = 21$) (Table 1; Figure 1). Fish caught in the marine envrionment were assumed to originate from the nearby rivers, and the sea trout were classified into three separate groups (hereafter termed populations): Hals River, Skillefjord River and Alta River.

The Hals River has a mean annual water flow of 4.3 ms^{-1} and an annual within-river angling catch of sea trout averaging 157 kg (www. ssb.no). The river has a 20 km stretch accessible to anadromous
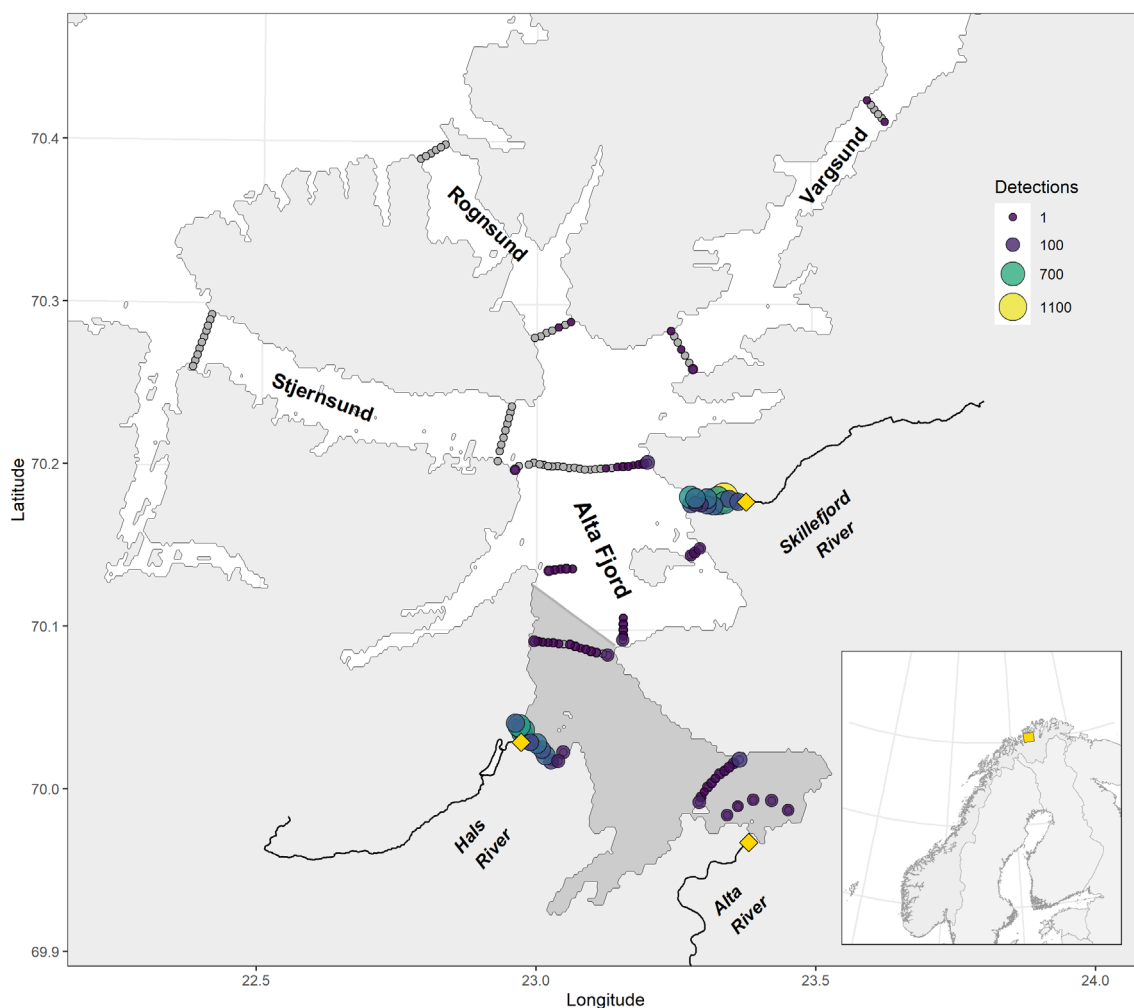
FIGURE 1 Map of the Alta Fjord system. Shaded area depicts the part categorized as a National Salmon Fjord. Points show the positions of the acoustic receivers, with the number of hourly detections at each receiver coded by size and colour. Receivers with no detections are shown in dark grey. Yellow diamonds denote the location of the Hals River, the Alta River and the Skillefjord River outlets. Inserted map denotes the location of the Alta Fjord system (yellow square) in Fennoscandia

TABLE 1 Overview of *Salmo trutta* post-smolts tagged with acoustic tags in the Alta Fjord system and whether they were included or excluded in the analyses

Population	Tagged	Included	Excluded	FW-return	Alta River	Other areas
Hals River	35 (175 ± 15)	13 (178 ± 17)	22 (173 ± 13)	6	3	4
Skillefjord River	35 (178 ± 17)	27 (179 ± 16)	8 (176 ± 19)	13	9	14
Alta River	22 (179 ± 19)	5 (169 ± 25)	17 (182 ± 17)	3	4	2

Note. Mean fork lengths L_F and standard deviations of the different groups are given in parentheses. FW-return refers to the number of *S. trutta* assumed to end their migration in fresh water. Alta River refers to the number of *S. trutta* that entered the Alta River at some point during the migration. Other areas refer to the number of *S. trutta* detected within or in proximity to the other study rivers.

salmonids. The marine habitats north and south of the Hals River outlet are shallow and characterized by patches of sandy bottoms. The Skillefjord River is located at the base of a small fjord arm (Skillefjord) of the Alta Fjord. The river has a mean annual water flow of 3.1 ms^{-1} and an annual within-river angling catch of sea trout averaging 92 kg (ww.ssb.no). The river has a 13 km stretch accessible to anadromous salmonids. The Alta River is the largest river draining into the Alta Fjord, with a mean annual flow of 88 ms^{-1} and an annual within-river

angling catch of sea trout averaging 2816 kg (www.ssb.no). The river has a 46 km stretch accessible to anadromous salmonids.

2.3 | Fish capture and tagging

Fish captured at sea were caught in bag-style fjord nets, which were inspected and cleaned at least once per day. Fish in good condition

were selected for tagging and transported by boat to the nearest shore or marina in large (≥100 l) holding tubs, with continuous water exchange to ensure good water quality. Fish captured within the Alta River were caught using a fyke net or by electrofishing.

For surgery, the fish were anaesthetised using benzocaine (0.1–0.2 ml Benzoak $^\circledR$ l^{-1}, c. 3 min immersion in aqueous solution), and placed with the ventral side up with the head and gills submerged in a v-shaped surgical tray. The tags were implanted into the body cavity through an approximately 1 cm long incision made with a scalpel posterior to the pelvic girdle. The incision was thereafter closed using a braided silk suture (5-0 Ethicon Inc., Sommerville, NJ, USA). Tagged fish were subsequently 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. Fish caught near the Hals River were released in the Hals River outlet or in the nearby marina during bad weather, whereas fish caught in the Skillefjord were released approximately 500 m from the catch site (Figure 2). Fish caught in the Alta River were released approximately 200 m downstream of the capture site in calm shore waters. The acoustic tags deployed outside the Hals River, in Skillefjord and in the Alta River in July ($n = 91$) transmitted an identification number and depth (pressure) (model D-LP7; diameter: 7.3 mm; length: 21.5 mm, mass in water: 1.1 g; transmission rate: 40–100 s random interval; lifespan: 5 months, Thelma Biotel AS, Trondheim, Norway). The tag deployed in the Alta River in April ($n = 1$) only transmitted an identification number (model ID-LP7; diameter: 7.3 mm; length: 18 mm, mass in water: 1.1 g; transmission rate: 30–90 s random interval; lifespan: 5 months, Thelma Biotel AS).

2.4 | Receiver deployment

A total of 144 acoustic receivers (model TBR700, Thelma Biotel AS) were deployed in 15 arrangements, hereafter termed arrays, within the Alta Fjord system (Figure 1). This included high-density receiver arrays placed near the Hals River outlet and in Skillefjord, nine across-fjord receiver arrays positioned throughout the fjord system, three receiver arrays placed strategically within the Alta Fjord and one receiver array placed around the Alta River estuary (Figure 1). In addition, two acoustic receivers were placed within the Alta River. In the Hals River and Skillefjord River, no receiver was placed in fresh water, but one receiver was positioned at the outlet of each river. Receivers deployed in the across-fjord arrays were positioned approximately 400 m apart, thus providing good across-fjord coverage given the expected detection range of 200–800 m in the Alta Fjord (Jensen et al., 2014).

2.5 | Data filtering

The data set was filtered manually before analyses. Only tag numbers corresponding to tags included in the study were evaluated, and tags from other ongoing studies and acoustic noise were removed from the data set without evaluation. After the initial filtering, the data set
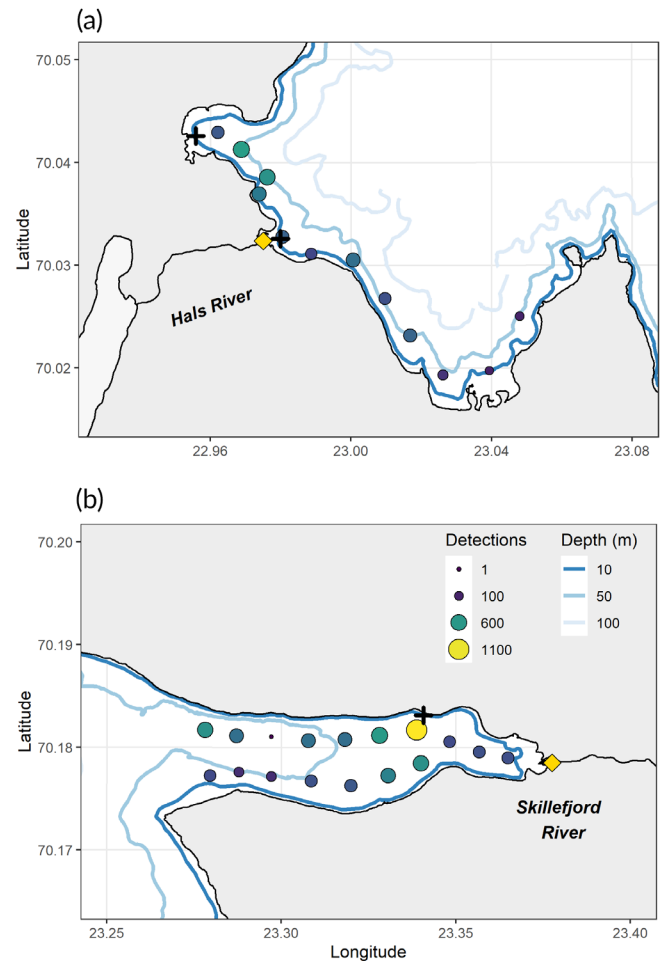
FIGURE 2 Maps of the area near the Hals River (a) and of Skillefjord (b). Points show the positions of the acoustic receivers, with the number of hourly detections at each receiver coded by size and colour. Blue lines represent the 10, 50 and 100 m bathymetry contours. Yellow diamonds denote the location of the river outlets, and crosses denote the release locations

consisted of 179,192 detections. Based on these, hourly positions, depths and habitats (near shore or pelagic) were estimated. This down sampling to hourly data was done to reduce the impact of multiple detections within a short period of time, i.e., a biased sampling distribution when the fish resided close to the receivers. Hourly positions were calculated using a weighted mean (Simpfendorfer et al., 2002), whereas arithmetic means were used to derive hourly swimming depths. Habitat use was only estimated for the hourly positions at the receiver arrays that provided complete coverage across the fjord (Figure 1). Detections at the receivers located closest to land (approximately 200 m from the shore) were classified as near shore, whereas detections at all remaining receivers were classified as pelagic. If fish were located both in the pelagic and near shore habitats within the same hour, the habitat was set as missing.

Of the 92 tagged sea trout, 45 generated sufficient data to be included in the analyses. This included 13 fish tagged outside the Hals River Bay, 27 fish tagged in Skillefjord and 5 tagged in the Alta River (Table 1). The 47 fish omitted from the data set consisted of 23 sea

trout that were never detected at sea, 13 sea trout that were only registered for shorter periods (days) before disappearing and 11 sea trout that were only detected shortly after tagging before the tags were registered as stationary on the bottom (*e.g.*, due to tag rejection, mortality or predation). The fork length L_F of the 45 sea trout included in the analyses ranged between 140 and 216 mm (mean ± S. D. = 177 ± 17 mm). No significant difference in L_F was detected between sea trout from the three populations (Fisher-Putman permutation test: *P*-value = 0.64) or between the sea trout included and excluded from the analyses (Fisher-Putman permutation test: *P*-value = 0.85).

2.6 | Data analyses

All statistical analyses were conducted using the R software version 4.0.2.

2.6.1 | Track estimation

Individual tracks were estimated by first executing a linear interpolation between all hourly positions. If the corresponding track resulted in fish crossing land between detections, the shortest possible in-water path was generated. This was done by first generating an adjacency matrix from a spatial grid encompassing the Alta Fjord system, weighted by the distance between grid cells. Subsequently, the shortest path was derived using Dijkstra's algorithm for weighted graphs using the *shortest_path* function from the *igraph* package (Csardi & Nepusz, 2006). Track endpoints were set as the last detection at sea, or as the first detection in fresh water if none of the following detections were in the marine environment.

2.6.2 | Site fidelity

To investigate site fidelity, the probability of sea trout leaving their home areas was modelled using binomial generalized linear models (*GLM*), with *Population*, fork length L_F and *Track duration* in days as fixed effects (Table 2). For each population, the home area was defined as the receiver array close to the tagging sites (Figure 1), and sea trout was considered to have left if they were detected at other arrays.

2.6.3 | Total migration distance

The total migration distance of individual fish was measured as the total distance travelled between (*i.e.*, not within) receiver arrays (Figure 1). This was done due to the nested spatial distribution of receivers in the study area and effectively prevented overestimating the distance travelled by sea trout that resided in areas with a high density of receivers for prolonged periods. The total migration distance was then modelled using linear models (*LM*) with *Population*, L_F and *Track duration* in days as fixed effects (Table 2). To prevent violations of model assumptions a log transformation was applied to the response variable.

2.6.4 | Distance from natal river

Distance from origin (*i.e.*, river closest to the tagging sites) was calculated to all positional estimates, along the shortest possible path. To quantify seasonal variation in how far the fish dispersed, daily maximum distance from origin was modelled using a set of generalized additive mixed-effect models (GAMM), with L_F as a fixed effect, *Day*

TABLE 2 Overview of models used to describe the migration and habitat use of *Salmo trutta* post-smolts tagged with acoustic tags in the Alta Fjord system

Model type	Response variable	Fixed effects	95% CI	Smoother	RE	R^2	ΔAICc
GLM	Probability of leaving home area	Population † L_F Track duration †	0.26–4.74 −0.01–0.13 0.03–0.18			0.30	−0.2
LM	log (Total migration distance)	Population † L_F Track duration †	0.66–2.61 −0.01–0.05 0.05–0.10			0.49	−0.9
GAMM	Daily distance from origin	L_F	−0.02–0.14	Day(Skillefjord)† Day(Hals)†	ID †	0.59	—
LMM	log (Depth)	Population L_F Day of the year Solar elevation † Temperature † Salinity †	−0.002–0.179 0.002–0.007 −0.001–0.002 0.004–0.005 0.048–0.070 0.017–0.026		ID †	0.05 (0.11)	−2.52

Note. † denotes model terms included in the most parsimonious model. 95% C.I. denotes the 95% confidence intervals for regression coefficients. RE gives the random effects used on the models' intercept. R^2 gives the adjusted *r*-squared for the GLM, LM and GAM and the marginal R^2 for the LMM, with conditional R^2 in parenthesis. ΔAICc denotes the difference in AICc value between the most parsimonious model and the one providing the second-lowest AICc value.

of the year as a population-specific smoothing term and *Fish ID* as random effect on the model's intercept to account for repeated observations of individual fish (Table 2). GAMMs were fitted using the *mgcv* package (Wood, 2011).

2.6.5 | Habitat use

When investigating habitat use (near shore *vs.* pelagic), only detections at the three complete receiver arrays within the Alta Fjord were included due to the low number of detections in the outer straits (Figure 1). For each fish detected at these arrays, the proportional number of near shore and pelagic registrations were investigated, and potential differences in habitat use were tested using a χ^2 test.

2.6.6 | Depth use

To determine what influenced the depth use of sea trout, a set of linear mixed-effect models (*LMM*) were used. The most complex model included *Population*, L_F, *Day of the year*, *Solar elevation*, *Temperature* at the surface and *Salinity* at the surface as fixed effects; and *Fish ID* as random effects on the model's intercept (Table 2). *Solar elevation* in degrees was derived using the *suncalc* package (Thieurmel & Elmarhraoui, 2019) and used to determine if sea trout displayed diurnal variation in depth use. This was done because the study was conducted during parts of the year when the sun is constantly above the horizon at theses latitudes (70° N), which prevented assigning a diel period (*i.e.*, day and night) to the depth observations. For *Temperature* and *Salinity* at the surface, numerical model data obtained on an hourly basis from the A12 model grid of the IMR NorFjords-160 hydrodynamical model which works with a 160×160 m horizontal resolution and 35 vertical layers were used (for details see Myksvoll *et al.*, 2020; Skarðhamar *et al.*, 2018). These data were also used to summarize the temperatures and salinities experienced by the sea trout. To prevent violations of model assumptions a log transformation was applied to the response variable.

2.7 | Model selection

In the models that included repeated observations of individual fish, temporal autocorrelation was investigated and, if necessary, corrected for using a first-order autoregressive process that accounts for the immediately preceding value. In the mixed-effect models, parameters were estimated by the restricted maximum likelihood to prevent potential biases (Zuur *et al.*, 2013). For the linear models, the fit of all model combinations was assessed using the *dredge function* from the *MuMIn* package (Barton, 2020) and the models that provided the lowest conditional AIC (AICc) value were considered the most parsimonious. In the additive model, model terms were selected based on their significance.

3 | RESULTS

A total of 11,898 hourly observations were made from $n = 45$ sea trout post-smolts in the marine environment from 26 June to 2 September. Of these, 9563 (80%) and 2094 (18%) were made in July and August, respectively. During the marine migration, sea trout experienced temperatures ranging from 7.3 to 16.3°C (mean ± S.D. = 10.9 ± 1.4°C) and salinities ranging from 14.7 to 33.7 (mean ± S.D. = 30.7 ± 1.7).

Track duration ranged between 2 and 65 days (mean ± S.D. = 33 ± 19 days). Overall, 22 sea trout (49%) were assumed to have returned to the three study rivers, with migrations lasting from 8 to 65 days (mean ± S.D. = 44 ± 16 days). This included 6 sea trout from the Hals River, 13 from the Skillefjord River, and 3 from the Alta River (Table 1). Of the Hals River sea trout assumed to have returned to fresh water, three were last detected at the Hals River outlet, whereas the remaining three individuals were last observed within the Alta River. Of the Skillefjord River sea trout assumed to have returned to fresh water, five were last observed at the Skillefjord River outlet, whereas eight were last detected within the Alta River. In contrast, all sea trout from the Alta River that returned to freshwater were last detected within the Alta River ($n = 3$). The authors found that 16 of the 45 (36%) sea trout entered the Alta River at some point during the tracking period, with date of first river entry ranging from 26 July to 30 August. This included four sea trout from the Alta River (80% of the fish tagged there), nine from Skillefjord (33%) and three from the Hals River (23%) (Table 1). Of the 16 fish that entered the Alta River, eight re-entered the marine environment after residing in freshwater from 1 to 10 days.

3.1 | Horizontal migration

During the tracking period, sea trout spent most of their time in the inner parts of the fjord system, and only 4 of the 45 sea trout (9%) were detected at the outer fjord straits and only for shorter periods (Figure 1). The highest densities of detections were at the receiver arrays close to the tagging sites in Skillefjord (51%) and adjacent to the Hals River (31%) (Figure 1). When present in these areas the sea trout displayed no apparent attraction towards the receivers closest to the rivers (Figure 2), and the mean distance from the river outlet was 2.2 km (range = 0.5–3.8 km) in Skillefjord and 1.1 km (range = 0.1–3 km) in Hals.

Overall, there was a large variation in horizontal migration, both within and among populations, with some individuals from all three populations migrating between distant receiver arrays (Figure 3). In all three populations, movements between river outlets were evident, and 44% ($n = 20$) of the fish were observed within or in proximity to rivers other than their natal river (Table 1). This movement trend was particularly high for sea trout from the Skillefjord River, where 52% ($n = 14$) were observed in proximity to the other rivers (Table 1). For the Hals and Alta River sea trout, 31% ($n = 4$) and 40% ($n = 2$) visited areas close to the other rivers in the study (Table 1). From here on,
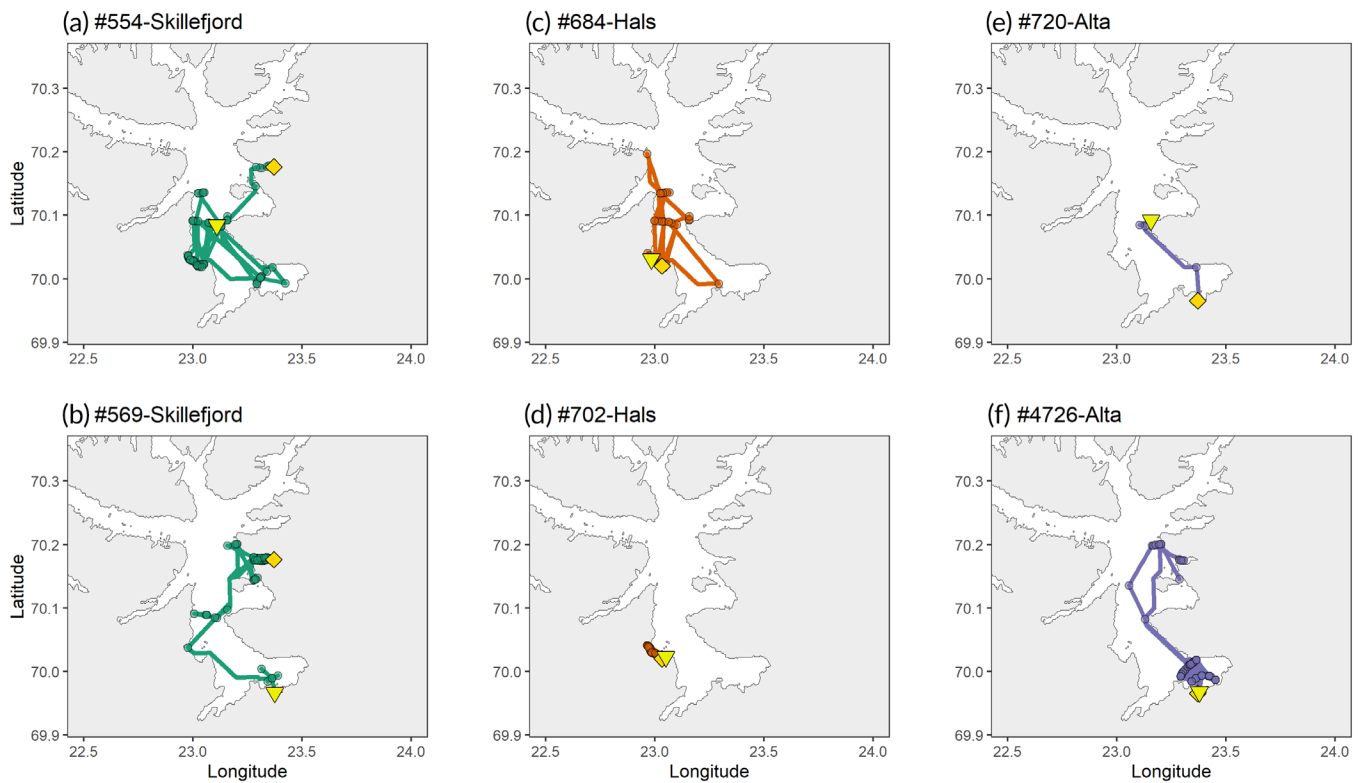
FIGURE 3 Examples of *Salmo trutta* post-smolt migrations observed with acoustic telemetry in the Alta Fjord system. (a, b) fish from the Skillefjord River, (c, d) fish from the Hals River and (e, f) fish from the Alta River

fish tagged in the Alta River are included in the descriptions of the migration metrics but omitted from the statistical models due to the low sample size ($n = 5$).

3.1.1 | Site fidelity

Overall, 76% ($n = 34$) of the sea trout left their home area, with 85% ($n = 23$) of the Skillefjord River fish, 62% ($n = 8$) of the Hals River fish and 60% ($n = 3$) of the Alta River fish being detected at receiver arrays beyond their local area. The difference between sea trout from Skillefjord and Hals was confirmed significant by the generalized linear mixed-effect model (*GLM*) analysing the probability of leaving the home area. The model that provided the best fit included a significant effect of *Population*, with fish from the Skillefjord River displaying a much higher tendency to leave their local area compared to fish from the Hals River ($\beta \pm$ S.E. $= 2.23 \pm 1.10$, *P*-value $= 0.04$); and a positive effect of the *Track duration*, with fish tracked for longer periods displaying a greater likelihood of being detected outside their home area ($\beta \pm$ S.E. $= 0.09 \pm 0.04$, *P*-value $= 0.02$). No effects of fork length L_F were detected (Table 2).

3.1.2 | Total migration distance

The total migration distance (distance migrated between receiver arrays) ranged between 0 and 308.1 km (mean $\pm$ S.D. $= 72.4 \pm 68.7$ km,

$n = 45$). The most parsimonious linear model (*LM*) explaining total migration distance for Skillefjord and Hals fish included a difference between *Populations*, with sea trout from the Skillefjord River migrating further than fish from the Hals River ($\beta \pm$ S.E. $= 1.63 \pm 0.48$, *P*-value $= 0.002$), and a positive effect of *Track duration* in days (7.7% increase per day, $\beta \pm$ S.E. $= 0.07 \pm 0.01$, *P*-value $<10^{-8}$). No effect of L_F was detected (Table 2).

3.1.3 | Distance from natal river

Maximum distance from the origin ranged between 2.7 and 39.3 km (mean $\pm$ S.D. $= 18.9 \pm 12.3$ km, $n = 45$). For the Skillefjord fish ($n = 27$), maximum dispersion ranged between 3.3 and 39.3 km (mean $\pm$ S.D. $= 22.3 \pm 12.6$ km), whereas for sea trout from the Hals River ($n = 13$) maximum dispersion ranged between 2.73 and 24.3 km (mean $\pm$ S.D. $= 12.5 \pm 9.0$ km) (Figure 4a). For the daily maximum distance from origin, the parsimonious generalized additive mixed-effect model (*GAMM*) included a significant effect of *Population* as a smoothing term and *Fish ID* as random effects on the model's intercept. The population-specific smoothing terms were significant for both Skillefjord (EDF $= 6.54$, $P < 10^{-15}$) and Hals (EDF $= 1.31$, $P = 10^{-4}$), and revealed a strong seasonal difference with fish from the Skillefjord River dispersing further away for their origin than fish from the Hals River from mid-July onwards (Figure 4b). No effect of L_F was evident (Table 2).
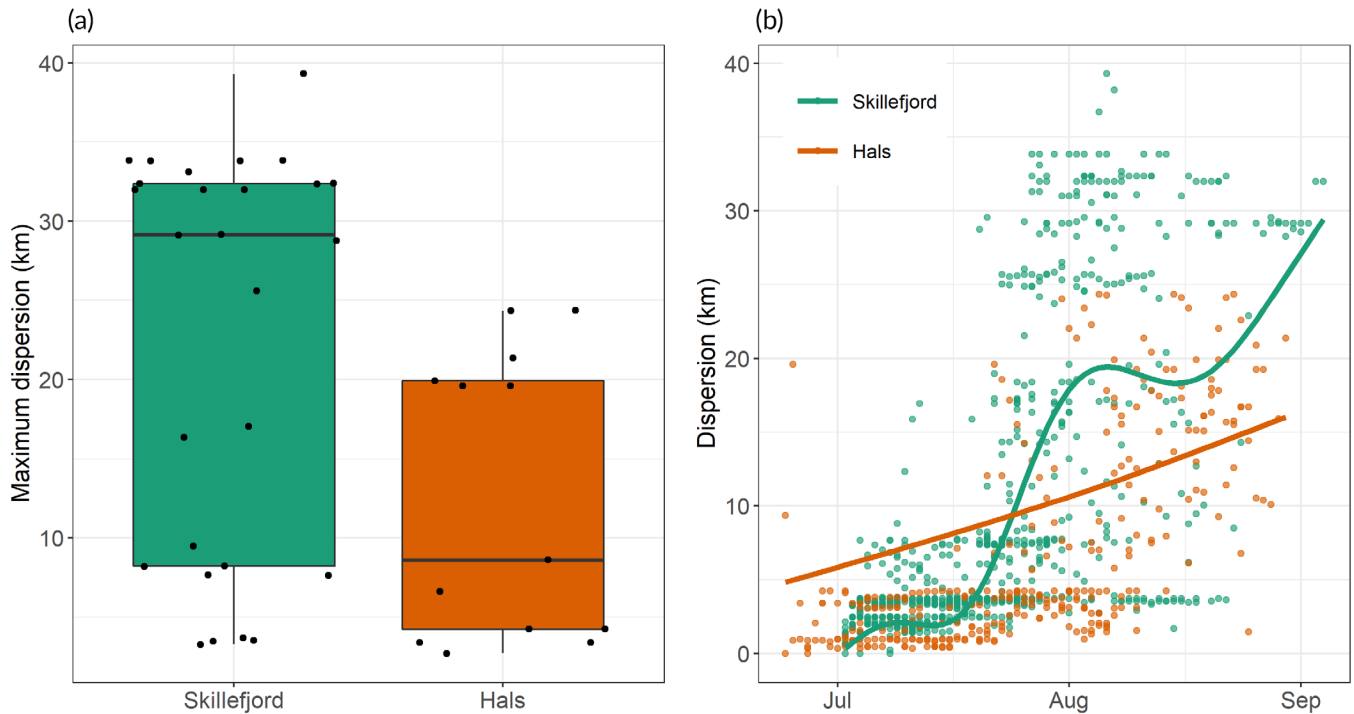
FIGURE 4 Distance from the origin for *Salmo trutta* post-smolts from the Skillefjord River (green) and the Hals River (orange), observed with acoustic telemetry in the Alta Fjord system. (a) The maximum dispersion distance of individual fish. (b) The daily distance from the origin for individual fish with lines depicting population-specific smoothers

3.2 | Habitat and depth use

Of the 45 sea trout, 36 were detected on at least one of the fjord-covering receiver arrays with a total of 772 hourly detections. Of these, 60 included detections both in near shore and in pelagic habitats within the same hour and were consequently omitted from the analysis. Of the remaining 712 detections, 398 were at the inner-most transect, 161 at the middle transect and 153 at the outermost transect in the Alta Fjord (Figure 1). Sea trout spent significantly more time in near shore areas (mean = 66 ± 27%, range = 11–100%) compared to pelagic habitats (χ^2 (n = 36, df = 35): 135.3, *P*-value $<10^{-3}$). No correlation was present between the number of hourly recordings and time spent in near shore areas (Spearman rank correlation: *P* = −0.07).

During the marine migration, hourly depth recordings of sea trout ranged between 0.2 and 16.0 m (mean = 1.7, S.D. = ±1.1 m). The fish displayed a strong surface orientation with individuals spending on average 77% of their time in the uppermost 2 m of the water columns (range = 55–100%, SD = 11%) (Figure 5). The parsimonious linear mixed model (*LMM*) explaining hourly depth use included a positive effect of *Solar elevation* (0.5% increase per degree, β ± S.E. = 0.0045 ± 0.0005, *P*-value $<10^{-16}$), *Temperature* (6.1% increase per °C, β ± S. E. = 0.0589 ± 0.0055, *P*-value $<10^{-16}$) and *Salinity* (2.1% increase per unit, β ± S.E. = 0.0204 ± 0.0031, *P*-value $<10^{-16}$). To compare the fixed effects included in the most parsimonious model, an additional model was constructed with standardized fixed effects. This revealed a 6.6% increase in depth per *Solar elevation* standard deviation (β ± S.
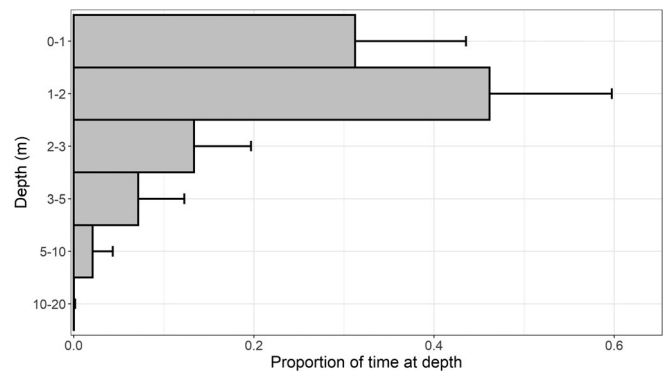
FIGURE 5 Depth use of *Salmo trutta* post-smolts observed with acoustic telemetry in the Alta Fjord system. Bars depict the mean proportion of time spent at different depths during their marine migration, with whiskers indicating standard deviations

E. = 0.064 ± 0.007, *P*-value $<10^{-16}$), a 9.3% increase per *Temperature* standard deviation (β ± S.E. = 0.089 ± 0.008, *P*-value $<10^{-16}$) and a 4.8% increase per *Salinity* standard deviation (β ± S.E. = 0.047 ± 0.007, *P*-value $<10^{-16}$). This indicated that sea trout utilized slightly deeper depths in warmer and more saline waters, and during periods with higher solar elevation. Notably, L_F, with larger individuals found at slightly deeper depths compared to smaller fish (β ± S.E. = 0.004 ± 0.001, *P*-value = 0.003), and *Population*, with sea trout from Skillefjord recorded deeper than fish from Hals (β ± S.E. = 0.089 ± 0.044, *P*-value = 0.054), were either significant or close to signifi-cant predictors of depth use at a 0.05 significance level. Nonetheless,

the model that included these additional fixed effects had a higher AICc value compared to the most parsimonious model (Δ AICc = −6.9).

4 | DISCUSSION

During the marine migration, sea trout post-smolts displayed a certain affinity towards areas close to their natal river, however, large variation in migratory behaviour was present both within and among populations. Many of the sea trout migrated far from their origin, some occasionally visited areas in proximity to the other rivers and some fish even entered rivers not associated with their tagging location. This suggests that neighbouring sea trout populations in subarctic fjords may need to be considered as a larger metapopulation in a management context.

During their marine migration, the sea trout post-smolts were mostly observed in the inner part of the Alta Fjord, with only a few individuals observed at the outer straits. This fjord-bound migration coincides with previous observations of sea trout from the Alta Fjord and other Norwegian fjord systems (Atencio et al., 2021; Flaten et al., 2016; Jensen et al., 2014), and likely reflects favourable feeding habitats as well as suitable abiotic conditions within the fjords. In comparison, sea trout from Denmark have been recorded to migrate between 130 and 580 km away from their natal river, likely because they encounter a less suitable environment once they enter the sea, thus promoting longer-distance migrations in search of favourable habitats (Kristensen et al., 2019).

In addition to the tendency to stay within the fjord, a substantial proportion of the sea trout (24%) displayed a spatial distribution limited to their home area. Sea trout are often observed to reside close to their natal river, and in some populations individuals are assumed to spend most of their time in estuaries, likely due to superior foraging conditions compared to adjacent marine habitats (Davidsen et al., 2014). Although a substantial utilization of local areas was evident in the current study, there was no indication of a particular attraction towards the receivers closest to the river for neither the Skillefjord nor the Hals fish. Furthermore, the tendency to utilize local areas varied significantly among populations. Fish from Skillefjord had a greater tendency to leave their home area, migrating longer distances and dispersing further from their origin, particularly from mid-July and onwards, than fish from Hals. It is possible that this observed difference could be a result of spatiotemporal variations in habitat quality between sites, and that habitats in proximity to the Hals River outlet may offer more suitable ecological conditions throughout the summer. This may indicate that even in relatively confined fjord systems, local habitat variations may promote population-specific migration patterns.

In addition to these described interpopulation differences, the sea trout post-smolts in this study displayed substantial intrapopulation variation in migratory behaviour. Individuals from all three populations displayed migrations throughout large parts of the Alta Fjord. Large variation in migration distance is common within sea trout

populations, and for veteran migrants it has been documented that migratory behaviour is condition-dependent, with individuals in a poorer nutritional state performing longer migrations (Bordeleau et al., 2018; Eldøy et al., 2015). In this study, no attempt was made to attribute migratory behaviour to body condition. The only physical variable related to individual fish investigated was body length, which did not influence neither migration distance nor dispersion from origin. This absence of a size effect on the migratory behaviour of first-time migrants concurs with a previous study, where sea trout post-smolts' tendency to either stay within the fjord system or travel to the open sea was independent of body size (del Villar-Guerra et al., 2014). Future studies on the migratory behaviour of sea trout post-smolts should therefore investigate which factors drive this variability, as this would improve our understanding of the spatial ecology of sea trout, which in turn could enable more efficient management and conservation.

While at sea, anadromous salmonids spend most of their time in the upper part of the water column (e.g., Spares et al., 2012; Strøm et al., 2017), and for sea trout a strong surface orientation is well documented across geographical regions and life stages (Eldøy et al., 2017; Gjelland et al., 2014; Kristensen et al., 2018). In the current study, the sea trout post-smolts spent most of their time in the uppermost 2 m of the water column, with temperature and salinity slightly influencing the depth use of individuals. Previous studies have documented that veteran sea trout utilize deeper waters during periods with high surface temperatures, and it has been suggested that this behaviour could be explained by sea trout seeking out depths with preferred temperatures (Eldøy et al., 2017; Rikardsen et al., 2007). Although our results concur with these findings, other factors, such as the presence of predators and the vertical distribution of prey, are considered as more important predictors of the depth use of sea trout. This is primarily because sea trout in the Alta Fjord spent most of their time at sea close to the surface, where there is little vertical temperature variation during summer (Skarðhamar et al., 2018), hence it is unlikely that the slight temperature effect on depth use is caused by thermal preferences. Nonetheless, the factors determining the vertical movement of sea trout should not be viewed in isolation, as most aspects of their migratory behaviour are likely shaped by complex interactions between predator and prey abundances and abiotic conditions (Kristensen et al., 2019).

Diel vertical movement is a widespread phenomenon among fishes (e.g., Righton et al., 2016; Walli et al., 2009), and for anadromous salmonids it is generally considered to reflect feeding behaviour or predator avoidance as a response to diurnal variation in light availability (Strøm et al., 2017). The current study was largely limited to the period of the year when the sun is constantly above the horizon at these latitudes (i.e., midnight sun); nonetheless, a diurnal effect on depth use was still evident with fish utilizing slightly deeper depths during periods with higher solar elevation. This coincided with a previous study on veteran sea trout from northern Norway, where a slight difference in depth use between day and night persisted through the year (Eldøy et al., 2017). This may indicate that either sea trout are able to adjust their vertical behaviour to subtle difference in light

intensity or diel variation in depth use may represent a more general behavioural pattern rather than an explicit response to daily variation in light (Eldøy *et al.*, 2017).

For anadromous salmonids, the bulk of the lifetime growth is obtained at sea, and for sea trout, growth in the marine environment correlates with the duration of the summer feeding migration (Berg & Jonsson, 1990; Jensen *et al.*, 2018). Currently, a major concern for sea trout populations is how increased infections by salmon lice influence the duration of the marine residency (Thorstad *et al.*, 2015). In a recent infection experiment it was documented that the time spent at sea may be reduced by up to 80% under heavy salmon lice burdens (Serra-Llinares *et al.*, 2020). Although the marine residency times reported in the current study are slight underestimations, because most of the sea trout were tagged at sea, the true durations of the marine migrations are likely representative of the natural behaviour of sea trout at high latitudes, as salmon lice infections are low in subarctic areas (Nilsen *et al.*, 2020). Nonetheless, with the projected expansion of aquaculture farming in subarctic areas (Vollset *et al.*, 2021), a potentially dramatic increase in salmon lice burden and other stressors can be expected. This could lead to substantial negative effects on sea trout populations by altering the migratory behaviour of individuals, and reducing their marine growth and survival.

One major caveat of this study is the uncertain origin of sea trout from the Hals and Skillefjord Rivers. All individuals from these sites were tagged while at sea. The sampling of sea trout at sea (late June–early July) coincided with the peak smolt migration in the Hals River (Jensen *et al.*, 2020), and therefore it is likely that most of the sea trout caught in the marine environment were correctly assigned. If this assumption is false, it could potentially weaken the study result regarding behavioural difference among and within populations. Nonetheless, it would not affect the conclusion that sea trout post-smolt from different populations utilized similar and overlapping parts of the fjord system, emphasizing the need for a metapopulation approach when managing the marine phase of these sea trout populations. Furthermore, it may be possible that the results are somewhat biased by the sampling methods. Whereas the post-smolts caught in Skillefjord and Hals were all caught by bag-style fjord nets, during overlapping sampling periods, most sea trout from the Alta River were sampled with a fyke net, within the river, later in the year. Consequently, it is possible that the fish sampled in the Alta River represent a different constituent of the sea trout population, than the fish sampled in Skillefjord and Hals. Nonetheless, as the sea trout from the Alta River were excluded from most of the analyses, any sampling bias would have limited impact on the conclusions.

In summary, sea trout post-smolts spent most of their time close to their natal river. Nonetheless, longer migrations were observed in all three study populations and 44% of the sea trout migrated between river outlets. While at sea, substantial variation in horizontal migration was present both within and between populations. The observed interpopulation variation in migratory behaviour is likely influenced by differences in habitat quality between sites, indicating that local ecological conditions may determine the migration strategy of sea trout post-smolts.

AUTHOR CONTRIBUTIONS

J.L.A.J. and P.A.B. designed the sampling. J.L.A.J., P.A.B., and T.B. conceived the idea for the manuscript. J.F.S. analysed the data. J.F.S, J.L.A, T.B and A.N. interpreted the data. J.F.S led the writing of the manuscript, with contribution from T.B, J.L.A.J., and E.N. All authors approved the final version of the manuscript.

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