Bjerck *et al. Animal Biotelemetry (2024) 12:34*
https://doi.org/10.1186/s40317-024-00390-1

Animal Biotelemetry

RESEARCH

Open Access

Depth use of wild Atlantic salmon post-smolts migrating through fjords

Helge B. Bjerck[1*], Henning A. Urke[2], Thrond O. Haugen[3], Jo Arve Alfredsen[4] and Torstein Kristensen[1]

Abstract

Juvenile Atlantic salmon (*Salmo salar*), known as post-smolt as they enter the sea, undergo an arduous migration from their natal rivers to their feeding grounds in the North Atlantic Ocean. It has become increasingly important to understand how post-smolts use the fjord environment as they migrate in order to properly assess the potential threats posed by large-scale salmon farming. Chief among these threats is the increased numbers of ectoparasitic salmon lice (*Lepeophtheirus salmonis*) inhabiting the water column, which are known to have specific depth preferences based on light, temperature, and salinity. Here, we present data on the depth use of wild Atlantic salmon post-smolts migrating through fjords. We aimed to investigate to what extent depth use varied throughout the fjord and from year to year. Using acoustic telemetry, tagged fish from four rivers in two fjords in western Norway were monitored as they migrated towards the open sea during two consecutive years. We found that post-smolts predominantly migrated in the top three meters of the water column throughout the length of both fjord systems. Among 61 successful migrants and 7013 detections, 98% of detections were in the top three meters of the water column. This corresponds well with past findings showing similar depth use in hatchery-reared smolt and in adult Atlantic salmon kelts returning to their feeding grounds after spawning. We found little evidence of a consistent diel pattern in depth use. Our results support assumptions of representative sampling when trawling the upper portion of the water column for post-smolts in order to estimate sea lice infection rates and may improve the precision of efforts to model salmon lice infection risk. The results may also be valuable in evaluating other threats to wild salmon.

Keywords Atlantic salmon, Smolt, Migration, Acoustic telemetry, Depth

Background

Juvenile Atlantic salmon, known as post-smolt as they enter the sea, undergo an arduous migration that is timed to coincide with the spring swell of productivity in the North Atlantic Ocean [1]. This migration requires a physiological and morphological transformation known as smoltification that allows them to osmoregulate in seawater and prepares them for their pelagic migratory lifestyle. In Norway, the smolt migration generally occurs between April and June when the fish are 1–6 years old and between 10 and 20 cm long [2, 3].

This migration is fraught with danger [4]. In addition to the threats of predation, starvation, and exhaustion, the rapid growth of the salmon farming industry over the past 40 years has led to an increase in the numbers of parasitic copepods (salmon lice, *Lepeophtheirus salmonis*, *Caligus elongatus*) that inhabit the water column throughout the coastal zones where salmon farming occurs [5]. Infection by these salmon lice can lead to substantial direct physiological costs along with risks of secondary infections, increasing the probability that post-smolts succumb to predation and exhaustion

---

*Correspondence:
Helge B. Bjerck
helge.bjerck@aqualife-rd.no
[1] Faculty of Biosciences and Aquaculture, Nord University, Bodø, Norway
[2] Aqua-Life R&D AS, Trondheim, Norway
[3] Faculty of Environmental Sciences and Natural Resource Management, Norwegian University of Life Sciences (NMBU), Ås, Norway
[4] Faculty of Information Technology and Electrical Engineering, Norwegian University of Science and Technology (NTNU), Trondheim, Norway

[6]. The pelagic infectious life-stages of salmon lice are known to have specific depth preferences based on light, temperature, and salinity. In the absence of a salinity gradient, salmon lice seem to prefer staying within the top two meters of the water column [7, 8], while they will aggregate at the halocline if a strong salinity gradient is present [9, 10]. It has therefore become increasingly important to understand how the depth use of migrating salmonids react to these same environmental variables.

The depth use of migrating salmon post-smolts also provides valuable information for evaluating the impact of other threats to wild salmon, including the risk of migrating post-smolts transmitting the monogenean ectoparasite *Gyrodactylus salaris* between freshwater environments, the effects of disposing mine tailings in fjords on post-smolt, predation, and changing physiochemical coastal conditions due to climate change or other anthropogenic alterations (e.g. [11]).

In order to better understand these impacts, baseline data on the depth use of migrating salmon post-smolts are much needed. Previous research suggests a preference for migrating within the top few meters of the water column. Efforts to sample post-smolts via trawling find success in the upper 10 m of the water column in the open sea [12, 13] and in fjords [14, 15]. Previous work using active tracking of acoustically tagged hatchery-reared post-smolts has indicated that these migrate in the top four meters of the water column and that they swim closer to the surface when the light intensity is low [16, 17]. Salmon post-smolts tagged with data storage tags have recorded temperatures consistent with a shallow depth use, with a clear diel pattern, along with occasional deep dives [18, 19]. Most recently, Newton et al. [20] measured the depth of wild post-smolts at a transect crossing the Moray Firth, roughly 70 km from the estuary. These smolts were observed at a mean depth of 0.8 m and displayed a diel rhythm of roughly half a meter. However, direct measurements of the depth use of wild in situ Atlantic salmon post-smolts in Norwegian fjords have yet to be reported.

Here, wild Atlantic salmon post-smolts from four populations in two different fjords in western Norway, Hardangerfjord and Nordfjord, were tagged with acoustic transmitters equipped with a pressure sensor for measurements of swimming depth, with 2 years of data from each population. A passive receiver network was deployed to gather data on these post-smolts throughout their fjord migration. Both of the studied fjords are in areas of Norway where the sea lice-induced mortality on migrating smolts is estimated to be greater than 10% [21], with estimates exceeding 30% in some years [22].

Though a passive receiver network does not allow for the near continuous observations offered by data storage tags (e.g. [18]) or the manual tracking of acoustically tagged fish (e.g. [16]), it allows for the sampling of depth use of migrating salmon smolts across a wide span of time and space [23]. Further, active tracking is a laborious procedure such that the number of fish that is feasible to track is limited, while passive receiver networks scale well with larger sample sizes. Simultaneously, advances in the miniaturization of acoustic tags now allow for the possibility of tagging wild smolts with depth-sensor tags. Previously, this was only possible to do with the typically larger hatchery-reared smolts, which may or may not represent wild fish (e.g. [24, 25]).

Key questions that we aimed to elucidate included (1) what depths do post-smolts use as they migrate through fjord systems? (2) does the depth use differ among fjords, among different parts of the fjord, or through time? (3) how do variable environmental conditions such as time of day and salinity influence depth use?

Methods

Study system

This study was conducted in two different fjords in western Norway, Nordfjord and Hardangerfjord (Fig. 1). With lengths of approximately 110 and 160 km, respectively, Nordfjord and Hardangerfjord are among the longest fjords in Norway. Each provides a relatively complex migration route for the post-smolts to navigate, with widths ranging from 2 to 7 km and many branching fjord arms and inlets. Typical of Norwegian fjords, both fjords are very deep and have steep drop-offs near to the shore. Nordfjord is 560 m at its deepest while Hardangerfjord is 850 m deep at its deepest.

Smolts from two rivers in each fjord were tagged in both 2018 and 2019: Stryn and Eid in Nordfjord, and Eio and Granvin in Hardangerfjord. All of these rivers have their outlets in the inner fjord, such that smolts emigrating from these rivers must swim more than 50–120 km to reach the open sea. Similarly, each of these rivers have comparable hydrodynamics as they are all relatively short and drain from a large lake surrounded by mountains.

Due to the influx of freshwater from precipitation and snowmelt from the surrounding mountains during springtime, a brackish layer of highly variable extent is created in the upper water column of the fjords. Due to interannual and geographical variation in timing and magnitude of freshwater input, alongside variable hydrographic conditions in the marine environment, the magnitude of this brackish layer can be highly variable at the relevant timescales of post-smolt migration. As smolts from these rivers generally do not begin their migration before the spring snowmelt has begun [26], post-smolts can use this brackish layer to graduate their acclimation to seawater (see Additional file 1).

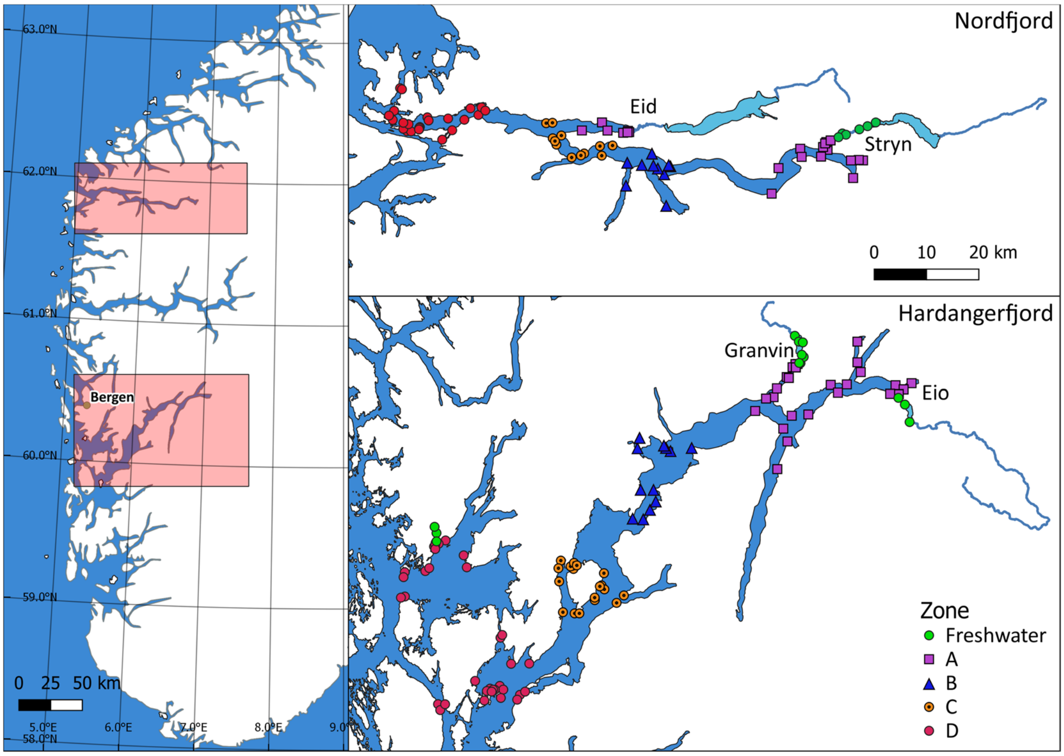

Fig. 1 Map of study system showing locations of acoustic receivers along with the location of each river, reproduced from Bjerck et al. [26]. Figure produced using QGIS v3.10.2, qgis.org

Receiver deployment

In Hardangerfjord and neighboring Bjørnafjord, a total of 106 Thelma Biotel receivers (TBR700) were deployed. In Nordfjord, 71 Innovasea (VR2W) receivers were deployed (Fig. 1). All receivers were moored and attached to ropes with the hydrophones oriented in a downward position, with buoys ensuring that the receivers were positioned 3–4 m below the surface. Within each fjord, the receivers were grouped into zones A-D such that zone A consisted of the area surrounding each estuary, zone D consisted of the outer fjord near to the open sea, and zones B and C were intermediary zones between zone A and D (Fig. 1). These same groupings were used for the survival analysis in Bjerck et al. [26], which incidentally showed zone-specific detection probabilities of 0.65 and 0.61 in zones B and C in Hardanger and detection probabilities of 0.63 and 0.82 in zones B and C in Nordfjord. Nearly all smolts were detected in zone A as they passed through the estuary. As zone D has a similar receiver density to zones B and C, we expect similar detection probabilities here (see Additional file 1 in Bjerck et al. [26]).

Fish sampling and tagging

In April of each year, pre-smolts were captured using DC electrofishing (Ing. Paulsen, Norway, FA4, 1600V, 80Hz) in each river. The same sections of each river were electrofished from year to year. The fish were then kept in 60-L holding tanks with flow of river water overnight and tagged the following day. These fish were tagged with ThelmaBiotel acoustic tags (D-LP7), as described in Bjerck et al. [26]. Briefly, after fish were anaesthetized using 60 mg/L tricaine methanesulphonate (MS-222) a small incision was made slightly offset from the ventral line, circa 2 cm behind the pectoral fin. Tags were then inserted intraperitoneally and the incision was then closed with three interrupted double surgical knots and sealed with a tissue adhesive. Tagged fish were released back into the river 1–4 h after recovery from anesthesia. The tags used have a weight in air of 2.0 g and a length of 21.5 mm and are designed to transmit both the ID of the tag and the depth of the tag with a resolution of 0.2 m every 30–90 s. The pressure sensors within these tags have much higher internal resolution, but the acoustic protocol restricts the tags to transmit data as a single byte in order to minimize the amount of information being sent per transmission. This means that the maximum depth they are able to record is 51 m. The tags transmitted signals with signal strength 139 dB Re 1 μPa @ 1 m and they were set to automatically deactivate after 155–200 days. This signal strength corresponds with a detection range on the order of 200 m, though this is known to vary substantially through time and space with changing ocean conditions [27–29]. In total, 248 smolts were tagged with depth transmitters across all rivers and years (Table 1). The average total length of smolts tagged with depth transmitters was 14.7 cm (SD = 1.1 cm) and the average weight was 25.1 (SD = 6.7) grams. Resulting tag burdens (mean = 8.8%, SD = 1.9%) were relatively high but this was likely not problematic [26, 30, 31]. The tagging protocol was approved by Norwegian authorities for animal welfare (Norwegian Food Safety Authority, FOTS IDs: 12002 and 15471).

Quality control

As these tags measure depth by measuring water pressure, air pressure was controlled for by retrieving hourly weather data from the Norwegian Meteorological Institute (seklima.met.no). In Nordfjord, weather data from the Sandane Airport (SN58100) were used and, in Hardanger, weather data from Kvamsøy (SN50070) were used. There was little variation between these two stations despite the 160 km separating them such that greater spatial resolution was not considered necessary. Further, variation in the calibration of the depth sensor was corrected for by retrieving the factory test value of each tag from Thelma Biotel and the air pressure from the closest weather station to the factory (Selbu II, SN68290). The resulting formula for calculating the presumed depth of the fish in meters from the raw data was then

$$D = 0.2 \times D_{\mathrm{r}} - \frac{p_{\mathrm{e}} - 1000}{100} - \frac{p_0 - p_{\mathrm{f}}}{100}, \qquad (1)$$

where D_{r} is the recorded value (in units of 0.2 m), p_{e} is the closest air pressure reading to the tag detection in millibars, p_0 is the test value recorded for the tag at startup at the factory in millibars, and p_{f} is the mean air pressure at the factory on the day of production in millibars. For the fraction of detections where this correction produced a negative depth, 0.05 m was added to the depth. This is half of the potential error due to the resolution of the measurements.

The spatio-temporal migration trajectories of each individual were inspected visually in order to identify false detections and mortalities/tag losses. Detections occurring at unlikely or impossible locations in relation to the rest of an individual's trajectory were removed. Mortality was identified based on depth data, as predated fish would often first exhibit erratic depth movements and then stop at a constant depth (or varying according to tidal cycles). Efforts were made to remove detections occurring after mortality or tag loss from the analysis.

Further, only smolts that were detected as successful migrants [i.e., smolts that were detected in the outer reaches of the fjord (zone D in Fig. 1)] and which had at least 10 detections in the fjord were included in the analysis.

Generalized linear mixed effects modeling

In order to investigate to what extent variables of interest accounted for variation in depth use, a generalized linear mixed effects model with log-link as the link function was fitted to the data with ID as a random intercept effect using the function glmer in the R package lme4 [32]. Candidate models reflecting hypotheses pertinent to the study objectives were subjected to model selection by using the Akaike Information Criterion (AIC) aiming at finding the model(s) that most efficiently explained the variance in depth use. Models attaining ΔAIC-values < 2 were considered to have substantial support in the data [33]. Variables fitted in the model included fjord zone, fjord, river of origin, waterway distance to the river mouth of origin, fish length at tagging, tag burden, day of year, the position of the sun with respect to the horizon, and a parameterized version of the position of the sun.

In order to test if depth use was correlated with light conditions (sensu [16]), the sun's vertical position was

Table 1 Summary of numbers of individuals tagged along with numbers of individuals after quality control, along with fish size at tagging (mean ± SD) for individuals before quality control

River year	# Tagged	# after QC	Length (cm)	Weight (g)	Tag burden
Eid 2018	24	15	13.76 ± 0.65	20.95 ± 2.97	0.10 ± 0.02
Eid 2019	32	11	15.05 ± 0.94	28.02 ± 6.08	0.08 ± 0.02
Eio 2018	31	5	15.28 ± 1.2	29.54 ± 5.82	0.07 ± 0.01
Eio 2019	44	5	14.62 ± 1.01	26.95 ± 10.36	0.08 ± 0.02
Granvin 2018	32	9	14.73 ± 0.88	24.86 ± 3.96	0.09 ± 0.01
Granvin 2019	21	5	15.47 ± 1.24	28.46 ± 6.1	0.08 ± 0.02
Stryn 2018	13	3	13.79 ± 1.17	21.88 ± 6.85	0.10 ± 0.02
Stryn 2019	51	8	14.46 ± 0.96	25.04 ± 5.41	0.09 ± 0.01
Total	248	61			

Tag burden is defined as the ratio of the weight of the tag to the weight of the fish at tagging in air (mean ± SD) used as a predictor. The position of the sun with respect to the horizon in degrees for a given time and position was determined through the use of the R package suncalc [34]. This was then parameterized with the function:

$$\text{par} \cdot \text{sun} = {}^{1}\!\Big/_{1 + e^{-\text{sun}\cdot\text{pos}/3}}, \tag{2}$$

such that the parameterized values flattened out when darkness and true daylight arrived but changed continuously during dusk and dawn (see Additional file 1). The parameterized values therefore reflect more of a day/night switch than the raw values which change continuously through the day and night. This approach was used as, due to the high latitude of the study system, the angle at which the sun moves with respect to the horizon is very acute, leading to prolonged dusk/dawn periods. Additionally, later in the season, true darkness becomes an impossibility at these latitudes as the sun reaches its nadir just below the horizon.

Results

After quality control, 7013 detections across 61 individuals remained (Table 1). However, the number of observations per individual ranged widely, with a median of 64 observations per individual. Median depths for individuals with at least 10 observations ranged between 0.03 and 2.1 m. The mean of median depths across these individuals was 0.56 m. 98% of these observations were at 3 m or less (Fig. 2). Some outliers ranged between depths of 10–50 m, but in all but one case, the post-smolt did not return to the upper layers of the water column (Fig. 3), indicating that these outliers are likely associated with mortality.

These 61 smolts moved rapidly through the fjord, with mean migration speeds of 0.17 m per second (1.12 body lengths per second). No receivers accounted for more than 17.5% of the detections occurring after the estuary, with most receivers contributing a few detections.

The most supported model included an interaction effect between the sun position and fjord zone with individual ID as a random effect. Both the intercepts and the slopes of these effects were allowed to vary with individual ID in the selected model. See Additional file 1: Table S1 for the model structures and AIC values of all fitted models. Adding effects of fjord or year did not improve the model (Additional file 1: Table S1) indicating that there was no substantial difference in smolt behavior between years or fjords. Tag burden or fish length also seemed to have no effect on depth use. The fixed-effects in the model explained 11.9% of the variation in depth-use and, by including the random-effects, the model explained 53.1% of the

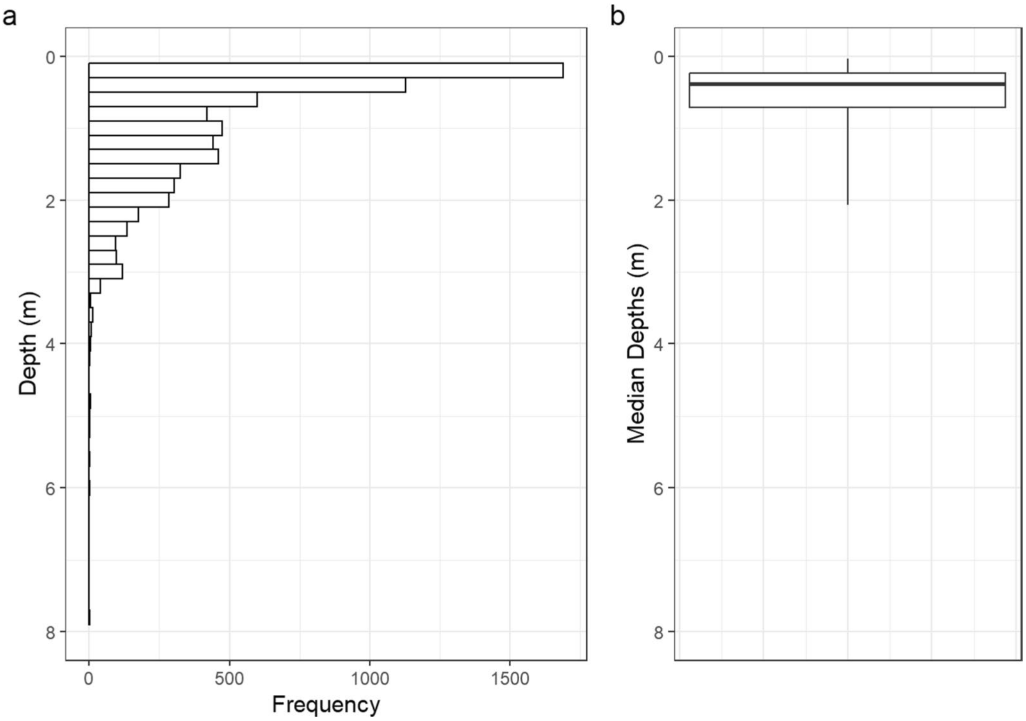

Fig. 2 Histogram of observed depth use across all acoustically tagged post-smolts that passed quality control (**a**) along with a boxplot showing the distribution of median depths for all individuals that passed quality control, where the upper and lower hinges correspond the 25th and 75th percentile and the whiskers correspond to the range of the data (**b**)

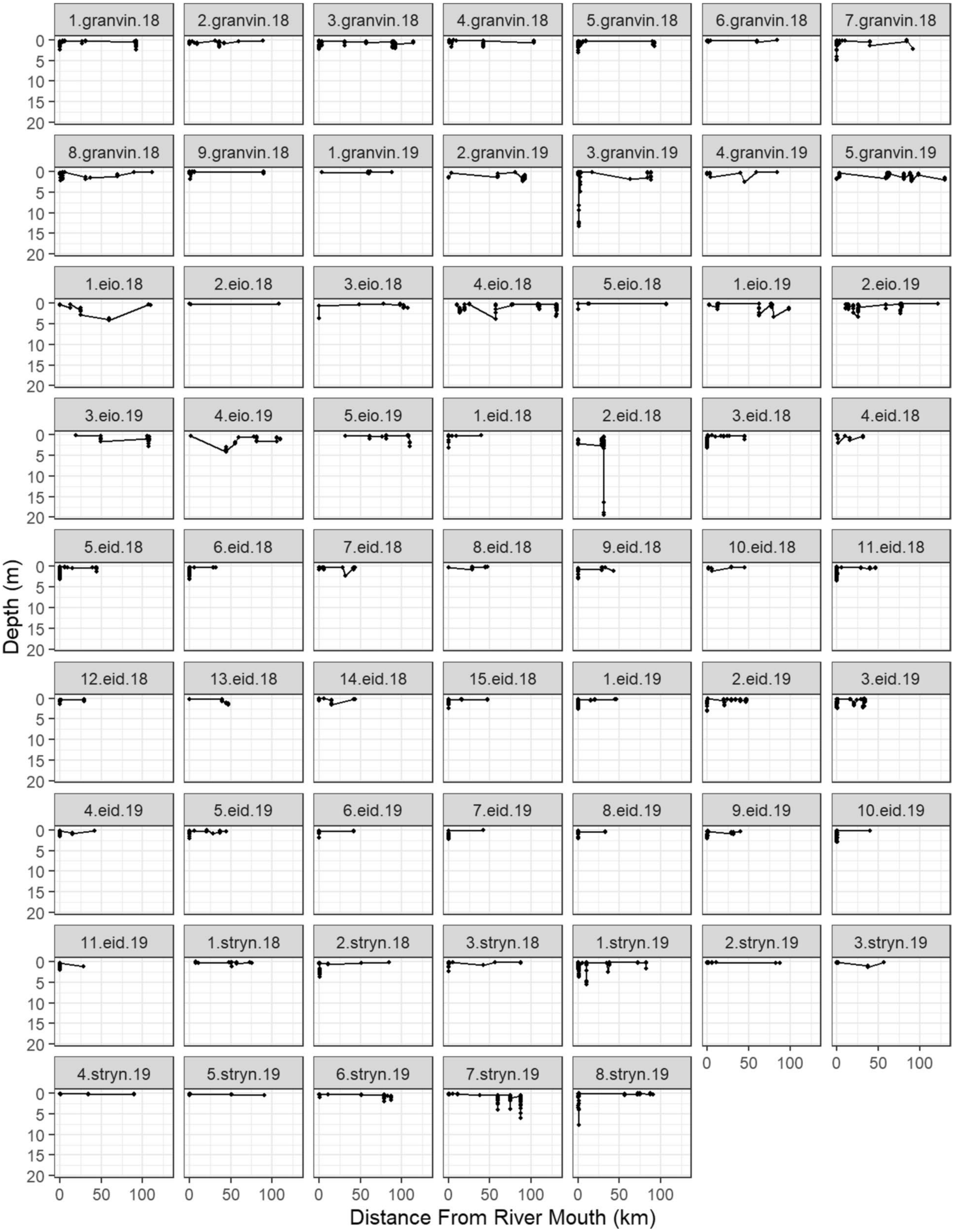

Fig. 3 Observed depth of each acoustically tagged post-smolt after quality control as a function of their distance from their respective river mouths. Labels indicate the ID of the fish along with their river of origin and the year of tagging

variation (Table 2). The selected model did not attain overwhelmingly higher AIC-support compared to other candidate models. In total, two additional candidate models attained ΔAIC-values less than or equal to 2. A common feature of all these models was the inclusion of fjord zone and sun position as fixed effects.

This model predicted that the average depth at daytime (sun positioned 18 degrees above the horizon) in zone A was 0.81 m, while the average depth at nighttime (sun positioned 12 degrees below the horizon) in zone D was 0.31 m (Table 3, Fig. 4).

Discussion

This study aimed to document the depth use of Atlantic salmon smolts migrating through fjords and to understand how this depth use varied through time and space. We found that outmigrating smolts were overwhelmingly detected within the top 3 m of the water column throughout the fjords. To our knowledge, this is the first study to report depth-use data for wild Atlantic salmon post-smolts as they migrate through fjords, though the behavior observed here is remarkably similar to that observed in wild smolts on the coasts of Scotland and Ireland [20, 35]. Other studies focusing on hatchery-reared post-smolts have also reported similar results [17, 36–38], indicating that wild and hatchery-reared post-smolt have the same depth use despite the differences in size and early-life experience. Similarly, Atlantic salmon kelts [39] and domesticated salmon in net pens seem to also use the upper few meters of the water column [40], though kelts are known to occasionally dive to depths greater than 200 m while out in the open sea [39, 41].

Table 2 Model parameter estimates of the most supported model fitted to depth-use data for Atlantic salmon post-smolts in two western Norway fjord systems during 2018 and 2019. P-values in bold are significant at $p < 0.05$

Fixed effect terms	Response = log (depth)		
	Estimates	CI	*p*
Intercept	−0.48	−0.70 to −0.26	**< 0.001**
Sun position (scaled)	0.06	−0.12 to 0.24	0.512
Zone [B]	−0.23	−0.73 to 0.26	0.353
Zone [C]	−0.57	−1.10 to −0.05	**0.033**
Zone [D]	−0.72	−1.08 to −0.35	**< 0.001**
Sun position × zone [B]	0.62	0.32–0.92	**< 0.001**
Sun position × zone [C]	0.27	−0.02 to 0.57	0.071
Sun position × zone [D]	0.24	0.04–0.44	**0.021**
Random effects			
σ^2	0.51		
$\tau_{00\ \text{full.id}}$	0.28		
$\tau_{11\ \text{full.id.scale.sun.pos}}$	0.16		
$\tau_{11\ \text{full.id.zoneb}}$	0.74		
$\tau_{11\ \text{full.id.zonec}}$	0.92		
$\tau_{11\ \text{full.id.zoned}}$	0.63		
ρ_{01}	0.25		
	−0.80		
	−0.85		
	−0.67		
ICC	0.47		
$N_{\text{full.id}}$	61		
Observations	7013		
Marginal R^2/conditional R^2	0.119/0.531		

Estimates are on ln-scale. Sun position scaling parameters: mean = 13.4; SD = 20.6. σ^2 = residual variance; τ_{00} = among-individual intercept variance; τ_{11} = among-individual slope variance; ρ_{01} = the random-slope-intercept-correlation; ICC = intraclass correlation coefficient

Table 3 Mean predicted depth across all individuals at nighttime (sun positioned 12 degrees below the horizon) and at daytime (sun positioned 18 degrees above the horizon) in each zone, along with standard deviations in parentheses

Zone	Nighttime depth (m)	Daytime depth (m)
A	0.79 (0.62)	0.81 (0.6)
B	0.24 (0.13)	0.63 (0.43)
C	0.33 (0.36)	0.4 (0.16)
D	0.31 (0.28)	0.42 (0.27)

We found little support in the data for any effects of fjord, day of the year, fish length, tag burden, or river of origin on depth use, though model convergence issues precluded the testing of overly complex models. Given the low amounts of variation in depth use observed, if these variables truly do have an effect on depth use, they must necessarily be small as well.

This study's most supported depth-use model showed that both fjord zone and the position of the sun had statistically significant effects on the depth use of post-smolts. However, these effects were small and largely inconsistent across individuals (Fig. 4). Previous work showing diel migration behavior has had access to direct measures of light intensity [36], while we inferred light intensity through the time of day and the position of the detection. As this region of Norway is notoriously cloudy, actual light intensities may vary substantially with the position of the sun. As the work of Davidsen et al. [16] implies, deeper depth use during daytime may be a direct reaction to light intensity rather than a true diel rhythm, reflecting that this behavior may be a tactic for reducing the risk of avian predation. That the final model included the raw values for the position of the sun rather than the parameterized values reflects that this effect is not a simple day/night switch and that the angle at which the sun's rays penetrate the ocean surface is important. Notably, salmon lice seem to have the opposite diel rhythm,

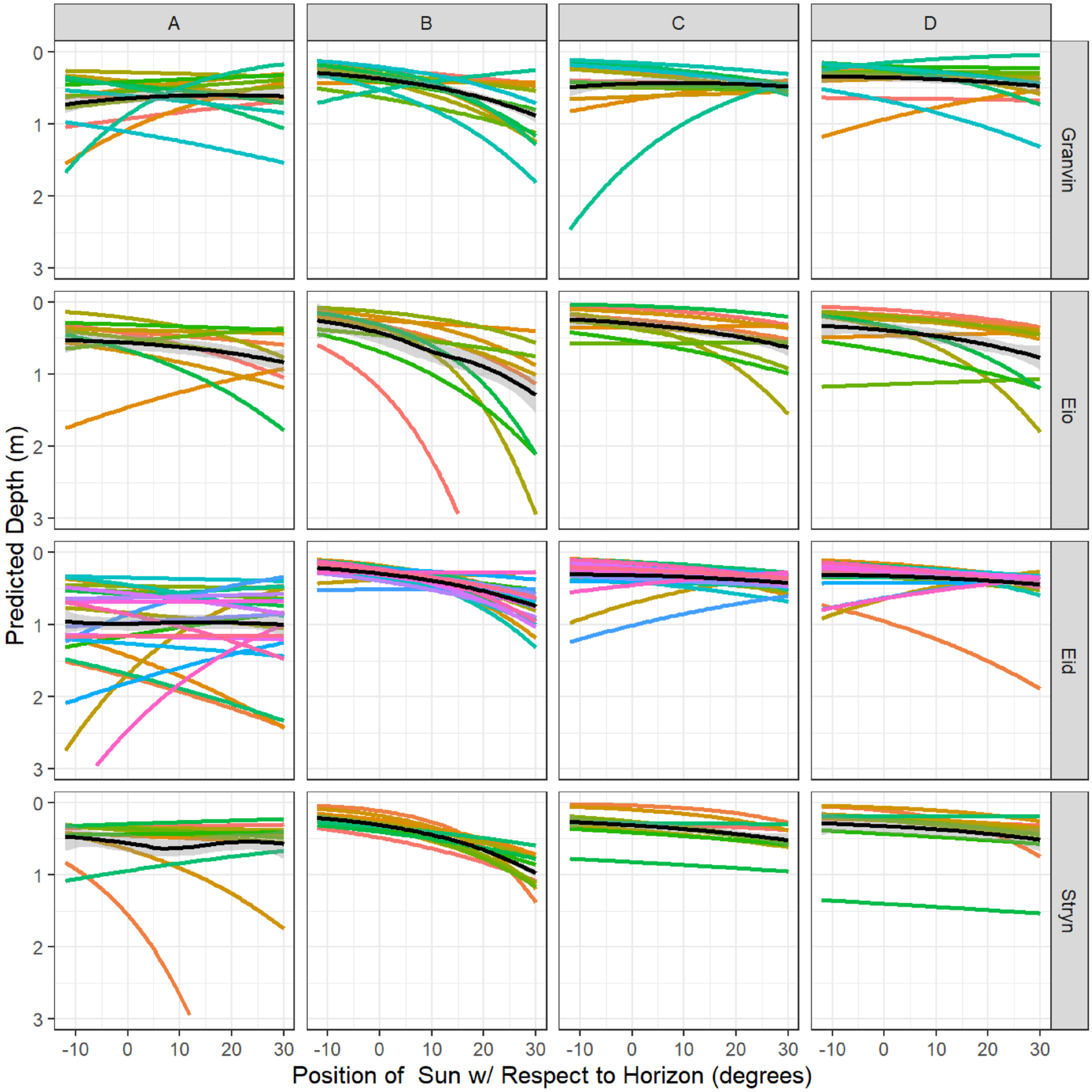

Fig. 4 Predicted effect of the position of the sun with respect to the horizon on the depth use of each acoustically tagged post-smolt (presented as individual lines) for each combination of fjord zone (**A**-**D**, see Fig. 1) and river. The thick black line shows the mean predicted effect of sun position on depth use across individuals within each facet. Modeling did not indicate that there were significant differences between rivers; the panels shown here are only meant to aid in visualization. Predictions were made from the selected depth-use model presented in Table 2 and include both the fixed effect of sun position, the fixed effects of fjord zone, and the random intercept and slope effects with respect to sun position per individual

going to the surface in response to light and descending 1–3 m in the dark [7, 10].

The effect of fjord zone on depth use showed that smolts tended to swim slightly deeper in zone A, near the estuary. This effect was largely driven by the higher variance in depth use observed in the estuary. As all of the migrating smolts were detected in these bottlenecks, detections in the estuary accounted for a large portion of the detections in zone A. When the detections in the estuary were removed, the effect of fjord zone on depth use was no longer significant. The higher variance in depth use observed in the estuary is not unexpected, especially if the extent of brackish water limits preferred depths as implied by the salinity data shown in the Additional file 1. Greater variability in depth use in the estuary has also been observed in smolts travelling through the Penobscot Bay [38] and the Moray Firth [20]. That said the estuaries of the rivers studied here are much smaller; they are on the order of 100–1000 m in length, depending on river and the level of the tide. The estuary also tends to be rife with predators; per kilometer, this is the most dangerous area for migrating smolts [4].

Regardless, the magnitude of the observed effects of fjord zone and sun position ranged from 0.1 to 0.4 m (Table 3). This was on the order of our expected error due to the resolution of our measurements, wave action, and/or spatial variation in air pressure, and was arguably not a biologically significant change in depth use.

Only one dive deeper than 15 m was recorded in the data after quality control. Though there were several deep dives in the raw data, in all but this one case the tags were not detected in the upper water column again. It was therefore assumed that these dives constituted the movements of predators and were therefore removed from the analysis. Work with data-storage tags has shown that post-smolts often undertake deep dives, but not during the first weeks of migration [18, 42]. It may be that this behavior does not manifest until the post-smolts are in the open sea, beyond the reach of our receiver network. That said, Newton et al. [20] observed one smolt at a depth greater than 25 m which subsequently returned to shallow depths in the Moray Firth. Given the non-continuous nature of the data, it may be unlikely to record these kinds of dives if they are brief and sporadic.

Post-smolts collected by trawling in this area of Norway are known to primarily feed on fish larvae and Euphausiids as they migrate [15]. Though these prey items can be found at the depths at which post-smolts were observed, they seem to be found in substantially higher densities at deeper depths, especially during the day [43–45]. This indicates that migrating at shallow depths is not a behavior meant to maximize the rate at which prey items are encountered. The rate at which these smolts migrate also implies that these smolts are primarily concerned with reaching the open ocean and do not spend great amounts of time foraging [26].

Limiting the analysis to only those smolts that were credibly detected in the outer fjord was a conservative approach to ensure that the data used in the quantitative analyses actually represented migrating salmon smolts rather than movements of predators (see e.g. [46]), with the assumption that it is unlikely that a predator of a tagged smolt will continue to exhibit a migratory trajectory similar to a post-smolt with the tag within its stomach. The use of acoustic tags designed to detect predation has revealed that this can happen within freshwater [47], but this has yet to be documented within the fjord environment. Acoustic tagging of brown trout (*Salmo trutta*) from the rivers of Granvin and Eio, one of the primary potential predators of migrating smolts in these populations, showed that the majority of those that migrated did not venture out in the outer fjord [48], with similar results in Sognefjorden, a fjord in between the fjords studied here [49], and in northern Norway [50, 51].

To our knowledge, correcting for the variable calibration of the tags is not standard practice, but probably should be a part of the workflow, especially for species that inhabit shallow waters. The mean offset for the smolts used in the analysis was 19.8 cm and the maximum was 37.8 cm. In other words, this accounted for a substantial amount of the variability in the data. Our recommendation is to check with the tag manufacturer how their tags are calibrated and to take note of the initial depth readings of the tag while the fish is at a known depth, for example while the tagged fish is recovering from anesthesia in a holding tank. Similarly, air pressure was adding a mean of 13.1 cm to recorded depths, ranging from -13.8 to 38.8 cm. Correcting for air pressure should also likely be a part of the workflow, especially if detections are occurring across a wide span of time and space.

Our data justify the practice of surface trawling for monitoring of sea-lice infestation data for migrating salmon post-smolts employed by the National Monitoring Program of Salmon Lice (NALO). Trawling of the top 3–4 m of the water column should produce representative samples of in situ migrating post-smolts, regardless of the time of day for the trawling operation.

In conclusion, post-smolts seem to be traversing large fjord systems with large environmental variability in salinity and temperature with a clear propensity for migrating within the top two meters of the water column. This indicates that post-smolts likely rely on environmental cues near the surface for navigation. This result also suggests that susceptibility to sea lice infections may be modeled using a simple behavioral model for post-smolts, along with relevant input from environmental data and sea lice depth preferences.

Supplementary Information

The online version contains supplementary material available at https://doi.org/10.1186/s40317-024-00390-1.

Additional file 1. Table S1: Difference in AIC values from the most supported model for all model structures tested during model selection. **Fig. S1**: The relationship between the time of day in hours versus **a** the position of the sun with respect to the horizon and **b** the parameterized values of the position of the sun for each recording of depth after quality control. **Fig. S2**: Interpolated salinity through each fjord in each year based on CTD measurements in the month of May, where **a** shows

Hardanger 2018, **b** is Nordfjord 2018, **c** is Hardanger 2019, and **d** is Nordfjord 2019. The orange and red contour lines show 12 and 20 salinity, respectively. The vertical black lines show the distances at which the CTD measurements were taken for each plot. **Fig. S3**: Violin plots showing observed depths of smolts when low salinity water was or was not available, defined as some part of the water column having salinity lower than 20 ppt. In red are detections from Stryn 2017, which had to be removed from the analysis as the tags used reported depth in 0.51 m increments as opposed to 0.2 m increments, while in red are all detections from other river years. The area of each violin plot is scaled according to how many data points are in it.

Acknowledgements
The authors would like to thank the river-owner's organizations in all rivers, as well as all aquaculture companies present in the regions for facilitating our work and the deployment of equipment. A large number of people contributed during the fieldwork, a big thank you to all of them. Special thanks to John Birger Ulvund for conducting all surgery implanting the tags in the fish.

Author contributions
H.B.B. wrote the first draft, analyzed and interpreted the data, and assisted with sampling and data collection. H.A.U. designed and planned the study, assisted with interpretation of data, and carried out fish sampling and data collection. T.O.H. assisted with the design of the study, and assisted with the analysis and interpretation of data. J.A.A. assisted with the design of the study and of the methodology. T.K. assisted with the design and planning of the study, assisted with fish sampling and data collection, and assisted with the interpretation of data. All authors contributed to editing the final draft.

Funding
Open access funding provided by Nord University. The study was conducted as a part of two long-term studies on salmonids: KLAFF and SalmonTracking 2030. The former is funded by County Governor of Vestland, Blom Fiskeoppdrett AS, Nordfjord Laks AS, Mowi AS, Coast Seafood AS, Selstad AS, Nordfjord Forsøksstasjon AS and the Eid and Stryn river-owner organizations and the latter is funded by PO3/4 Kunnskapsinkubator and FHF—Norwegian Seafood Research Fund (901575).

Availability of data and materials
The data presented here is available for dissemination upon reasonable request.

Declarations

Ethics approval and consent to participate
The sampling and tagging protocol was approved by Norwegian authorities for animal welfare (FOTS IDs: 12002 and 15471).

Consent for publication
Not applicable.

Competing interests
The authors declare no competing interests.

Received: 2 September 2024 Accepted: 7 November 2024

References

1. Rikardsen AH, Dempson JB. Dietary life-support: the food and feeding of Atlantic salmon at sea. In: Aas Ø, Klemetsen A, Einum S, Skurdal J, editors. Atlantic salmon ecology. London: Wiley; 2011. p. 115–43.
2. Otero J, L'Abée-Lund JH, Castro-Santos T, Leonardsson K, Storvik GO, Jonsson B, et al. Basin-scale phenology and effects of climate variability on global timing of initial seaward migration of Atlantic salmon (*Salmo salar*). Glob Change Biol. 2014;20(1):61–75.
3. Thorstad EB, Whoriskey F, Rikardsen AH, Aarestrup K. Aquatic nomads: the life and migrations of the atlantic salmon. In: Aas Ø, Einum S, Klemetsen A, Skurdal J, editors. Atlantic salmon ecology (Internet). Oxford: Wiley-Blackwell; 2010 [cited 2020 Oct 4]. p. 1–32. Available from: https://doi.org/10.1002/9781444327755.ch1.
4. Thorstad EB, Whoriskey F, Uglem I, Moore A, Rikardsen AH, Finstad B. A critical life stage of the Atlantic salmon (*Salmo salar*): behaviour and survival during the smolt and initial post-smolt migration. J Fish Biol. 2012;81(2):500–42.
5. Dempster T, Overton K, Bui S, Stien L, Oppedal F, Karlsen Ø, et al. Farmed salmonids drive the abundance, ecology and evolution of parasitic salmon lice in Norway. Aquac Environ Interact. 2021;1(13):237–48.
6. Medcalf K, Hutchings J, Fast M, Kuparinen A, Godwin S. Warming temperatures and ectoparasitic sea lice impair internal organs in juvenile Atlantic salmon. Mar Ecol Prog Ser. 2021;18(660):161–9.
7. Hagemann A, Kvæstad B, Venås B. Effect of diel light cycles on vertical migration patterns of *Lepeophtheirus salmonis* (Krøyer, 1837) copepodids measured in an in situ mesocosm. Aquac Int. 2024;32(6):7369–85.
8. Crosbie T, Wright D, Oppedal F, Dalvin S, Myksvoll M, Dempster T. Impact of thermoclines on the vertical distribution of salmon lice larvae. Aquac Environ Interact. 2020;16(12):1–10.
9. Crosbie T, Wright D, Oppedal F, Johnsen I, Samsing F, Dempster T. Effects of step salinity gradients on salmon lice larvae behaviour and dispersal. Aquac Environ Interact. 2019;23(11):181–90.
10. Heuch P. Experimental evidence for aggregation of salmon louse copepodids (*Lepeophtheirus salmonis*) in step salinity gradients. J Mar Biol Assoc U K. 1995;75(4):927–39.
11. Drinkwater KF, Frank KT. Effects of river regulation and diversion on marine fish and invertebrates. Aquat Conserv Mar Freshw Ecosyst. 1994;4(2):135–51.
12. Sheehan TF, Renkawitz MD, Brown RW. Surface trawl survey for U.S. origin Atlantic salmon Salmo salar. J Fish Biol. 2011;79(2):374–98.
13. Shelton RGJ, Turrell WR, Macdonald A, McLaren IS, Nicoll NT. Records of post-smolt Atlantic salmon, *Salmo salar* L., in the Faroe-Shetland Channel in June 1996. Fish Res. 1997;31(1–2):159–62.
14. Nilsen R, Serra-Llinares RM, Sandvik AD, Elvik MS, Kj R. Lakselusinfestasjon på vill laksefisk langs norskekysten i 2019; 2019.
15. Hellenbrecht LM, Utne KR, Karlsen Ø, Glover KA, Wennevik V. Diet analysis of Atlantic salmon (*Salmo salar*) post-smolts after the ecological regime shift in the Northeast Atlantic. Fish Res. 2023;262:106672.
16. Davidsen JG, Plantalech Manel-la N, Økland F, Diserud OH, Thorstad EB, Finstad B, et al. Changes in swimming depths of Atlantic salmon *Salmo salar* post-smolts relative to light intensity. J Fish Biol. 2008;73(4):1065–74.
17. Plantalech Manel-La N, Thorstad EB, Davidsen JG, Økland F, Sivertsgård R, Mckinley RS, et al. Vertical movements of Atlantic salmon post-smolts relative to measures of salinity and water temperature during the first phase of the marine migration. Fish Manag Ecol. 2009;16(2):147–54.
18. Einarsson SM, Guðjónsson S, Jónsson IR, Guðbrandsson J. Deep-diving of Atlantic salmon (*Salmo salar*) during their marine feeding migrations. Environ Biol Fishes. 2018;101(12):1707–15.
19. Reddin DG, Downton P, Friedland KD. Diurnal and nocturnal temperatures for Atlantic salmon postsmolts (*Salmo salar* L.) during their early marine life. Fish Bull. 2006;104(3):415–28.
20. Newton M, Barry J, Lothian A, Main R, Honkanen H, Mckelvey S, et al. Counterintuitive active directional swimming behaviour by Atlantic salmon during seaward migration in the coastal zone. Grabowski J, editor. ICES J Mar Sci. 2021;78(5):1730–43.
21. Nilsen F, Ellingsen I, Finstad B, Helgesen KO, Karlsen Ø, Sandvik AD, et al. Vurdering av lakselusindusert villfiskdødelighet per produksjonsområde i 2018. Rapp Fra Ekspertgruppe Vurder Av Lusepåvirkning Append. 2018;2:62.
22. Vollset KW, Nilsen F, Ellingsen I, Karlsen Ø, Paterson RA, Qviller L, et al. Produksjonsområdebasert vurdering av lakselusindusert villfiskdødelighet i 2023 [Internet]. 181. Ekspertgruppe for vurdering av lusepåvirkning; 2023 [cited 2024 Oct 15]. Available from: https://brage.nina.no/nina-xmlui/handle/11250/3104585.
23. Heupel MR, Semmens JM, Hobday AJ. Automated acoustic tracking of aquatic animals: scales, design and deployment of listening station arrays. Mar Freshw Res. 2006;57(1):1.

24. Jonsson B, Jonsson N, Hansen LP. Differences in life history and migratory behaviour between wild and hatchery-reared Atlantic salmon in nature. Aquaculture. 1991;98(1–3):69–78.
25. Urke HA, Kristensen T, Ulvund JB, Alfredsen JA. Riverine and fjord migration of wild and hatchery-reared Atlantic salmon smolts. Fish Manag Ecol. 2013;20(6):544–52.
26. Bjerck HB, Urke HA, Haugen TO, Alfredsen JA, Ulvund JB, Kristensen T. Synchrony and multimodality in the timing of Atlantic salmon smolt migration in two Norwegian fjords. Sci Rep. 2021;11(1):6504.
27. Dallolio A, Bjerck HB, Urke HA, Alfredsen JA. A persistent sea-going platform for robotic fish telemetry using a wave-propelled USV: technical solution and proof-of-concept. Front Mar Sci. 2022;7(9):857623.
28. Kessel ST, Cooke SJ, Heupel MR, Hussey NE, Simpfendorfer CA, Vagle S, et al. A review of detection range testing in aquatic passive acoustic telemetry studies. Rev Fish Biol Fish. 2014;24(1):199–218.
29. Gjelland KØ, Hedger RD. Environmental influence on transmitter detection probability in biotelemetry: developing a general model of acoustic transmission. Rands S, editor. Methods Ecol Evol. 2013;4(7):665–74.
30. Newton M, Barry J, Dodd JA, Lucas MC, Boylan P, Adams CE. Does size matter? A test of size-specific mortality in Atlantic salmon *Salmo salar* smolts tagged with acoustic transmitters. J Fish Biol. 2016;89(3):1641–50.
31. Lothian AJ, Rodger J, Wilkie L, Walters M, Miller R, Muller K, et al. A comparison of acoustic tag sizes on wild Atlantic salmon *Salmo salar* L. smolt migration success and behaviour. Ecol Freshw Fish. 2024;2024:e12798.
32. Bates D, Mächler M, Bolker B, Walker S. Fitting linear mixed-effects models using lme4. Stat [Internet]. 2014 June 23 [cited 2020 Apr 23]; Available from: http://arxiv.org/abs/1406.5823.
33. Burnham KP, Anderson DR, editors. Information and likelihood theory: a basis for model selection and inference. In: Model selection and multimodel inference [Internet]. New York, NY: Springer New York; 2004 [cited 2024 Jun 25]. p. 49–97. Available from: https://doi.org/10.1007/978-0-387-22456-5_2.
34. Thieurmel B, Elmarhraoui A. Suncalc: compute sun position, sunlight phases, moon position and lunar phase [Internet]. 2019. Available from: https://CRAN.R-project.org/package=suncalc.
35. Doogan A, Cotter D, Bond N, Ó'Maoiléidigh N, Brophy D. Partitioning survival during early marine migration of wild and hatchery-reared Atlantic salmon (*Salmo salar* L.) smolts using acoustic telemetry. Anim Biotelemetry. 2023;11(1):39.
36. Davidsen JG, Rikardsen AH, Halttunen E, Thorstad EB, Økland F, Letcher BH, et al. Migratory behaviour and survival rates of wild northern Atlantic salmon *Salmo salar* post-smolts: effects of environmental factors. J Fish Biol. 2009;75(7):1700–18.
37. LaBar GW, McCleave JD, Fried SM. Seaward migration of hatchery-reared Atlantic salmon (*Salmo salar*) smolts in the Penobscot River estuary, Maine: open-water movements. ICES J Mar Sci. 1978;38(2):257–69.
38. Renkawitz MD, Sheehan TF, Goulette GS. Swimming depth, behavior, and survival of atlantic salmon postsmolts in penobscot bay, maine. Trans Am Fish Soc. 2012;141(5):1219–29.
39. Hedger R, Hatin D, Dodson J, Martin F, Fournier D, Caron F, et al. Migration and swimming depth of Atlantic salmon kelts *Salmo salar* in coastal zone and marine habitats. Mar Ecol Prog Ser. 2009;19(392):179–92.
40. Johansson D, Ruohonen K, Kiessling A, Oppedal F, Stiansen JE, Kelly M, et al. Effect of environmental factors on swimming depth preferences of Atlantic salmon (*Salmo salar* L.) and temporal and spatial variations in oxygen levels in sea cages at a fjord site. Aquaculture. 2006;254(1–4):594–605.
41. Hedger R, Rikardsen A, Strøm J, Righton D, Thorstad E, Næsje T. Diving behaviour of Atlantic salmon at sea: effects of light regimes and temperature stratification. Mar Ecol Prog Ser. 2017;4(574):127–40.
42. Guðjónsson S, Einarsson SM, Jónsson IR, Guðbrandsson J. Marine feeding areas and vertical movements of Atlantic salmon (*Salmo salar*) as inferred from recoveries of data storage tags. Jech JM, editor. Can J Fish Aquat Sci. 2015;72(7):1087–98.
43. Ferreira ASDA, Stenevik EK, Vollset KW, Korneliussen R, Folkvord A. Vertical migration of Norwegian spring-spawning herring larvae in relation to predator and prey distribution. Mar Biol Res. 2012;8(7):605–14.
44. Nielsen T, Andersen C. Plankton community structure and production along a freshwater-influenced Norwegian fjord system. Mar Biol. 2002;141(4):707–24.
45. Zhou M, Zhu Y, Tande K. Circulation and behavior of euphausiids in two Norwegian sub-Arctic fjords. Mar Ecol Prog Ser. 2005;300:159–78.
46. Daniels J, Sutton S, Webber D, Carr J. Extent of predation bias present in migration survival and timing of Atlantic salmon smolt (*Salmo salar*) as suggested by a novel acoustic tag. Anim Biotelemetry. 2019;7(1):16.
47. Lennox RJ, Nilsen CI, Nash A, Hanssen EM, Johannesen HL, Berhe S, et al. Laboratory and field experimental validation of two different predation sensors for instrumenting acoustic transmitters in fisheries research. Fisheries. 2021;46(11):565–73.
48. Lægreid ML. Migrations and utilization of the fjord habitat by anadromous brown trout (*Salmo trutta*) from three watercourses in Hardangerfjord, Norway [Internet]. [Ås]: Norwegian University of Life Sciences; 2020. Available from: https://hdl.handle.net/11250/2681551.
49. Hawley KL, Urke HA, Kristensen T, Haugen TO. Balancing risks and rewards of alternate strategies in the seaward extent, duration and timing of fjord use in contemporary anadromy of brown trout (*Salmo trutta*). BMC Ecol Evol. 2024;24(1):27.
50. Eldøy SH, Davidsen JG, Thorstad EB, Whoriskey F, Aarestrup K, Næsje TF, et al. Marine migration and habitat use of anadromous brown trout (*Salmo trutta*). Jonsson B, editor. Can J Fish Aquat Sci. 2015;72(9):1366–78.
51. Strøm JF, Jensen JLA, Nikolopoulos A, Nordli E, Bjørn PA, Bøhn T. Sea trout *Salmo trutta* in the subarctic: home-bound but large variation in migratory behaviour between and within populations. J Fish Biol. 2021;99(4):1280–91.

Publisher's Note