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Original Article

Micro- and macro-habitat selection of Atlantic salmon, *Salmo salar,* post-smolts in relation to marine environmental cues

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Atlantic salmon is an economically and culturally important species. The species encounters several natural and man-made threats during its migration between fresh water and the ocean, which in combination may explain its ongoing decline. With the aim to better understand whether post-smolt behaviour is influenced by physical oceanographic conditions, the migratory behaviour of 173 post-smolts in a high-latitude Norwegian fjord was investigated, combining acoustic telemetry with site- and time-specific environmental variables from an oceanographic model. Most post-smolts (94%) performed a unidirectional migration out the fjord. Progression rates were relatively high (0.42–2.41 km h^{-1}; 0.84–3.78 *BL* s^{-1}) and increased with distance from the river. While post-smolts had an affinity for lower salinities in the inner fjord, statistical models failed to detect any significant relationship between the small-scale (within arrays) migratory behaviour and salinity, temperature, or coastal surface currents within the fjord. In the outer part, the post-smolts predominantly exited the fjord system through the strait with the highest surface salinities and lowest temperatures, independently of the current direction. Our findings indicate that the *macro*-habitat selection of the Atlantic salmon post-smolts was influenced by environmental factors: the post-smolts directed their migration towards "ocean cues." However, this was not confirmed on the *micro*-habitat level.

Keywords: coastal migrations, fish behaviour, oceanographic modelling, salmonids, telemetry.

Introduction

Atlantic salmon, *Salmo salar,* is an anadromous species distributed across the North Atlantic Ocean. Since the early 1980s, numerous populations of Atlantic salmon in both North America and Europe have experienced prolonged population declines (ICES, 2020). These declines have been caused by local as well as broad-scale factors, such as ecosystem changes in the marine environment (e.g. Beugrand and Reid, 2012; Mills *et al*., 2013) and freshwater habitat loss (e.g. Forseth *et al*., 2017). However, in areas with intense Atlantic salmon farming, parasite induced mortality from the salmon lice *Lepeophtheirus salmonis* (Thorstad and Finstad, 2018; Bøhn *et al*., 2020) and genetic introgression from escaped farmed salmon (Glover *et al*., 2013, 2018) pose the greatest threats to wild populations (Anon, 2020). Open-net aquaculture farming of Atlantic salmon occurs in near-shore areas along most of the Norwegian coastline, producing over a million metric tonnes annually (SSB, 2019). The high densities of fish in the aquaculture facilities can produce unnaturally high numbers of salmon lice, and hence a large proportion of wild Norwegian Atlantic salmon migrate through areas with high numbers of infective salmon lice during their migration towards the open ocean. This is particularly problematic for first time migrating post-smolts, which represents the most vulnerable life-stage of Atlantic salmon (Thorstad and Finstad, 2018).

Telemetry studies have shown that Atlantic salmon take relatively direct routes towards the ocean and, in Norway, post-smolts usually spend between a few days and 4 weeks in the fjord systems before leaving the coast (Thorstad *et al*., 2012; Halttunen *et al*., 2018). During this period, post-smolts utilize both nearshore and pelagic habitats (Thorstad *et al*., 2007; Davidsen *et al*., 2009), primarily residing in the upper 3 m of the water column with occasional dives to deeper depths (Davidsen *et al*., 2008; Plantalech Manel-la *et al*., 2009). Despite that several aspects of the initial phase of the ocean migration of Atlantic salmon are well-documented (Thorstad *et al*., 2012), most studies have focused on populations south of the Arctic circle, and knowledge of the migratory behaviour of post-smolts from the northernmost populations remains poorly understood (but see Davidsen *et al*., 2009). This knowledge gap is problematic as several important aspects of post-smolts life-history and behaviour differ with latitude. For example, individuals from more northern areas enter the sea later in the summer, at a bigger size and at an older age compared to more southern populations (Klemetsen *et al*., 2003). Among Norwegian Atlantic salmon, high-latitude populations are currently less threatened, partially due to less

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anthropogenic impact in the coastal areas (Anon, 2020). However, the Norwegian aquaculture industry has an incentive for growth, with particular interest in expansion to more pristine areas in the north. Hence, detailed information of the behaviour of post-smolts from high-latitude populations is needed for preserving the state of these populations.

In recent years, several studies have linked the migration of post-smolts to environmental factors, by simulating migration trajectories based on behavioural rules and hydrodynamic data (e.g. Mork *et al*., 2012; Moriarty *et al*., 2016; Ounsley *et al*., 2020). By comparing simulated migration trajectories to existing observational data, these studies have documented regional differences in migratory behaviour in relation the environmental cues. For example, favourable current patterns may guide the migration of post-smolts from some areas (Mork *et al*., 2012), while in other regions, post-smolts must display a directed migration, against the prevailing current, to reach their ocean feeding grounds (Ounsley *et al*., 2020). While these simulation studies provide plausible mechanisms for the migratory behaviour of post-smolt from their natal river to ocean feeding areas, more specific information on which environmental factors influence post-smolt behaviour in coastal zones and within fjords remains less studied (but see Newton *et al*., 2021). This is largely due to the lack of detailed site- and time-specific hydrodynamic data along the migration routes of the fish. However, with the recent developments in numerical ocean modelling it is now possible to link fish observations to real-time high-resolution hydrodynamic data (Newton *et al*., 2021). In a management context, this direct coupling may be of special importance in coastal areas with Atlantic salmon farming, as variable currents, hydrography (salinity and temperature), and water mass dynamics are also fundamental to the aquaculture-driven lice infestation pressure imposed on wild salmonids (Sandvik *et al*., 2016; Myksvoll *et al*., 2018; Skarðhamar *et al*., 2018; Asplin *et al*., 2020). To achieve sustainable aquaculture production in the future, knowledge of salmon lice dispersal from farms, as well as the migration routes of post-smolts from river to the open ocean, is crucial for planning and optimizing farm location structure in fjords.

The present study investigates the migratory behaviour of post-smolts tagged with acoustic transmitters in relation to high-resolution numerical model simulations of salinity, temperature, and current flow. The study was performed in a high-latitude fjord system with large variation in environmental conditions within and between years (Skarðhamar *et al*., 2018; 2019; Asplin *et al*., 2020). The main aim was to analyze the underlying factors that influence individual fish behaviour during the initial phase of their ocean migration. More specifically, it was tested if post-smolts prefer certain environment conditions (salinity, temperature, and current), and if such preferences change as the fish progress through the fjord system. It was hypothesized that:

H1: Atlantic salmon post-smolt have a micro-habitat preference (within array) for (a) higher salinity water, (b) lower temperatures, and (c) outward running currents (“migrate towards salty and cold ocean habitat and going with the flow”).

H2: Atlantic salmon post-smolts have a macro-habitat preference (strait selection) for (a) higher salinity water, (b) lower temperatures, and (c) outward running currents (“migrate towards salty and cold ocean habitat and going with the flow”).

H3: Atlantic salmon post-smolt have a macro-habitat choice that minimizes the travel distance to the open ocean (the “efficient in-transit-corridor-hypothesis”).

Material and methods

Study area

The study was conducted in 2017 and 2018 in the Alta Fjord system, northern Norway (70°N, 23°E; Figure 1). The Alta River is the largest watercourse draining into the fjord system, with a catchment area of 7400 km^2, mean annual flow of 75 m^3 s^{-1}, and its lower 46 km accessible to anadromous fish (Ugedal *et al*., 2008). The river influences the currents, temperature, and salinity of the fjord basin (Skarðhamar *et al*., 2018). The Alta Fjord is ca. 30 km long and maximum 15 km wide and connects to the Norwegian Sea by the three fjord straits: Stjernsund (23 km long, with 92 km from the Alta River to the open ocean, direction W), Rognsund (16 km, 100 km from Alta River to open ocean, direction NW), and Vargsund (22 km, 117 km from Alta River to open ocean, direction NE; Figure 1). Stjernsund is the deepest strait (460 m) with a 190 m deep sill, while the other two straits are shallower with sill depths of ca. 50 m. The Alta Fjord and the three straits are, hereafter, referred to as the Alta Fjord system. The Alta Fjord system is the deepest in its central parts (488 m) and has few shallow areas that are mainly located in the innermost part of the fjord (Figure 1).

Fish capture and tagging

During the two study years, 444 wild Atlantic salmon were tagged, with a mean fork length (L_F) of 145 mm ($SD = 11$) and a mean weight of 30 g ($SD = 7$). Of these, 72 individuals were tagged in 2017 (28 June–28 July) and 372 in 2018 (22 April–16 July). In 2017, Atlantic salmon were caught either as smolts in the river using a fyke net located 8 km upstream from the river outlet ($n = 35$), or as post-smolts at sea in bag nets ($n = 22$) or by surface trawling ($n = 15$) on the eastern side between receiver array 2 and the Alta River outlet (Figure 1). During trawling, post-smolts were caught with a modified pelagic trawl that included a “FISH-LIFT” aquarium as a cod-end, making it possible to catch live and unharmed fish (Holst and McDonald, 2000). In 2018, Atlantic salmon were captured as smolts or pre-smolts, either by the fyke net ($n = 301$), or by electrofishing ($n = 71$) in various parts of the Alta River. During the sampling periods, the fyke and bag nets were checked 1–10 times a day. Fish caught in the bag nets were immediately tagged, whereas fish caught in the fyke net were held for up to 24 h in cages in the river before tagging. Fish caught by trawling were held in 400-l tanks on board the boat and tagged once the boat returned to shore. Fish caught in the river were released ca. 100 m downstream from the fyke net or at the electrofishing position, whereas fish caught at sea were transported and released in the Alta River estuary. Only fish that appeared to be in good condition, with no visible damages or behavioural deviations, were selected for tagging.

The fish were anesthetized prior to tagging by use of 2-phenoxy-ethanol (EC No 204–589–7, SIGMA Chemical Co.; www.sigmaaldrich.com, 0.5 ml l^{-1}, mean time 4 min) and placed in a water-filled tube with the head and gills submerged. Acoustic transmitters were surgically implanted into the body cavity through a ca. 1-cm long incision on the ventral surface posterior to the pelvic girdle. The incision was, thereafter, closed using one independent silk suture (5–0 Ethicon

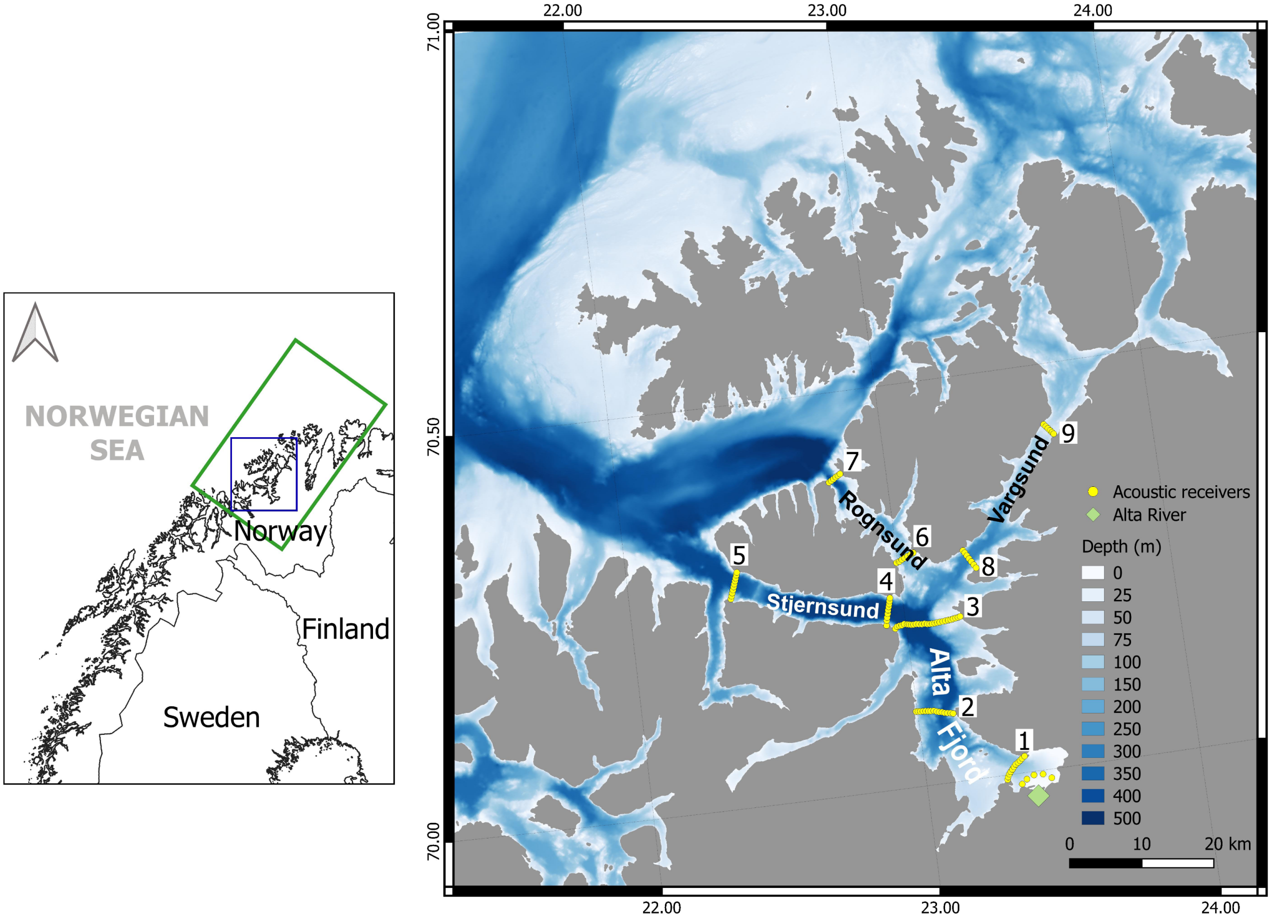

Figure 1. Bathymetric map of the Alta Fjord system in northern Norway (blue rectangle), with the acoustic receiver arrays as yellow dots (numbered 1–9). The diamond denotes the location of the Alta River outlet and the position of the receivers placed in the estuary. The green rectangle shows the outline of the numerical model grid.

braided silk suture, Ethicon Inc.; www.ethicon.com). Tagged fish were then placed in a 90-l holding tub for recovery and transported to the release site. The surgical procedure lasted approximately 2 min and all fish were allowed minimum a 15-min recovery period before they were released. A maximum of 40 tagged fish were released at each site per day to avoid tag code collisions. The fish were tagged with either acoustic identification transmitters ($n = 330$, tag type ID-LP7, transmission rate: 30–90 s random interval, power output: 139 dB re 1 uPa at 1 m, diameter: 7.3 mm, length: 17 mm, mass in air/water: 1.8/1.1 g, and lifespan: 5 months, Thelma Biotel AS, Norway; www.thelmabiotel.com) or depth transmitters ($n = 114$, tag type D-LP7, transmission rate: 30–90 s random interval, power output: 139 dB re 1 uPa at 1 m, diameter: 7.3 mm, length: 21.5 mm, weight in air/water: 2.0/1.1 g, and lifespan: 5 months, Thelma Biotel AS).

Receivers

In both 2017 and 2018, acoustic receivers (TBR-700, Thelma Biotel AS; and VR2-W, Vemco Inc., Nova Scotia, Canada; www.vemco.com) were deployed between May and early June (prior to tagging) and retrieved after the post-smolts had left the area between late September and early October. The study included data from 103 receivers deployed in 2017 and 110 receivers deployed in 2018. The receivers were placed in nine across-fjord arrays throughout the Alta Fjord system, in addition to five receivers at the river mouth and two receivers in the tidal zone of the Alta River (Figure 1). Each receiver was attached to an anchored rope, with the hydrophone pointing upwards, and suspended by a buoy at depths of 5 or 3 m in areas shallower than 20 m. Within each array, the receivers closest to land were placed 200 m from the shore and the remaining receivers were positioned approximately 400 m apart to match the minimum detection range of 200 m (Jensen *et al.*, 2014).

Data filtering and tag fates

The data from all acoustic receivers were filtered to remove obvious false detections. This procedure included removal of detections from tag numbers not included in the study and detections from tags that remained stationary for several days, as these were assumed to indicate either fish mortality or tag shedding. Further, the data from each registered fish was manually inspected to detect irrational registrations, e.g. if fish were registered before its tagging date, migrating from the outer to the inner parts of the fjord, at irrationally high speeds or without registration prior to or after a specific registration. Registrations within 24 h after tagging were also removed to avoid documenting tagging effects. After this filtering, the dataset included 19 885 registrations. Further, all but the first registration on a specific receiver was removed. In total, 769 post-smolt first detections on a specific receiver were retained after filtering, with 144 detections in 2017 and 625 detections in 2018. All depth registrations were considered valid after the data filtering. Of the 444 tagged Atlantic salmon post-smolts, 173 were detected at least once in the Alta Fjord system, whereas three individuals were only detected in the tidal zone of the river. Out of these, 35 (49% of the tagged post-smolts) were detected in 2017 and 138 (37%) in 2018 (Table 1).

Hydrodynamic modelling

Data on salinity, temperature, and currents were obtained from the IMR NorFjords160 model; a state-of-the-art, three-dimensional, free-surface, hydrostatic, and s-coordinate (terrain-following vertical coordinates), primitive equation ocean model based on the open-source Regional Ocean Modelling System (ROMS; Shchepetkin and McWilliams, 2005; Haidvogel *et al*., 2008; see also http://myroms.org). The model grid A12 used in this study covers the northern Norwegian coast and fjords of western Troms and Finnmark county (Figure 1) with 160 m × 160 m horizontal grid cell resolution and 35 vertical levels (finer vertical resolution close to the surface). At its open boundaries the model is driven with the most realistically forcing fields that are available: the larger and coarser NorKyst800 ocean model (Asplin *et al*., 2020; https://thredds.met.no), and the AROME-2.5km atmospheric model (Meteorological Co-operation on Operational Numerical Weather Prediction; Müller *et al*., 2017), both of which are used operationally at the Norwegian Meteorological Institute. The model includes tides as well as river run-off from daily discharge data (http://nve.no). The model has been shown to realistically reproduce hydrography and currents in the Alta Fjord and other Norwegian fjords and coastal areas, with typical accuracy within one unit of both salinity and temperature in the surface layer (Skarðhamar *et al*., 2018; Asplin *et al*., 2020; Dalsøren *et al*., 2020). Further model details and examples of recent applications can be found in Skarðhamar *et al*. (2018, 2019), Carvajalino-Fernández *et al*. (2020), Dalsøren *et al*. (2020), and Myksvoll *et al*. (2020).

The oceanographic analysis presented here is based on hourly values of modelled salinity, temperature, and current velocity at a depth of 1 m (Figure 2). This depth was chosen because the tagged Atlantic salmon post-smolts predominantly stayed in the upper water layers while migrating through the Alta fjord system, with 89 and 88% of the registrations close to the surface (< 2 m depth) in 2017 and 2018, respectively. In the statistical analyses (see next section) values were extracted at a depth of 1 m for each detection of post-smolt (at the closest hour), at all receiver positions (the grid cells closest to each hydrophone) in the associated array. The along-fjord component (*Current_InOut)* was used as current velocity, determined as the velocity component normal (perpendicular) to each array. This was done as we found it reasonable to only consider the currents in the main direction of the fish migration.

Statistical analysis

All statistical analyses were carried out in R version 3.5.1 (R-Developmental-Core-Team, 2019).

Migration route and progression rate

As approximately half of the fish were tagged at sea in 2017 (51%), the first day of migration was only estimated for fish

Table 1. Number of fish detected (No. fish), number of first detections on individual receivers (No. reg. in analysis), and average number of acoustic detections (minimum and maximum number) by individual fish (Av. no. det.) at the nine receiver arrays (1–3 in the main Alta Fjord, 4–5 in Stjernsund, 6–7 in Rognsund, and 8–9 in Vargsund, see Figure 1) in the Alta Fjord system during 2017 and 2018. *N* = total number of fish recorded on the receiver arrays.

Year		Receiver array									*N*
		Alta Fjord			Stjernsund		Rognsund		Vargsund		
		1	2	3	4	5	6	7	8	9	
2017	No. fish	30	28	16	12	2	4	4	5	0	35
	No. reg. in analysis	43	39	28	17	2	4	5	6	0	
	Av. no. reg.	10 (1–45)	9 (1–75)	11(1–50)	5 (1–11)	7 (3–10)	5 (1–10)	3 (1–7)	15 (1–64)	0	
2018	No. fish	87	116	100	68	72	20	11	5	1	138
	No. reg. in analysis	98	157	162	78	80	27	14	8	1	
	Av. no. reg.	6 (1–35)	12 (1–170)	17 (1–104)	8 (1–48)	7 (1–33)	9 (1–45)	8 (1–19)	11 (1–29)	3 (2–4)	

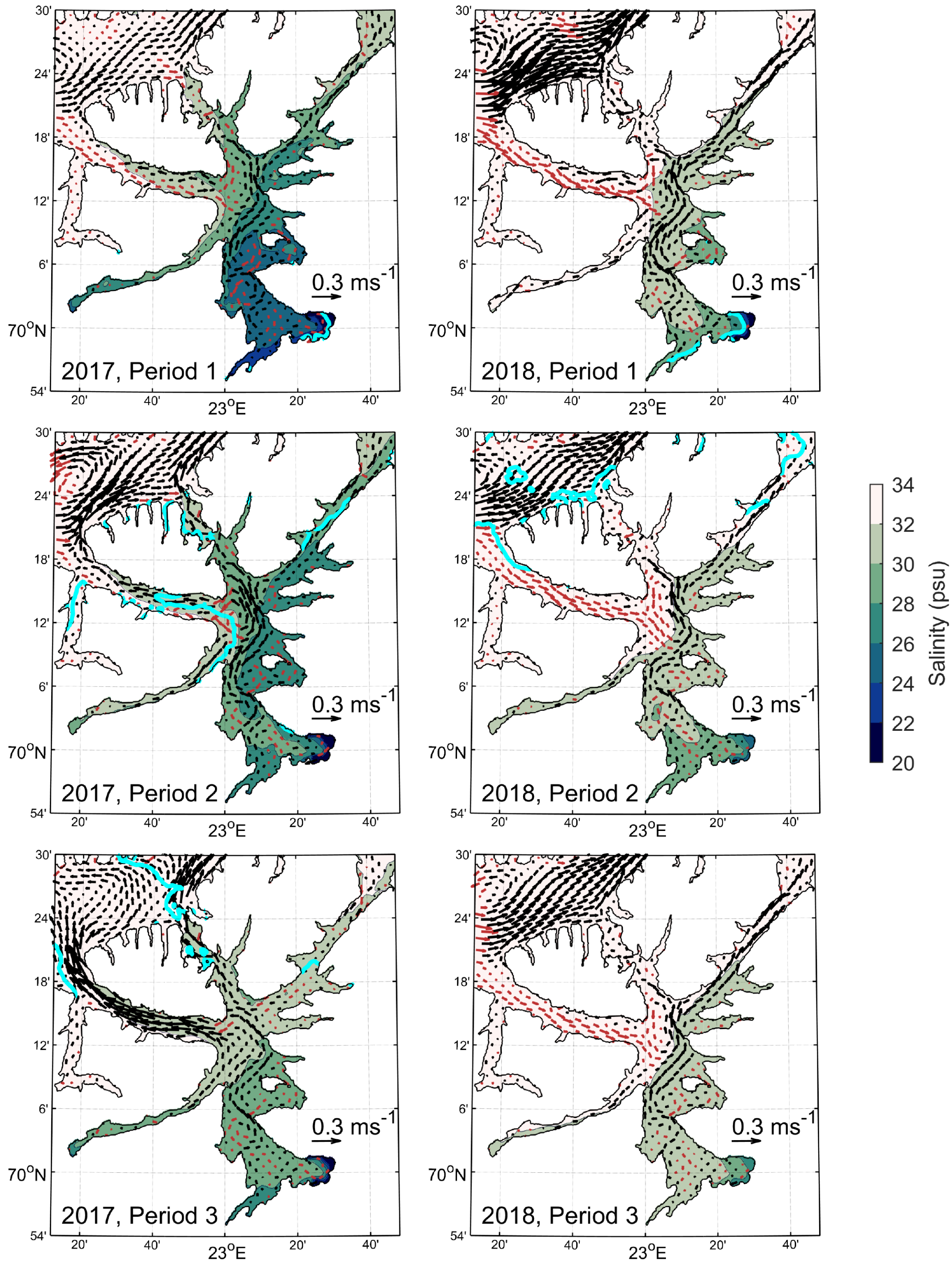

Figure 2. Distribution of modelled surface (1 m depth) salinity (colour gradient) and currents (outward flow as black vectors, inward flow as red vectors) in the Alta Fjord system. The fields are averaged for three periods (each 14 d, top to bottom) in summer 2017 (left) and 2018 (right); Period 1: June 26–July 9, Period 2: July 10–23, and Period 3: July 24–August 4. The cyan lines show the progression of the 10°C isotherm through the study period, with warmer water in the inner fjord and colder water towards the coast.

tagged in 2018 and defined by the first registration on receivers in the tidal zone of the river (Figure 1).

Post-smolts were assumed to exit through the fjord strait where they were last detected, even if these detections were at the inner strait arrays (array 4, 6, or 8; Figure 1). Time spent in the Alta Fjord system was defined as the difference in time from when the fish left the river, or when the fish were released at sea, to the last observation at one of the outer arrays in the straits (array 5, 7, or 9; Figure 1). For each fish, the shortest possible path in the sea was calculated by Dijkstra's algorithm using the *shorthest_path* function from the *igraph* package (Csardi and Nepusz, 2006), thus preventing the post-smolts from crossing the land-sea boundary (for further details see Strøm *et al.*, 2021).

Progression rates were calculated as the shortest distance over ground per hour and as body length (*BL*) per second for (i) the entire fjord system (from the first observation at sea to the outermost arrays in the straits), (ii) the main Alta Fjord

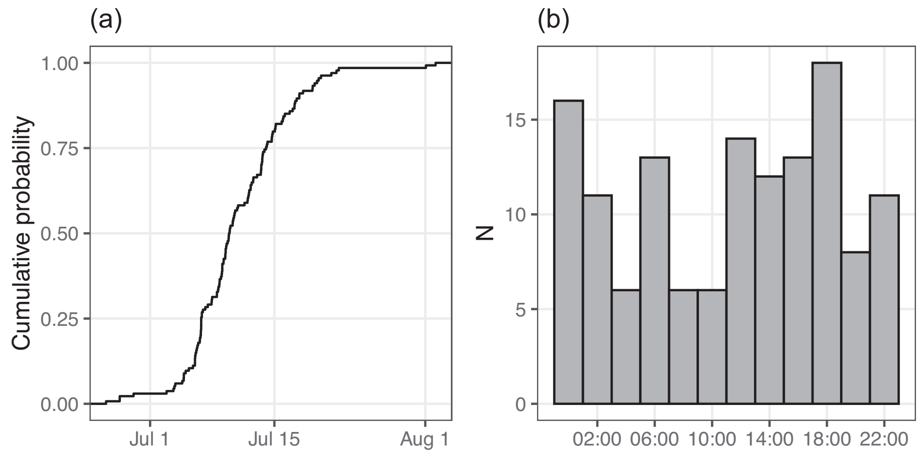

Figure 3. Outmigration of Atlantic salmon smolt acoustically tagged in the Alta River in 2018, depicted by the cumulative date of outmigration (a) and the diurnal timing of outmigration (b).

(from the first observation at sea to array 3, 4, 6, or 8), and (iii) for the straits (from the innermost to the outermost array in each strait; Figure 1). For the fish observed to pass through both segments of the fjord system, the difference in progression rate was tested using a paired Wilcoxon test.

Selection of micro-habitat based on environmental variables

Micro-habitat selection was defined by the placement of the fish in the environmental gradients (*Salinity, Temperature,* and *Current*) within each array. For example, a fish detected near a receiver with lower temperature compared to the average temperature on that array, would show a selection for cold water on this micro-habitat scale. We, therefore, used relative values (deviation from where the fish was, relative to the mean of the same array) for our calculations and models. These relative values are, hereafter, referred to as '$Environmental_{\ difference}$'

Linear mixed effect models (LMMs) were used to evaluate the $Environmental_{\ difference}$, i.e. the potential selection of environmental conditions by the fish during their migration. For our models, the $Environmental_{\ difference}$ was calculated for all individual fish passing any receiver, using data on *Salinity*, *Temperature*, and *Current*, from the exact time when the fish passed by, rounded to the nearest hour. Identical models were applied for the three different environmental variables. Hence, we used the difference in *Salinity, Temperature*, and *Current* as the response variable in separate models, with *Year* as a factorial predictor, *Distance* (from the river mouth*)* and *Season* (day of the year) as continuous predictors, and individual fish (*fishID*) as random effects. In order to to investigate explicitly if overall microhabitat selection occurred, *Distance* and *Season* were standardized with a mean of zero and standard deviation of one. This centring of the continuous predictors allowed easier interpretation of model coefficients and intercepts, i.e. to what extent these were significantly different from zero, which would indicate that fish selected specific environmental conditions (micro-habitat use) during their fjord migration.

$$Environmental_{difference} \sim Year + Distance + Season + (1|fishID)\,. \quad (1)$$

Values for *Salinity*, *Temperature*, and *Current* velocity were extracted from the NorFjords160 model, using hourly values of the variables from the grid cell closest to each acoustic receiver in the arrays (precision = 114 m), rounding the time when a fish passed to the nearest hour (precision = 30 min).

Graphical representation of environmental conditions and fish micro-habitat choice

To illustrate the conditions that the fish met during their migration, we plotted the *Salinty, Temperature*, and *Current* at each transect, divided into three periods of 14 d. We added the mean *Salinty, Temperature*, and *Current* that the fish experienced in the same periods.

Selection of macro-habitat

We defined macro-habitat choice by the fish from their use of the outer straits, i.e. from where they were last detected. We used the proportions of fish that used the three different straits. In addition, we related the choice of macro-habitat to the environmental variables (*Salinity, Temperature*, and *Current*) present in each strait and when the fish passed our receivers.

Results

Area-wide environmental conditions

The modelled surface salinity (1 m depth) ranged from about 15 to 34 (brackish to full marine salinity) with strong horizontal gradients both from the inner to the outer parts of the fjord system as well as across-fjord within the Alta Fjord (Figure 2). The strongest influence of fresh water occurred in 2017 (Figure 2), due to high water levels in the Alta River that year.

The modelled surface (1 m depth) temperature in the Alta Fjord system ranged from approximately 8°C in June to 14°C in August, with the inner parts being 1–3°C warmer than the outer straits. The temperature increased through the study period in both years (Figure 2), but 2018 was 1–2°C warmer than 2017 in August, despite similar initial temperatures in June (about 9°C within the Alta Fjord).

The modelled surface flow was highly variable in direction, meandering through the wide but topographically complex Alta Fjord (Figure 2) with typical current velocities up to 0.3 ms^{-1}. In the outer parts of the system, the along-fjord current varied between fjord straits and years (Figure 2). In the westernmost strait, Stjernsund, there was an increasing tendency

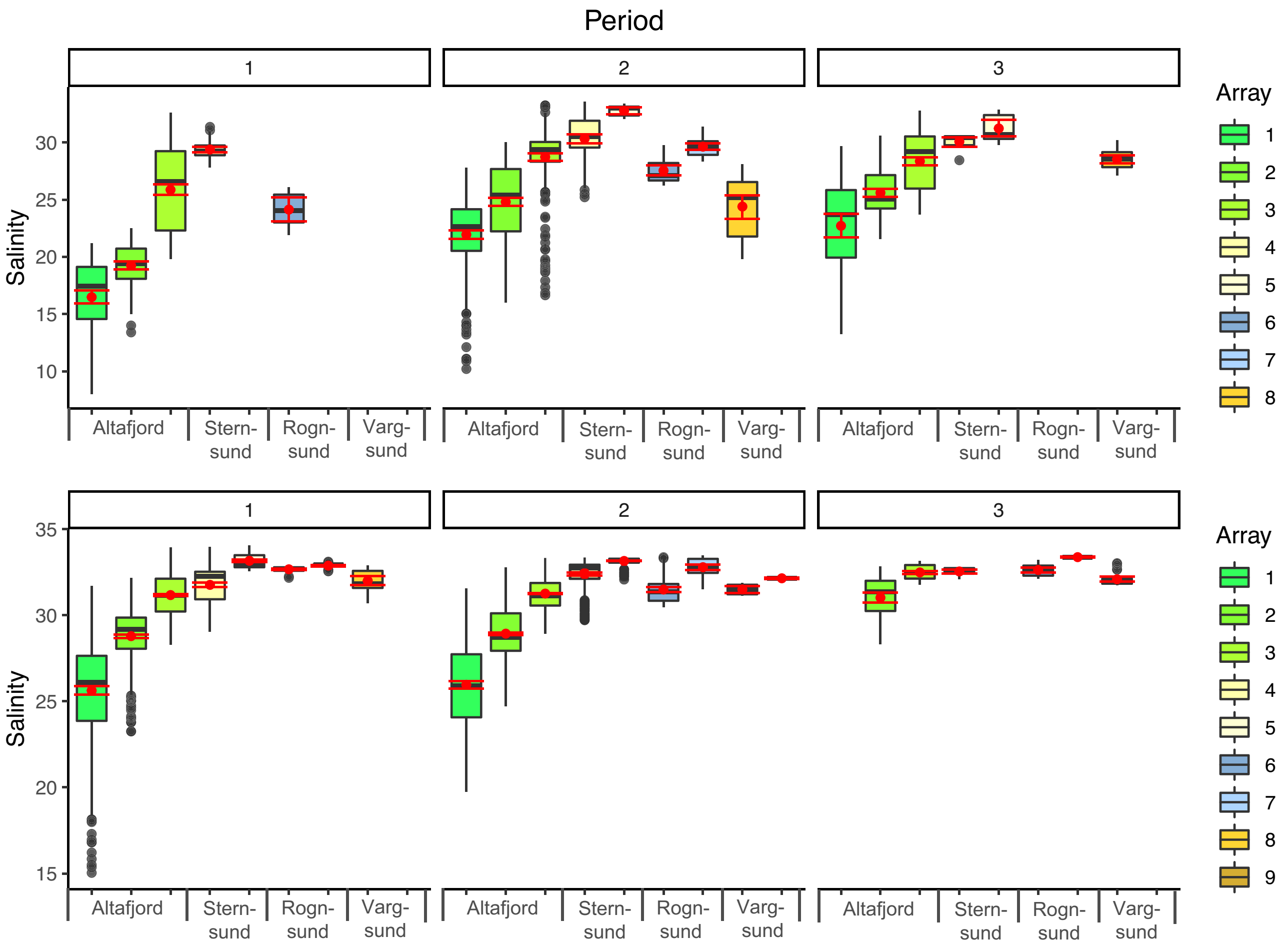

Figure 4. Boxplot of the modelled surface salinity (1 m depth) at the nine acoustic receiver arrays (the colours refer to the geographic location of each array) in the Altafjord, Stjernsund, Rognsund, and Vargsund in three periods (each 14 d) covering the season of outmigration of Atlantic salmon in 2017 (upper panel) and 2018 (lower panel). Red points show mean salinity with 95% (bootstrapped) *CI*s when individual fish passed a particular hydrophone, averaged over each period. The graph shows whether the fish´s micro-habitat selection (the salinity where they swam) deviated from the salinity available across the same array.

for outward currents in 2017, while inward currents dominated in 2018 (Figure 2). In Rognsund and Vargsund, outward currents dominated in both years (Figure 2).

Timing of migration from the river

In 2018, the Atlantic salmon smolts left the Alta River between 26 June and 2 August ($n = 134$), with July 10 as the median date for outmigration (Figure 3a). Most smolts left the river during the midnight sun period (mid-May to the end of July), and the fish showed no clear preference for leaving the river at a particular time of the diurnal cycle (Figure 3b).

Duration of migration in the fjord and progression rate

For the fish observed to exit the fjord system through the fjord straits ($n = 86$), time spent in the Alta Fjord ranged from 28.2 to 170.9 h (mean = 68.5, *SD* = 25.4), with post-smolts progression rates ranging from 0.40 to 2.08 km h^{-1} (mean = 0.99, *SD* = 0.32). This corresponded to size relative rates of 0.84–3.78 *BL* s^{-1} (mean = 1.89, *SD* = 0.62). In the main Alta Fjord and in the fjord straits, post-smolts progression rates ranged from 0.10 to 3.04 km h^{-1} (mean = 0.88, *SD* = 0.45, $n = 135$), and from 0.42 to 2.41 km h^{-1} (mean = 1.26, *SD* = 0.54, $n = 60$), respectively. For the fish that we recorded progression rates for both in the main Alta Fjord and the fjord straits ($n = 60$), progression rates were significantly higher in the fjord straits (Paired Wilcoxon test: $V = 426$, $p < 10^{-3}$).

Selection of micro-habitat based on environmental conditions

Salinity

In general, the fish passed the receiver arrays at salinities from 16 to 33 and 26 to 33 in 2017 and 2018, respectively, with increasing salinities from the inner to the outer part of the fjord systems (Figure 4). Overall, the fish displayed no significant micro-habitat selection with regards to salinity (Table 2): the 95% *CI*s of the intercept in the LMM with difference in salinity as a response variable ranged from −0.4112 to 0.1510. Furthermore, no significant effect was evident of *Year, Season*, or *Distance* (Table 2). This lack of explanatory power by the predictor variables was confirmed by the fixed effect component explaining less than 1% of the model's variance (Table 2). In comparison, the full mixed effect model, with *Fish ID* as a random effect, explained approximately 14% of the observed variation (Table 2). Despite this lack of statistical significance,

Table 2. Parameter values from the LMMs for *Salinity, Temperature*, and *Current*. The last two columns show the percentage of the variation explained by the model. R^2_M provides the percentage of the variation explained by the fixed effects, whereas R^2_C denotes the variance explained by the full model, including *Fish ID* as random effects.

Salinity	Value	SE	t-value	*p*-value	R^2_M	R^2_C
Intercept	− 0.1301	0.1431	− 0.9092	0.3636	0.0075	0.1389
Season	0.0985	0.0622	1.5820	0.1142		
Year	0.2496	0.1600	1.5595	0.1207		
Distance	− 0.0127	0.0478	− 0.2651	0.7910		
Temperature	Value	SE	*t*-value	*p*-value	R^2_M	R^2_C
Intercept	− 0.0276	0.0325	− 0.8493	0.3961	0.0009	0.0239
Season	− 0.0103	0.0141	− 0.7341	0.4632		
Year	0.0053	0.0363	0.1461	0.8840		
Distance	− 0.0014	0.0131	− 0.1062	0.9155		
Current	Value	SE	*t*-value	*p*-value	R^2_M	R^2_C
Intercept	− 0.0031	0.0099	− 0.3121	0.7551	0.0024	0.0907
Season	− 0.0045	0.0043	− 1.0617	0.2888		
Year	− 0.0047	0.0110	− 0.4315	0.6666		
Distance	0.0025	0.0035	0.0035	0.7058		

the graphical representation of micro-habitat selection with regards to salinity revealed that in period 1, when the salinity was at its lowest, the Atlantic salmon post-smolts consistently swam in less saline water compared to what was available in the innermost two arrays (Figure 4). The effect size was relatively small, about 0.5–1, but the 95% *CI*s in general did not overlap with the median salinity for these arrays. The same result was seen in period 2 in 2017. In the outer parts, i.e. in the fjord straits, the salinity was close to full ocean salinity (> 30) with little variation, and no systematic deviations in salinity from where the fish swam compared to the rest of the array (Figure 4) were observed.

Temperature

In general, the fish passed the receiver arrays at temperatures of about 10–12 and 8–13°C in 2017 and 2018, respectively, with higher temperatures typically found in the inner part of the fjord system (Figure 5). Fish displayed no significant micro-habitat selection with regards to temperature (Table 2): the 95% *CI*s of the LMM's intercept ranged from −0.0913 to 0.0362. The model documented no significant effects of Y*ear, Season*, or *Distance,* and the full model including *Fish ID* as random effects explained only about 2% of the observed variation (Table 2). This minimal temperature selection by the fish was confirmed by the graphical representation, which revealed no differences in temperature where the fish swam and the median temperature on the same array during all three 14 d periods throughout the season (Figure 5).

Current

In general, the fish passed the receiver arrays following a slight positive/outward current, *i.e.* current strengths of about −0.2 to + 0.4 and −0.1 to + 0.2 m s^{-1} in 2017 and 2018, respectively. There was however no significant overall microhabitat selection by the fish with regards to current (Table 2): the 95% *CI*s of the intercept in the LMM ranged from −0.0224 to 0.0162. No significant effects were evident of Y*ear, Season*, or *Distance* (Table 2), with the fixed effect components explaining approximately 0.2% of the model's variance (Table 2). In comparison, the full model, with *Fish ID* as a random effect, explained approximately 9% of the observed variation (Table 2). The graphical representation revealed no clear spatiotemporal trends in current strength during the post-smolt migration (Figure 6). There was minimal selection of current speed and direction by the fish, and practically no difference in current speed where the fish swam and the current strength available on the same array (Figure 6).

Selection of macro-habitat—migratory behaviour in the fjord

Of the 173 Atlantic salmon post-smolts detected at sea, 171 were observed at multiple locations throughout the Alta Fjord system. Most post-smolts performed a unidirectional migration from the inner to the outer parts of the fjord. However, 10% of the fish tagged in 2017 ($n = 3$) and 6% in 2018 ($n = 8$), displayed more atypical behaviours with either back and forth movements through the fjord system or detours into several of the fjord straits. In 2017, the post-smolts were relatively evenly distributed across the three arrays closest to the river outlet (arrays 1–3), whereas a larger proportion followed the western side when leaving the fjord in 2018 (Figure 7).

In total, 131 fish were last detected at the inner or the outer arrays in the fjord straits. In both years, the westernmost fjord strait Stjernsund was used as the primary exit point, with 59% ($n = 13$) and 83% ($n = 91$) of the post-smolts leaving the fjord system through this strait in 2017 and 2018, respectively (Figure 7). In comparison, 23% ($n = 5$) and 16% ($n = 17$) exited the fjord system through the middle strait Rognsund in 2017 and 2018, while 18% ($n = 4$) and 1% ($n = 1$) exited through the easternmost strait Vargsund in the same years.

Selection of macro-habitat—choice of fjord strait based on environmental conditions

In both 2017 and 2018, most Atlantic salmon post-smolts left the Alta Fjord system through the westernmost fjord strait

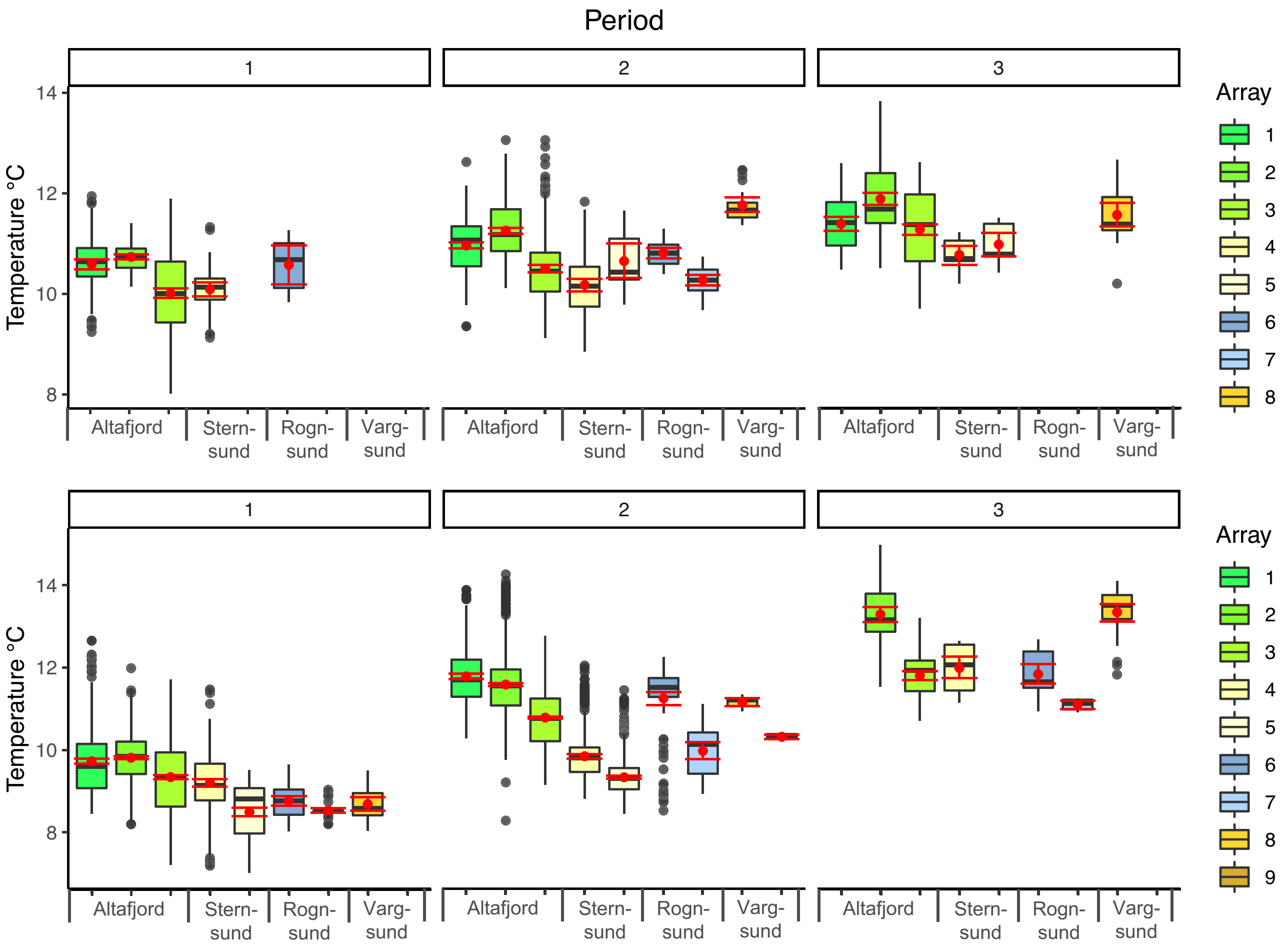

Figure 5. Boxplot of the modelled surface temperatures (1 m depth) at the nine acoustic receiver arrays (the colours refer to the geographic location of each array) in the Altafjord, Stjernsund, Rognsund, and Vargsund in three periods (each 14 d) covering the season of outmigration of Atlantic salmon in 2017 (upper panel) and 2018 (lower panel). Red points show mean temperature with 95% (bootstrapped) *CI*s when individual fish passed a particular hydrophone, averaged over each period. The graph shows whether the fish´s micro-habitat selection (the temperature where they swam) deviated from the temperature available across the same array.

Stjernsund (as detailed above). Overall, fish migrating through Stjernsund experienced higher salinity and lower temperatures compared to fish that migrated through the other fjord straits (Figure 8). Although Stjernsund offered the least favourable current patterns of the three straits, particularly in 2018 when inwards currents dominated (*cf*. Figure 2), 45% (n = 80) of the detections coincided with outflowing currents (Figure 8). In comparison, 70% (n = 35) of the detections in Rognsund, and 33% of the detections in Vargsund (n = 5), coincided with outflowing currents (Figure 8).

Discussion

This study tested aspects of long-held hypotheses regarding the post-smolt migrations of Atlantic salmon by combining the relatively new technologies of acoustic telemetry and advanced oceanographic modelling. The aim of the study was to better understand if post-smolt coastal behaviour is influenced by environmental variables such as water salinity, temperature, and current speed, both on a micro- and a macro-habitat scale. This information may be valuable to resource managers as they strive to reduce human impacts on the highly vulnerable post-smolt life stage of Atlantic salmon.

General migratory behaviour

During their migration through the fjord system, most Atlantic salmon post-smolt displayed a rapid, directional migration, and for the fish that was observed to enter the ocean, time spend in the fjord system ranged between 1 and 7 d. This, in combination with the observation that most post-smolts exited the fjord through Stjernsund, which is the shortest route from the river and fjord to the ocean, supports the 'efficient-in-transit-corridor-hypothesis' (Hypothesis 3). It has been suggested that the marine migration patterns for stocks of juvenile Chinook salmon (*Oncorhynchus tshawytscha*) remain consistent despite fluctuations in environmental parameters (Tucker *et al*., 2012), and if there is some sort of inherent navigation ability in salmonids it could explain the post-smolts ability to navigate directly to the ocean. The documented behaviour concurs with the general assumption that Atlantic salmon post-smolts primarily utilize fjords as migration corridors (Hansen *et al*., 2003; Klemetsen *et al*., 2003). However, 6–10% of the post-smolts showed behaviours deviating from this unidirectional pattern. This may be explained by tagging effects, predation, or simply individual variation in behaviour. Previous diet and parasite studies have suggested that some post-smolts may forage in the Alta Fjord (Rikardsen *et al*., 2004; Knudsen *et al*., 2005), and a Canadian study

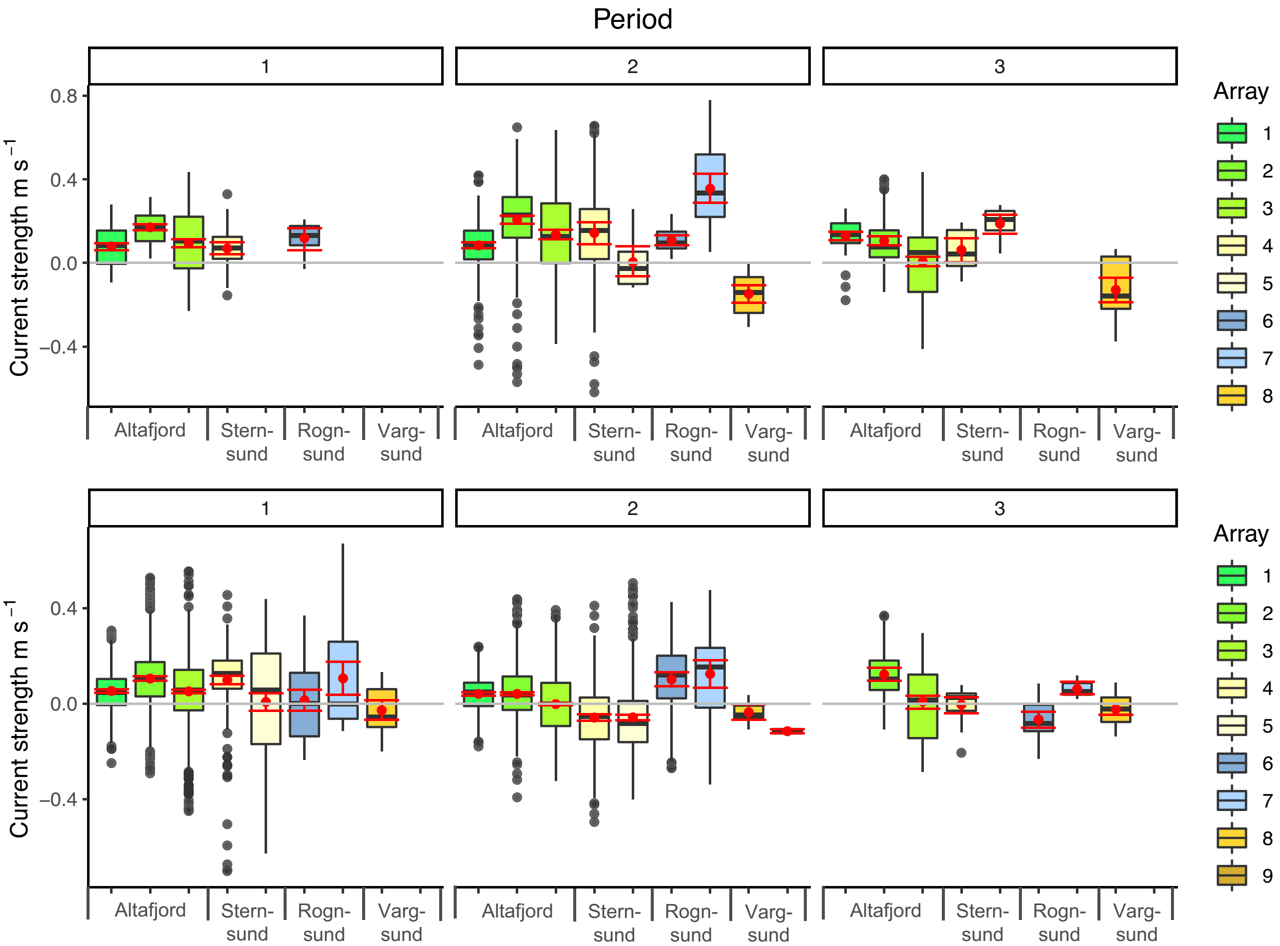

Figure 6. Boxplot of the modelled in-out current velocity component (1 m depth) at the nine acoustic receiver arrays (the colours refer to the geographic location of each array) in the Altafjord, Stjernsund, Rognsund, and Vargsund in three periods (each 14 d) covering the season of outmigration of Atlantic salmon in 2017 (upper panel) and 2018 (lower panel). Positive current velocity is towards the sea (out) and negative towards the river (in), grey horizontal line indicates no current. Red points show mean current velocity with 95% (bootstrapped) *CI*s when individual fish passed a particular hydrophone, averaged over each period. The graph shows whether the fish's micro-habitat selection (the current where they swam) deviated from the current strength and direction available across the same array.

also showed that some individuals deviate from the described type of unidirectional behaviour (Dempson *et al.*, 2011).

The progression rate of Atlantic salmon post-smolts in coastal areas normally range between 0.8 and 1.2 *BL* s^{-1}, but may vary extensively between sites and years (Thorstad *et al.*, 2012). In a previous study on post-smolts from the Alta River, individuals were observed to progress through the fjord systems at rates ranging from 1.8 to 3.0 *BL* s^{-1} (Davidsen *et al.*, 2009). While the progression rates observed in the current study (averaging 1.86 *BL* s^{-1}) were somewhat lower than reported by Davidsen *et al.*, (2009), we note that the limited data available shows that Atlantic salmon post-smolt display high progression rates when migrating through the Alta fjord system. We also show that post-smolts migrated with higher progression rates as they progressed through the fjord system. Increased progression rates of up to (an additional) 0.5 *BL* s^{-1} have been reported for post-smolts swimming towards higher salinities (Hedger *et al.*, 2008), which may explain the higher progression rates documented in the outer fjord straits.

Habitat selection for salinity

Our statistical models indicate that Atlantic salmon post-smolts do not select their micro-habitat (within arrays) based on a salinity gradient in the environment. Hence, we reject our hypothesis 1a. However, at the innermost 2–3 arrays in the fjord, there was a tendency for the fish to prefer low salinity waters (*cf*. Figure 4). This slight affinity towards less saline waters may show that the post-smolts need some time to adapt to marine conditions once they enter the fjord. An alternative explanation to why fish preferred less saline waters in the inner part of the fjord is that their positions at the arrays were determined by the outflowing brackish current. However, this was considered less likely due to the lack of current preferences at the innermost arrays. The lack of any salinity preference within the outer arrays may simply be due to the very small variation in salinity at these locations.

On the macro-habitat scale, further out in the fjord, most of the fish exited through the fjord strait Stjernsund. This strait had the highest salinity of the three exits, and it is possible that the tendency for the post-smolt to migrate though Stjernsund coincided with a switch from a tendency to favour fresh water early in the migration to later being triggered by the "ocean cue" of high salinity. The predominant selection by the fish to use the saltiest fjord strait indicates that Atlantic salmon post-smolts are guided by "ocean cues" and migrate towards salty waters (supporting our Hypothesis 2a). However, as discussed above, this "ocean cue" is not triggered immediately after the fish has left the river. Moreover, from our single population, 2-

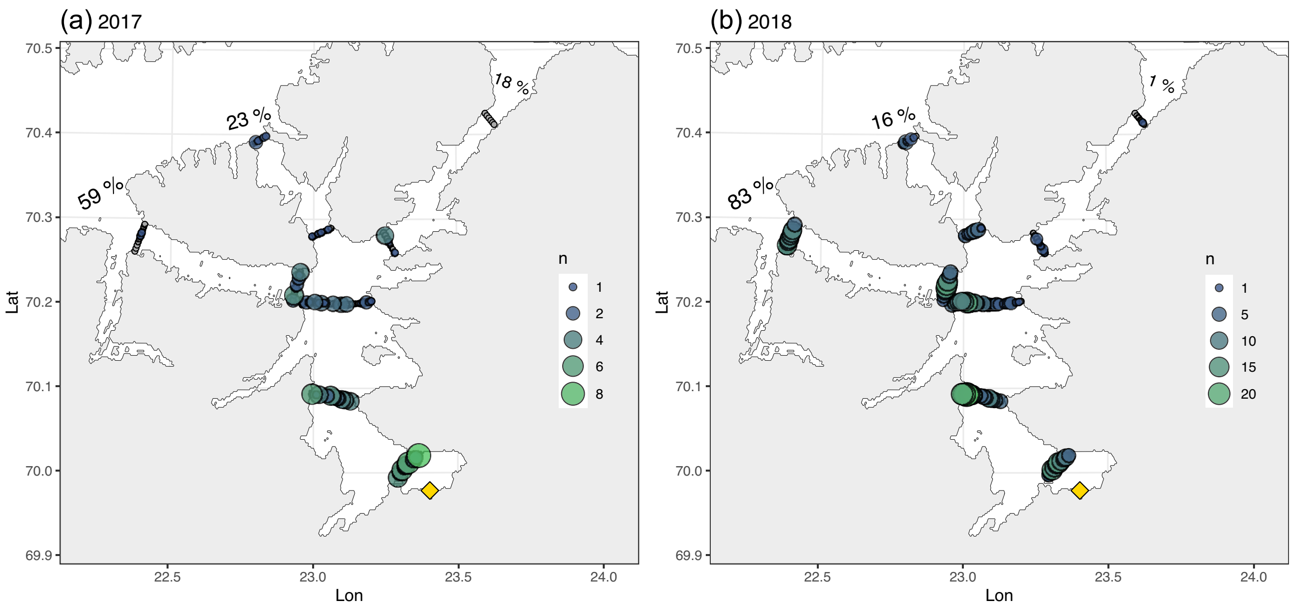

Figure 7. Number of detections of Atlantic salmon post-smolts from the Alta River on acoustic receivers placed in the Alta Fjord system during 2017 (left plot) and 2018 (right plot), indexed by colour and size. Yellow diamonds denote the location of the Alta River. Numbers denotes the proportions of Atlantic salmon post-smolts migrating through the different fjord straits.

year data set, we are not able to disentangle our environmental variables from each other due to confounding. This is further discussed below.

Habitat selection for temperature

The surface temperatures present in the Alta Fjord system during summer ranged between 8 and 14°C, and although temperatures varied to some extent within the arrays, there was no indication that post-smolts selected for certain temperatures on the micro-habitat scale. The hypothesis that the fish preferred water with lower temperature at the micro-habitat scale (Hypothesis 1b) was, therefore, rejected. Recent studies using archival telemetry have documented that while the thermal habitat of Atlantic salmon may vary extensively among life stages (Strøm *et al*., 2020), post-smolts are commonly observed to utilize waters with surface temperatures between 7 and 15°C (e.g. Reddin *et al*., 2006; Guðjónsson *et al*., 2015). The lack of a thermal preference observed on the micro-habitat scale in our data may, therefore, be a result of the full temperature range present with the fjord being highly suitable for Atlantic salmon post-smolts.

On the macro-habitat scale, the Atlantic salmon smolts predominantly exited the fjord through the coldest of the three straits. This suggests a preference for lower surface temperatures during the final stage of their fjord migration, supporting our Hypothesis 2b, at this scale. We argue that this may be an additional "ocean cue" for the fish (in addition to high salinity). However, due to the strong correlation between temperature and salinity it is not possible to disentangle lower temperature from higher salinity, as the ocean water included both these qualities.

Habitat selection for current

Swimming with the currents reduces the energy expenditure of fish. It has been suggested that Atlantic salmon post-smolt display a current-following behaviour during their migration to ocean feeding grounds (Mork *et al*., 2012), and that prevailing oceanic currents may facilitate their dispersion throughout their marine residency (Dadswell *et al*., 2010). In contrast, recent studies in coastal areas of the North Sea have documented that post-smolt consistently swim against prevailing currents during the initial part of the marine migration and it is likely that the correlation between surface currents and post-smolt behaviour is depending on site-specific oceanographic conditions (Ounsley *et al*., 2020; Newton *et al*., 2021). In the inner part of the Alta Fjord system, post-smolts have been suggested to follow the outflowing current from the Alta River (Davidsen *et al*., 2009). Explicitly, Davidsen *et al*. (2009) attributed the tendency for post-smolt to follow the western side of the fjord to winds from the east pushing the outflowing brackish current westwards. While we observed a large proportion of the post-smolts on the western side of the fjord in 2018, no relationship between where the fish positioned itself at a cross-section of the fjord (on arrays of acoustic receivers) and patterns in the in- or out-flowing water currents was present. Hence, in our data, the post-smolts did not select their path based on currents on the micro-habitat-scale, rejecting our Hypothesis 1c that the fish "goes with the flow."

On a macro-habitat scale, we observed that most fish exited the fjord through the westernmost fjord strait, Stjernsund. While a marked variation was present between study years, this strait was characterized by a dominant *inflowing* surface current of oceanic water and offered less favourable surface currents compared to the other straits (*cf*. Figure 2). We, therefore, reject hypothesis 2c that post-smolts "go with the flow." If currents directed towards the sea was the most important migration cue for the fish, the other straits should have been preferred by the fish. Therefore, higher salinity and lower temperature seem to overrule current flow as environmental signals that guide the migration of post-smolt from in the Alta Fjord system.

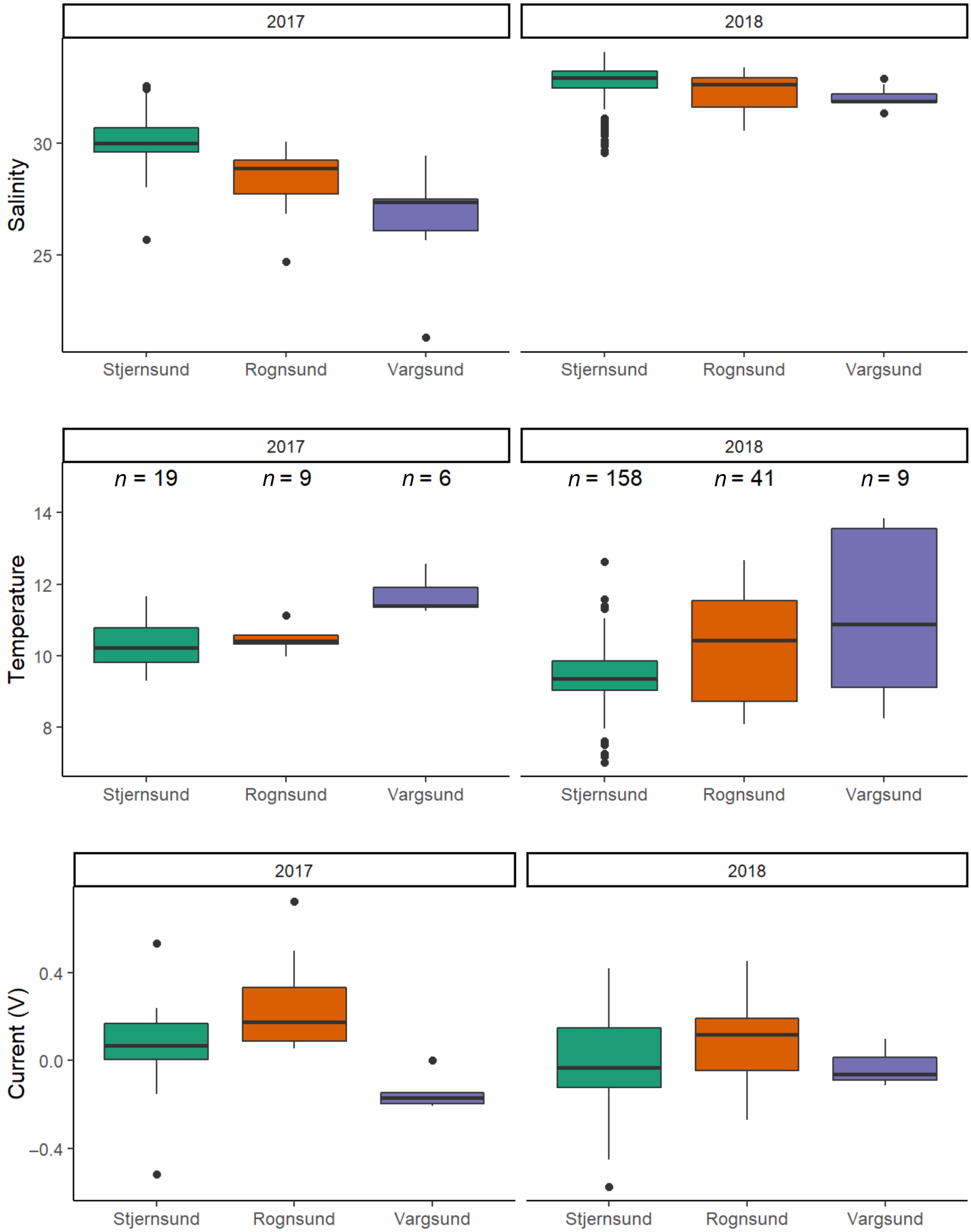

Figure 8. Modelled environmental variables (salinity, temperature, and current strength) at the acoustic receiver position at the time when acoustically tagged Atlantic salmon post-smolts were recorded during their migration through the three fjord straits (Stjernsund, Rognsund, and Vargsund) in 2017 (left panels) and 2018 (right panels).

Study limitations

While no consistent micro-habitat preference for neither salinity, temperature, nor current flow was observed in our data, we recommend that future studies may improve the methodology by deploying salinity and temperature sensors on the cross-fjord arrays of receivers. This will ensure that the numerical data used to describe fish behaviour corresponds to the environment experienced by the individuals. Moreover, this step should be used to control and validate data from the oceanographic modelling that we used for this study. For the macrohabitat choices between the straits, we are confident that the modelled variability of salinity and temperature between the straits are representative, since this depends on a larger scale and slower variability on the coast. Although we formulated precise hypotheses that separated the effects of salinity, temperature, and current strength, we are aware that these factors are confounded in our single population study over 2 years. Therefore, to further analyze which environmental cues that guide post-smolt Atlantic salmon on their migration, multi-population studies with different environmental conditions or meta-analysis will be necessary.

Conclusion

In conclusion, the present study represents a stepping-stone towards a more comprehensive understanding of post-smolt behaviour by combining acoustic telemetry and advanced fine-scale oceanographic modelling. It was shown that Atlantic salmon post-smolts did not select *micro*-habitat based on salinity, temperature, or current. However, the fish predominantly exited the fjord system using the shortest route towards the open ocean. While salmonids may have some sort of inherent navigation ability in the marine environment, post-smolts are naïve to the marine environment and may use the oceanic cues for guidance in finding the shortest route to the open ocean feeding grounds. Although no relationship was present between surface current and the larger scale migration route of post-smolts, most individuals entered the open ocean through the strait with the highest salinities and the lowest temperatures. This suggests that oceanic cues, cold and salt water, may be important in determining the *macro*-habitat choice of Atlantic salmon in the Alta Fjord system. In a management context, these results can be used to protect wild Atlantic salmon populations. To mitigate the problems with transfer of salmon lice from aquaculture facilities, the direct migration routes used by wild Atlantic salmon post-smolts should be avoided, preferably in combination with modelling of salmon lice larvae dispersal.

Authors' contributions

JLAJ and PAB conceived the ideas and designed the study; JLAJ, BJA, and JETS performed the fieldwork; TB, JFS, AN, JS, RP, and JLAJ analyzed the data; TB, JFS, and JLAJ prepared the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

Conflicts of interest

The authors have no conflict of interest to declare.

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Data availability statement

Data available upon request.

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