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A Physical Bottleneck Increases Predation on Atlantic Salmon Smolts During Seaward Migration in an Irish Index River

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ABSTRACT

Counting departing smolts and returning adults in index rivers is essential to estimate marine survival and track population trends of Atlantic salmon (*Salmo salar*). However, mortalities between counting facilities and a river mouth can skew survival estimates. We used acoustic and radio telemetry to investigate survival, mortality sources and behaviour of wild salmon smolts in the River Erriff, Ireland's index river, and Killary Fjord. Smolts were tagged with acoustic tags in 2017 ($n=40$) and 2018 ($n=35$) and radio tags in 2018 ($n=30$). Survival was low for acoustic-tagged smolts in 2017 (26%) and 2018 (47%), mainly due to riverine mortality. Terrestrial or avian predators consumed 65% of acoustic-tagged smolts in 2017 and 67% of radio-tagged smolts in 2018. Nocturnal migration and ebb tide transportation likely contributed to high estuary survival. High predation on smolts emphasised the importance of assessing freshwater mortality for effective salmon management.

1 | Introduction

The Atlantic salmon (*Salmo salar* L.) occurs naturally along east and west coasts of the North Atlantic Ocean and is culturally, economically and ecologically valuable (Drenner et al. 2012; Klemetsen et al. 2003). Despite its importance, the number of wild Atlantic salmon has declined throughout its range since the 1980s (Chaput 2012; ICES 2024; Nicola et al. 2018). The decline has spurred research to improve monitoring and forecasting of stock sizes (Chadwick 1985; ICES 2024; Potter et al. 2004; White et al. 2023). Models used to estimate pre-fishery abundance depend on multiple parameters including the number of smolts reaching the sea and the count of returning adults; these data are typically collected in river traps (Chaput et al. 2005; Chaput 2012; Forseth et al. 2013; Potter et al. 2004). Index rivers where both smolt output and adult returns are monitored allow for direct comparisons of these parameters and are crucial for

estimating marine survival and describing regional, national and international population trends (ICES 2024).

Migration of Atlantic salmon smolts from freshwater to sea and early marine journey are critical phases in their life history that are often associated with increased mortality rates (Hoar 1976; Thorstad et al. 2012). Smolts that move from freshwater to sea are exposed to predators in freshwater, marine and terrestrial environments (Aarestrup et al. 1999; Furey et al. 2015; Heggenes and Borgström 1988; Jepsen, Holthe, and Økland 2006; Jepsen, Flávio, and Koed 2019; Ruggles 1980). Hence, smolts often migrate at night to reduce their vulnerability to visual predators (Haraldstad et al. 2017; Ibbotson et al. 2006; Ibbotson, Beaumont, and Pinder 2011). Environmental conditions can also influence predation risk of smolts, as when low water levels during dry years increase predator hunting success (Martínez-Abraín et al. 2020).

Predators typically concentrate in areas where smolts are abundant or easy to capture (Holling 1959; López-Bao et al. 2011; Kennedy et al. 2018; Mather 1998), thereby creating bottlenecks for smolt survival. Smolt mortality is generally density-independent, so an increase in the number of smolts leaving a river correlates with an increased number of adult returns (Crozier and Kennedy 1993; Jonsson, Jonsson, and Hansen 1998; Thorstad et al. 2012). Consequently, addressing survival bottlenecks can enhance smolt survival and thereby benefit salmon populations (Flávio et al. 2020).

The advent of telemetry has greatly enhanced the ability to track smolt migrations, providing insights beyond what traditional in-river traps offer (Hussey et al. 2015; Thorstad et al. 2012). Unlike traps, which provide a snapshot of smolt migration at specific locations, telemetry allows for tracking the entire journey from river to sea to reveal important details about behaviour and survival (Thorstad et al. 2012). Acoustic and radio telemetry are two commonly used methods with their own advantages and disadvantages. Acoustic telemetry can be used in freshwater and marine environments, but not in air, while radiotelemetry works in freshwater and in air but not in marine environments (Thorstad et al. 2013). Both methods can be used passively or actively. Passive tracking uses automated listening stations (ALS) to log detections of tagged fish that swim within range, to provide continuous temporal data, but is limited by ALS placement. Active tracking requires manual tracking of tagged fish, with better spatial resolution, but is labour-intensive (Thorstad et al. 2013). Therefore, combining multiple tracking approaches can overcome limitations of each method (Chavarie et al. 2022; Flávio et al. 2021).

We used acoustic telemetry to investigate survival rates of Atlantic salmon smolts migrating through the River Erriff, a National Salmonid Index Catchment (NSIC) in Ireland, and subsequently through Killary Fjord in 2017 and 2018. Large smolt losses in the River Erriff led to the addition of radio telemetry in 2018 to identify the specific source of losses in the

river. Our objective was to explain variation in migrating fish survival by (1) estimating survival rates in both the river and fjord for Atlantic salmon smolts; (2) identifying sources of smolt mortality in the river; and (3) characterising smolt behaviour (diel and tidal patterns) and environmental conditions (water level) that affected smolt survival during migration. Our findings would enhance understanding of survival and sources of mortality for migrating smolts, thereby informing management practices aimed at improving salmon population monitoring in index rivers.

2 | Methods

2.1 | Study Area and Experimental Fish

The River Erriff is a spate river draining into the top of Killary Fjord, in the Republic of Ireland (Figure 1). The catchment drains 168 km², with a main channel 12.8 km long and a mean annual discharge of 8.16 m³ s⁻¹. Primary land use in the catchment is sheep grazing, with varying levels of stream boundary protection (Gargan et al. 2016). Some coniferous forestry plantations are in the catchment. The River Erriff is a 20–25-m wide 5th-order stream that features a mix of riffles, runs and pools. An important tributary to the River Erriff is the River Black, with a catchment area of 16 km². The River Black is a 6-m wide 3rd-order stream. A Wolf-style trap (Wolf 1951) is located at Tawnyard in the upper River Black, 11.5 km upstream from the estuary (Figure 1). The first 2.2 km downstream from the Tawnyard trap consists mainly of a long, sinuous glide 3–4 m deep, interrupted by a small bedrock cascade 165 m downstream from the trap. The remaining 1.46 km of the River Black before joining the River Erriff is a high-gradient riffle dominated by cobble, large rocks and bedrock, except for one large 150-m-long pool (by A1/R1; Figure 1). The River Erriff is 60% of the drainage area to Killary Fjord, a 16-km-long by 750-m-wide inlet with a mean depth of 15 m. The estuary comprises the first 2 km of Killary Fjord (river mouth to A7;

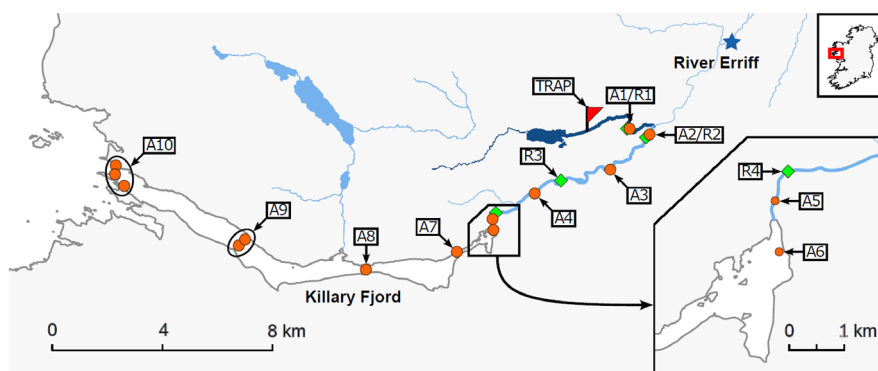


FIGURE 1 | The River Erriff (light blue), River Black (dark blue) and Killary Fjord, Republic of Ireland. The estuary part of Killary Fjord spans from the river mouth to A7. Flag indicates the trap in the River Black where smolts were tagged and released with acoustic tags in 2017 ($n = 40$) and 2018 ($n = 35$), and with radio tags in 2018 ($n = 30$). Orange points indicate acoustic automated listening stations (ALS), which were organised into 10 arrays: One in the River Black (A1), four in the River Erriff (A2 to A5), two in the estuary (A6 and A7) and three in Killary Fjord (A8 to A10). Note that A2 was only operational in 2018. Green diamond indicates radio automatic listening stations (ALS) deployed in the River Black (R1) and the River Erriff (R2 to R4). Blue star marks the location of the Derrinkee–Sandpit station from which water level data were sourced. The box in the upper right corner indicates the location of the River Erriff in Ireland, while the lower right box shows the deployments of acoustic and radio ALSs in the lower River Erriff and the start of the estuary.

Figure 1). The maximum depth at the fjord mouth is 45 m, which opens into the Atlantic Ocean.

Emigrating wild Atlantic smolts were captured at the Tawnyard trap, which operates from March 1 to May 30 each year. Based on smolt counts at the trap, the smolt run started on April 4 and ended on May 19 in 2017, whereas in 2018, the smolt run started on April 19 and ended on May 13 (Figure S1). The earlier smolt run in 2017 was potentially due to higher water temperatures.

In 2017, eight smolts were captured and tagged with acoustic transmitters at the trap on April 6 and 7 and 32 smolts were tagged during April 20–26. In 2018, 35 smolts were captured and tagged with acoustic transmitters during April 20–30 and with radiotransmitters on May 3 and 4 ($n = 20$ and 10, respectively). The trap was checked each morning for smolts, so smolts were held for up to 24 h. All smolts were released from the trap after tagging between 07:45 and 10:45 am, together with all residual untagged and PIT-tagged smolts from the trap. At capture, smolts were selected for tagging based on silvery appearance and streamlined body that was indicative of smoltification, to increase likelihood that tagged fish would migrate to sea (Hoar 1988). Fork length (L_F) and weight (W) were measured before tagging. Smolts shorter than 125 mm were not tagged to ensure an appropriate tag-to-body weight ratio (tag burden).

2.2 | Acoustic Telemetry

2.2.1 | Tagging Procedure

Atlantic salmon smolts were tagged with individually coded acoustic transmitters, from either Innovasea (V7, 1.6 g weight in air, 0.75 g weight in water, nominal ping rate 30–60 s, expected battery life 108 days, Innovasea Systems Inc., Canada) or Thelma (ID-LP7, 1.8 g weight in air, 1.1 g weight in water, nominal ping rate 20–60 s, expected battery life 100 days, Thelma Biotel, Norway). In 2017, 10 smolts were tagged with Thelma acoustic transmitters and 30 with Innovasea acoustic transmitters (Table 1). In 2018, 35 smolts were equipped with Thelma transmitters. Prior to surgery, fish were individually anaesthetised in a bath containing tricaine methanesulfonate 100 mg/L (mean time in anaesthetic 01 min 48 s). After fish were anaesthetised (loss of equilibrium and slow irregular operculum rate), fork length (L_F) and weight (g) were measured. Fish were then placed in a V-shaped surgical cradle, and an acoustic transmitter was implanted into the body cavity through an incision slightly to the side of the mid-ventral line, anterior to the pelvic girdle. The incision was closed with 1–2 sutures using a braided poly-filament absorbable suture (Ethicon, Vicryl 4/0). The operation time from when the fish was taken out of anaesthesia until the fish was put into recovery water ranged from 1 to 2 min (mean operation time 01 min 17 s). Surgical implantation was performed by a qualified fish surgeon in accordance with guidelines described in authorisation AE19118/P001 from the Health Products Regulatory Authority. Fish were released below the trap in daylight after they were fully recovered (20–30 min after surgery) in groups of 3–15 fish. All tags were tested to ensure they were operating properly before implantation.

2.2.2 | Acoustic Array

Automatic Listening Stations (Vemco Ltd. Models VR2W, VR2AR; www.vemco.com) were deployed to track fish movements in 10 arrays (Figure 1): one in the River Black (A1); four in the River Erriff (A2–A5); two in the estuary (A6 and A7); and three in Killary Fjord (A8–A10). River array A2 operated only in 2018. Arrays A1 to A8 were each one station, array A9 included two stations and array A10 included three stations. Receivers at A9 and A10 were placed 220 m apart to ensure complete coverage at each acoustic gate. Range testing was conducted in April 2014 when the acoustic array was first installed in the River Erriff and Killary Fjord. Acoustic data were downloaded, and stations were serviced in winter each year.

Manual tracking was conducted through the river and fjord after the smolt run to locate tags in the system and determine where smolts disappeared. In 2017, manual tracking was conducted on May 23 from the riverbank using a Vemco VR-100 hydrophone from the release site to river mouth by scanning non-riffle habitat for 3 min at each site. The stretch from the release site to the first acoustic array (A1) was scanned every 50 m. The same river stretch (release to A1) was also scanned by towing a hydrophone from a kayak. After A1, larger pools were scanned at the start, middle and end. Manual tracking in Killary Fjord was conducted by towing a hydrophone from a boat ($\sim 3 \text{ km h}^{-1}$) on June 13–14. Due to the low numbers of tagged smolts disappearing in the fjord in 2017 based on passive and manual acoustic tracking, manual acoustic tracking was not performed in the river and fjord in 2018. Instead, radiotelemetry was used in 2018 to identify sources of smolt mortality in the river.

2.3 | Radio Telemetry

2.3.1 | Tagging Procedure

Thirty Atlantic salmon smolts were tagged with radio transmitters (Model BD-2, Holohil Systems Ltd., Ontario, Canada). Transmitters weighed 1.2 g in air (tag dimensions: 16 mm L \times 8 mm W \times 3.5 mm H, antenna length: 15 cm), with an expected life of 6 weeks transmitting at 45 pulses per minute. Surgical procedures were the same acoustic tag implantation (mean time in anaesthetic 01 m 39 s), with the addition of a cannula procedure. A hollow needle was used for the cannula to allow the radio antenna to exit the body cavity posterior to the incision and trail back along the body of the smolt. The needle was removed after the antenna was run through the body wall. The incision was closed with 1–2 sutures using a braided poly-filament absorbable suture (Ethicon, Vicryl 4/0). Operation time ranged from 1 to 2 min (mean: 01 min 39 s). Surgical implantation used the same animal authorisation and release procedures as acoustic-tagged fish.

2.3.2 | Radio Tracking

In 2018, radio Automatic Listening Stations (Advanced Telemetry Systems Inc. Isanti, MN., USA, Model R4500SD)

TABLE 1 | Number, fork length (L_F), weight, tag burden and tag model used for acoustic-tagged and radio-tagged Atlantic salmon (*Salmo salar*) smolts released in the River Black, Republic of Ireland, in 2017 and 2018. Mean and standard deviation (SD) in parentheses.

Tagging Group	N	Released	Size at Tagging (Mean [SD])			Tag Manufacture (Model)
			F_L (cm)	Weight (g)	Tag Burden (%)	
2017-Acoustic	30	April 6–26	13.8 (± 0.7)	25.3 (± 3.8)	6.5 (± 0.9)	Innovasea (V7)
2017-Acoustic	10	April 20 and 25	13.9 (± 0.7)	24.7 (± 3.3)	7.4 (± 1.0)	Thelma Biotel (ID-LP7)
2018-Acoustic	35	April 20–30	14.4 (± 1.0)	29.6 (± 6.7)	6.4 (± 1.3)	Thelma Biotel (ID-LP7)
2018-Radio	30	May 3 and 4	14.1 (± 0.8)	27.2 (± 4.3)	4.5 (± 0.7)	Holohill (BD-2)

were deployed to track fish movements and determine sources of mortality in the river (Figure 1) in four radio arrays (R1–R4), each with one station. Tagged smolts were also tracked with a mobile station (Advanced Telemetry Systems Inc. Isanti, MN., USA. Model R2000), wherein fish positions were recorded using a handheld GPS. Manual tracking was conducted five times during May 8–16 to locate tagged fish and recover stationary tags in water or on land. Manual radio tracking began at the Tawnyard trap in the River Black, where smolts were tagged and released and continued along the riverbank to the river mouth. In open terrain, radiotransmitters could be detected up to 500m away, whereas in the river, the detection range was limited to ~200m due to riparian vegetation. Radio array efficiency (detection probability) was estimated using a Bayesian state-space implementation of the Cormack-Jolly-Seber (CJS) mark-recapture model.

2.4 | Data Analysis

Raw acoustic detection data were checked for abnormal behaviour using the R package *actel* (Flávio and Baktoft 2021). Abnormal behaviour included (1) skipping acoustic ALS arrays and passing undetected through multiple arrays; (2) long upstream movements by being detected in an acoustic array after being detected at one or several acoustic arrays farther downstream, which indicated the tag had been ingested by a predator (Flávio et al. 2021). Abnormal events were analysed in detail to identify and remove false detections. Statistical analyses used R version 4.4.0 (R Core Team 2024).

2.4.1 | Survival in River and Fjord

2.4.1.1 | Detection Probability and Apparent Survival. Survival in the river and fjord (objective 1) was estimated from acoustic telemetry data collected in 2017 and 2018. To account for the possibility that smolts passed arrays undetected, we used a Bayesian state-space implementation of the CJS mark-recapture model to estimate apparent survival (Φ) and probability of detection (p ; i.e., array efficiency) for tagged smolts. In the CJS model, detection of a tagged smolt at each array was considered a ‘recapture’ event (Cormack 1989). The state-space CJS model created separate models for the unobserved survival process and the observed detection process, to accommodate imperfect detection rates. Smolt fork length was

included as a possible effect on survival, but not on detection probability. Tag burden was not included in the model due to collinearity with fish size. The state-space CJS model was:

$$\text{logit}(p_{(y,e)}) = \mu_{p_{(y,e)}}$$

$$\text{logit}(\Phi_{L(y,e,f)}) = \mu_{\Phi(y,e)} + \beta \times L'_{(f)}$$

where y = year \times telemetry combination (2017 acoustic, 2018 acoustic, 2018 radio), e = array, f = individual smolt and $L'_{(f)}$ = standardised fork length of a tagged smolt ($L'_{(f)} = (L_{(f)} - \bar{L}) / \sigma_L$). Because L was standardised, apparent survival of an average-sized smolt (Φ) at each array (e) was estimated as:

$$\text{logit}(\Phi_{(y,e)}) = \mu_{\Phi(y,e)}$$

For the last array at the fjord mouth (A10), apparent survival was not separable from detection probability because no future events (recaptures) could inform the model. Therefore, combined survival and detection probability for the last segment of the fjord delta (δ_L ; A9–A10) was estimated as:

$$\text{logit}(\delta_{L(y,f)}) = \mu_{\delta(y)} + \beta \times L'_{(f)}$$

where combined survival and detection probability for an average-sized smolt (δ) was estimated as:

$$\text{logit}(\delta_{(y)}) = \mu_{\delta(y)}$$

The CJS model was fit in JAGS (Plummer 2003) using the R package ‘R2jags’ (Su and Yajima 2024). The model ran with three Markov chain Monte Carlo (MCMC) chains, 50,000 iterations (5000 were burn-in), a drop rate of five and uninformative priors. Non-convergence was examined using trace plots of MCMC chains, by checking that Gelman-Rubin (R-hat) statistics were < 1.1 using the function *gelman.diag* from the coda package (Plummer et al. 2006), and by examining unimodal distributions of model parameters (Brooks and Gelman 1998). Diagnostics examined did not suggest non-convergence (Supporting Information).

2.4.1.2 | Instantaneous Mortality Rates per Kilometre. For each migration stretch between arrays, instantaneous mortality (Z) per km was estimated by

combining distance with respective apparent survival (Φ 's) from the CJS model, following the formulae adapted from Miranda and Bettoli (2007):

$$Z = \frac{\ln\left(\frac{1}{\Phi}\right)}{d}$$

where d = distance covered (km) and Φ = apparent survival for the stretch. Although Z was estimated for short stretches (< 1 km), estimates may have been unreliable and were flagged in the results. Z was calculated as mortality rates relative to distance; hence, for shorter distances, even small variations in distance measurement—for example, due to receiver drift, variability in GPS accuracy, or detection range—can have a disproportionate impact on the estimate compared to longer stretches.

2.4.2 | Sources of River Mortality

A combination of active (manual) and passive tracking data was used to identify sources of mortality in the river (objective 2). Sources of mortality could not be assigned for acoustic-tagged smolts in 2018, because manual acoustic tracking was not conducted that year. Manual acoustic tracking was used to determine if tags in smolts had been removed from the river by terrestrial or avian predators, or remained stationary in the river as an unknown river mortality. The source of mortality of tagged smolts was assigned using criteria described by Flávio et al. (2021):

Acoustic study (2017):

1. If a tagged smolt disappeared between the release site and the final river array (A5) and the tag could not be located by manual tracking, the smolt was classified as eaten by an unknown terrestrial predator (mammal or bird).
2. If a tag was stationary in the river during manual tracking, the smolt was classified as an unknown river mortality.
3. If an acoustic-tagged smolt was found dead with no signs of predation or wounds, the smolt was classified as died from tagging.

Radio study (2018):

1. If a radio tag was recovered from spraint (otter or mink faeces), found with chew marks on a riverbank, or was buried deep in brush adjacent to the river but was not recovered, the smolt was classified as eaten by an otter (*Lutra Lutra*) or a mink (*Mustela vison*).
2. If a radio tag was recovered below a heron (*Ardea cinerea*) rookery or the signal originated from a heron nest, the smolt was classified as eaten by a heron.
3. If a radio-tagged smolt disappeared between the release site and the final river array (R4) and the tag could not be located by manual tracking, the smolt was classified as eaten by an unknown terrestrial or avian predator (mammal or bird).

4. If a tag was stationary in the river during manual tracking, the smolt was classified as an unknown river mortality.
5. If a radio-tagged smolt was found dead with no signs of predation or wounds, the smolt was classified as died from tagging.

2.4.3 | Smolt Behaviour

To test for differences in diel patterns during river migration by smolts, we used a generalised linear mixed-effects model (GLMM) with the logit link function and Bernoulli distribution. The response variable (Diel) indicated if smolts arrived at arrays during day (1) or night (0). Smolts arriving after sunset, but before sunrise, were assumed to have arrived during night, and those arriving after sunrise, but before sunset, were assumed to have arrived during the day. The model included tag group (Acoustic 2017, 2018; Radio 2018) and array (A1/R1, A2/R2, A3, A4/R3 and A5/R4). Closely located acoustic and radio arrays were combined into single factor levels (A1/R1 and A2/R2), except for A3, which had no nearby radio array. Fish ID was included as a random effect to account for multiple observations of the same individual. The GLMM was fit using the function *glmmTMB* in the *glmmTMB* package (Brooks et al. 2017):

$$Diel_{ij} \sim \text{Bernoulli}(P_{ij})$$

$$E(Diel_{ij}) = P_{ij}$$

$$\text{logit}(P_{ij}) = \text{Group}_{ij} + \text{Array}_{ij} + \text{FishID}_i$$

Model assumptions were validated by examining scaled quantile residuals using the function plot in the DHARMA package (Hartig 2022) and by plotting scaled quantile residuals against covariates included and not included in the model.

Diel patterns and tidal stage were evaluated for entry into Killary Fjord (i.e., the estuary) based on the time of first arrival at array A6 for acoustic-tagged smolts. To determine if arrival times at A6 were uniformly distributed or were concentrated at certain times of day, Watson's one-sample test was used (separately for 2017 and 2018) with the function *watson.test* in the circular package (Agostinelli and Lund 2023). To assess the effect of the tidal stage (high, ebb, low, or flood) on arrival times of smolts at A6, each arrival time was converted into an angle corresponding to its position within the tidal cycle. Watson's one-sample test was used (separately for 2017 and 2018) to determine if arrival angles were uniformly distributed or were concentrated at particular phases of the tidal cycle.

2.4.4 | Environmental Conditions

To determine if water levels influenced predation risk of smolts, mean water levels during the smolt run from April 6 to May 9 were compared between 2017 and 2018. The period from April 6 to May 9 was used to encompass the time from when smolts were first tagged and released to when smolts were first detected at the last river array (A5 or R4), as a relevant window for comparing water levels during river migration. Due to the lack of

water level data in the River Black, where smolts were tagged and released, data were used from the Derrinkee–Sandpit station, located ~7 km upstream from where the River Black drains into the River Erriff (www.waterlevel.ie; Figure 1).

Daily water levels were not related to individual smolt mortalities because time of death was not available for each smolt. Consequently, mortality events could not be connected to the corresponding daily water levels. Additionally, water levels were not compared between acoustic-tagged smolts released earlier in 2018 and radio-tagged smolts released later in 2018, because the lake upstream from the River Black likely buffered rainfall recorded at the Derrinkee–Sandpit station. Instead, mean water levels were compared between 2017 and 2018 using Welch's *t*-test (*t.test* function in the stats package; R Core Team 2024).

3 | Results

Fork lengths of acoustic-tagged smolts ranged from 129 to 152 mm in 2017 and 125 to 165 mm in 2018, and radio-tagged smolts ranged from 132 to 162 mm in 2018 (Table 1). Acoustic-tagged smolts in 2017 and 2018 and radio-tagged smolts in 2018 differed significantly in mean fork lengths ($F_{2,102} = 4.70$, $p = 0.011$). Acoustic-tagged smolts in 2018 (mean FL = 144 mm, SE = 1.65) were significantly longer than those tagged in 2017 (mean FL = 138 mm, SE = 1.05; Tukey's post hoc test: $p = 0.01$).

In contrast, radio-tagged smolts in 2018 (mean = 141 mm, SE = 1.40) did not differ significantly in size from acoustic-tagged smolts in 2017 ($p = 0.31$) or 2018 ($p = 0.32$). Smolts tagged with Thelma and Innovasea acoustic transmitters in 2017 did not differ significantly in length (Welch's *t*-test: $t = -1.2$, $df = 61.8$, $p = 0.24$). Tag burden (tag/body weight) of acoustic-tagged smolts ranged from 4.7% to 8.8% (mean = 6.7%, SD = 1.0%) in 2017 and 4.1%–9.0% (mean = 6.4%, SD = 1.2%) in 2018. Tag burden ranged from 3.1% to 5.7% (mean = 4.5%, SD = 1.0%) for radio-tagged smolts in 2018.

Acoustic detection probability (array efficiency) was high overall in 2017 and 2018 (Figure 2). In 2017, array efficiency was highest at the first river array A1 (95%) and lowest at the last river array A5 (87%). In 2018, array efficiency was lower at river arrays A3 (76%) and A5 (12%) than at other arrays that ranged from 90% at the mid-fjord array A9 to 97% at the first river array A1. Radio array efficiencies in 2018 were high and ranged between 91% (CI: 61%–100%) at R2 and 92% (CI: 62%–100%) at R3 (Table S1). The number of smolts detected at each acoustic and radio array can be found in Table 2.

Apparent survival was lowest in the first stretch of the River Black between release and array A1 (Release–A1) in 2017 ($\Phi_1 = 46\%$) and 2018 ($\Phi_1 = 71\%$; Figure 2). Below this stretch, apparent survival in 2017 was lower between A1 in the River Black and A3 in the River Erriff ($\Phi_2 = 79\%$) than other stretches in the River Erriff ($\Phi_3 = 96\%$; $\Phi_4 = 93\%$). In contrast, apparent survival

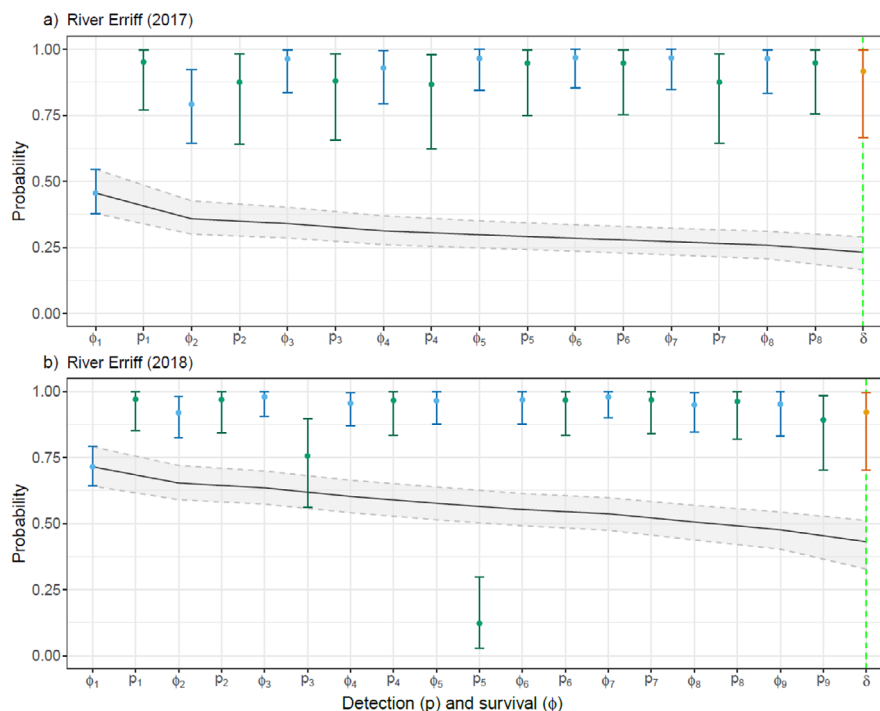


FIGURE 2 | Posterior distribution of Bayesian CJS estimated survival probability (Φ , blue), detection probability (p , green) and combined survival and detection probabilities (δ , orange) of Atlantic salmon (*Salmo salar*) smolts at arrays in the River Erriff and Killary Fjord, Republic of Ireland, in 2017 (a) and 2018 (b). A value of 1 represents high probability, and conversely 0 represents low probability. The line represents the cumulative survival probability and its corresponding 95% confidence interval up to the point of success. Since array A2 was not deployed in 2017, the values for p_1 , p_2 , p_3 , ..., p_8 represent detection probabilities for arrays A1, A3, A4, ..., A9, while ϕ_1 , ϕ_2 , ϕ_3 , ..., ϕ_8 denote survival probabilities for migration stretches Release–A1, A1–A3, A3–A4, ..., A8–A9. In 2018, the values correspond to the arrays and migration stretches in chronological order. For example, p_2 represents the detection probability for array A2, and ϕ_2 the survival probability for the stretch A1–A2. The dashed green vertical line represents the array that marked success of migration (i.e., array A10).

TABLE 2 | Number of Atlantic salmon (*Salmo salar*) smolts tagged and detected at acoustic (A1–A10) and radio (R1–R4) arrays in the River Black, River Erriff and Killary Fjord, in the Republic of Ireland. 2017A is acoustic-tagged smolts in 2017, 2018A is acoustic-tagged smolts in 2018, and 2018R is radio-tagged smolts in 2018. The number of smolts not detected at an array but detected at subsequent arrays is in parentheses. The number not detected is not known (unk) in the final array. Radio arrays are listed together with their nearest acoustic counterpart. Arrays A1 and R1 are located in the River Black where smolts were tagged and released, arrays A2–A5 and R2–R4 are in the River Erriff, arrays A6 and A7 in the estuary, and arrays A8–A10 in the fjord.

Group	Tagged	A1/R1	A2/R2	A3	A4/R3	A5/R4	A6	A7	A8	A9	A10
2017A	40	17 (0)	—	12 (1)	12 (1)	11 (1)	12 (0)	12 (0)	11 (1)	12 (0)	12 (unk)
2018A	35	24 (0)	22 (0)	17 (5)	21 (0)	2 (18)	20 (0)	20 (0)	19 (0)	17 (1)	17 (unk)
2018R	30	9 (0)	7 (0)	—	7 (0)	7 (unk)	—	—	—	—	—

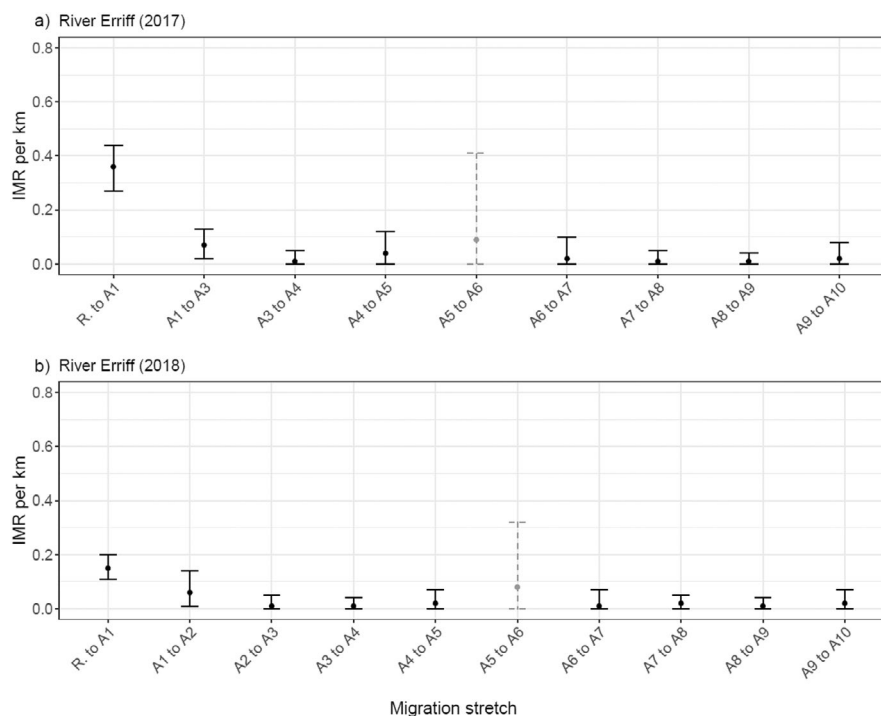


FIGURE 3 | Instantaneous mortality per km (Z) of Atlantic salmon (*Salmo salar*) smolts in migration stretches in the River Erriff and Killary Fjord, Republic of Ireland, in 2017 (a) 2018 (b). Points represent estimated Z with confidence intervals. Dashed grey lines indicate estimates for distances less than 500 m, which may be unreliable.

was high in the second stretch in 2018 ($\Phi_2 = 92\%$). A2 was not deployed in 2017, so apparent survival in the second stretch (Φ_2) was not comparable between 2017 ($\Phi_2 = A1-A3$) and 2018 ($\Phi_2 = A1-A2$). Apparent survival was high in 2017 in the estuary ($\Phi_5 = 97\%$; $\Phi_6 = 97\%$) and Killary Fjord ($\Phi_7 = 97\%$; $\Phi_8 = 96\%$) and in 2018 in remaining stretches in the River Erriff (Φ_3 to $\Phi_5 > 95\%$), the estuary ($\Phi_6 = 97\%$; $\Phi_7 = 98\%$) and Killary Fjord ($\Phi_8 = 95\%$; $\Phi_9 = 95\%$).

Cumulative survival from release to last river array (A5) was 31% in 2017 and 58% in 2018, while from release to mid-fjord array (A9), cumulative survival was 26% in 2017 and 47% in 2018. The Bayesian CJS model found that the effect of length on survival probability of smolts was unimportant ($\beta = 0.033$, CI: -0.25 to 0.35). Estimated apparent survival, delta, cumulative survival, detection probabilities and corresponding confidence intervals

are shown in Figure 2 and can also be found in Tables S1 and S2 in supplementary material.

Instantaneous mortality per km (Z) was highest in the first river stretch below release (Release to A1) in 2017 ($Z = 0.36$, CI: $0.27-0.44$) and 2018 ($Z = 0.15$, CI: $0.11-0.20$; Figure 3). In remaining stretches, Z ranged from 0.01 to 0.09 in 2017 and 0.01 to 0.08 in 2018.

In total, 26 of 40 acoustic-tagged smolts in 2017 (65%) and 20 of 29 radio-tagged smolts (excluding tagging-related mortality) in 2018 (67%) were lost to predation (Table 3). In 2017, 26 acoustic tags were not located by manual tracking or recorded on arrays, so were assumed to have been removed from the study area by terrestrial or avian predators. Two acoustic tags were stationary in deep in water in 2017, so were categorised

TABLE 3 | Sources of river mortality of acoustic- and radio-tagged Atlantic salmon (*Salmo salar*) smolts from active and passive tracking data in the River Black and River Erriff, Republic of Ireland. Data from 2018 acoustic tagging not shown because active acoustic tracking was not conducted this year. The percentage relative to the total number of tagged smolts is shown in parentheses.

Fate	Criteria	2017 Acoustic	2018 Radio
		<i>n</i> (%)	<i>n</i> (%)
Unknown Terrestrial or Avian Predation	Tag disappeared between the release site and final array and tag could not be located during active tracking	26 (65%)	2 (6.7%)
Otter or Mink Predation	Radio tag recovered from spraint; tag found with chew marks up on the riverbank; tag buried deep in brush adjacent to river but tag not recovered.	0 (0%)	15 (50%)
Heron Predation	Radio tag recovered below heron rookery or signal originating from heron nest.	0 (0%)	3 (10%)
Unknown River Mortality	Tag stationary in the channel for several days but water too deep for tag recovery.	2 (5%)	2 (6.7%)
Tagging Mortality	Dead fish with tag recovered with no signs of predation or wounds.	0 (0%)	1 (3.3%)
TOTAL		28 (70%)	23 (76.7%)

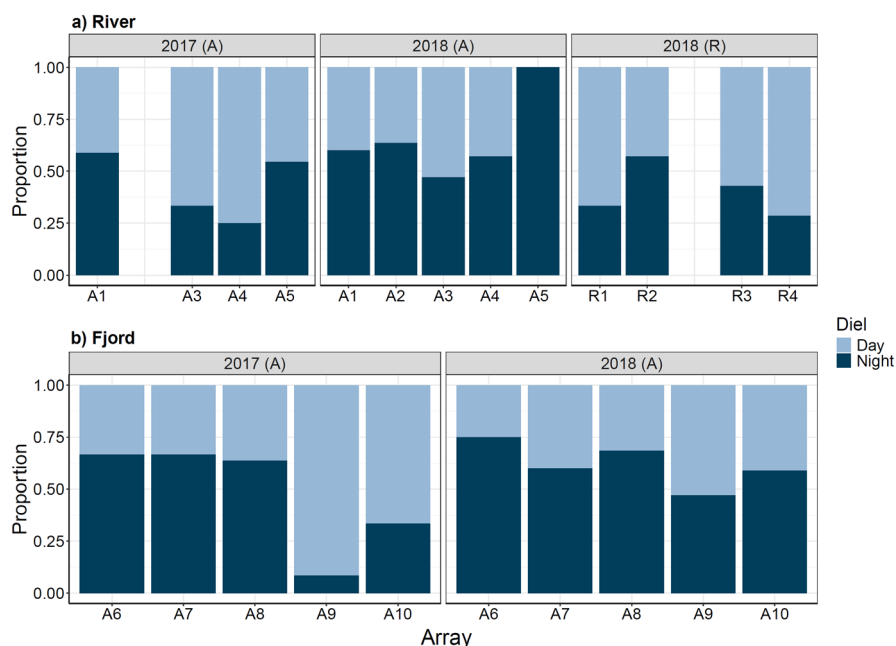


FIGURE 4 | Proportion of Atlantic salmon (*Salmo salar*) smolts arriving at arrays during day (light blue) and night (dark blue) in (a) the River Erriff and (b) Killary fjord, Republic of Ireland, 2017 and 2018. Smolts were tagged with acoustic tags in 2017 (2017 A) and 2018 (2018 A) and radio tags in 2018 (2018 R). Array A2 was not deployed in 2017. The order of radio arrays in 2018 (R) corresponds to closest acoustic arrays, with a blank space indicating the absence of a corresponding radio array for acoustic array A3.

as unknown river mortalities. In 2018, one radio-tagged smolt with an intact tag was recovered immediately downstream of the release site without visible marks of predation, so was classified as a tagging-related mortality. Of the remaining radio-tagged smolts in 2018, 24% (7/29) were detected on the last river array (R4), so were assumed to have completed their river migration. Eighteen radio tags were located within the immediate vicinity of the river during manual radio tracking. Of these, three were recovered on the ground under a large

heron rookery on a small island in the lough upstream of the release site, so were presumed to have been eaten by herons. Fifteen tags were attributed to otter or mink predation, 12 of which were recovered from the riverbank with chew marks (four in otter spraints) and 3 were buried deep in heavy bankside cover or brush and could not be recovered. Two radio tags were not located during manual tracking or on arrays and were assumed to have been removed from the water by terrestrial or avian predators. Two stationary radio tags could not be

recovered from deep water, so were categorised as unknown river mortalities.

In the river, the proportion of night arrivals by acoustic-tagged smolts at different arrays varied between 25% at A4 and 58% at A1 in 2017, and between 47% at A3 and 64% at A2 in 2018 (Figure 4). At array A5, only two smolts were detected in 2018, both arriving at night (Table 2). The proportion of night arrivals in the river by radio-tagged smolts in 2018 varied between 29% (R4) and 57% (R2). Diel patterns of smolts in the river did not differ significantly among groups ($\chi^2=3.74$, $df=2$, $p=0.15$) or arrays ($\chi^2=3.69$, $df=4$, $p=0.45$).

Acoustic-tagged smolts arrived at the first estuary array (A6) on average at 23:35 (SE=00:22) in 2017 and 00:17 in 2018 (SE=00:14; Figure 5a). Arrival times at A6 differed significantly from uniformity in 2017 ($U^2=0.21$, $0.025 < p < 0.05$) and 2018 ($U^2=0.35$, $p < 0.01$). More smolts entered the estuary on an ebb tide, with a mean entry time in the last quarter of the ebb tide (Figure 5b). Arrival times on the tidal cycle differed significantly from uniformity in 2017 ($U^2=0.19$, $0.025 < p < 0.05$) and 2018 ($U^2=0.27$, $p < 0.01$).

In Killary Fjord, the proportion of night arrivals was relatively high at arrays A6–A8 (64% at A8 and 67% at A6 and A7 in 2017; 60% at A7 and 75% at A6 in 2018; Figure 4). In contrast, the proportion of night arrivals was lower at the two most seaward arrays, particularly in 2017 (8% at A9 and 33% at A10; Figure 4; Figures S2–S4).

Overall, water levels were higher and fluctuated more in 2018 than in 2017 (Figure 6). The mean water level during the smolt run was significantly lower in 2017 (mean=0.15 m, SD=0.03) than in 2018 (mean=0.49 m, SD=0.46; $t=-4.30$, $df=33.3$, $p < 0.001$).

4 | Discussion

Smolt survival was lower in the River Erriff than Killary Fjord, likely because smolts must traverse a stretch of the River Black with a narrow, constricted bedrock cascade, thereby increasing

their vulnerability to predation. Predation can intensify in confined environments where structural elements favour prey capture (Mather 1998), such as in small streams (Aarestrup et al. 2005; Heggenes and Borgström 1988), swift currents (Roos 1959), shallow, narrow stream stretches (Almeida et al. 2012; Cho et al. 2009; Sortland et al. 2023), below lake outlets (Roos 1959) and in small restricted estuaries (Hvidsten and Møkkelgjerd 1987; Serrano et al. 2009). Higher predation downstream of the trap in our study could also indicate predator habituation to a consistent supply of smolts (Flávio et al. 2020), wherein predators learned to exploit the bedrock cascade as an optimal hunting location during the smolt run (Boulêtreau et al. 2018; Holling 1959; López-Bao et al. 2011). Our findings highlight that predation in small rivers and streams can be significant, especially where smolt movements are restricted by natural or man-made barriers. The high survival we found in the estuary contrasts with the high mortality often observed in estuaries and coastal areas near river mouths (Thorstad et al. 2012). However, widely ranging survival in estuaries among studies (Artero et al. 2023; Chaput et al. 2019; Halfyard et al. 2012, 2013; Lilly et al. 2022) suggests that survival likely depends on factors such as smolt fitness, local stressors, predator community, geography and physical conditions like salinity and turbidity (Chaput et al. 2019; Lilly et al. 2022; Thorstad et al. 2012). High survival in the estuary in our study could also be linked to smolt behaviour during migration.

Survival of acoustic-tagged smolts was lower in 2017 than 2018 in our study, perhaps because larger smolts had higher survival than small smolts (Flávio et al. 2021; Kallio-Nyberg et al. 2004; Gregory et al. 2019). In support of this theory, acoustic-tagged smolts were significantly larger in 2018 than in 2017. However, radio-tagged smolts were of similar size as acoustic-tagged smolts in 2018, but had the lowest river survival (24%). Furthermore, length was not related to survival probability of smolts, which suggests that smolt size did not influence survival in our study.

Tag burden can also affect smolt survival, with higher tag burden potentially reducing smolt survival (e.g., Bass et al. 2020;

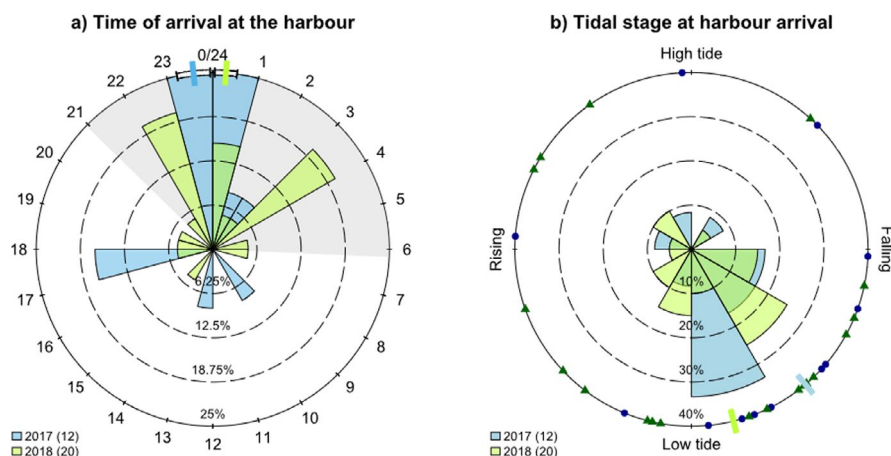


FIGURE 5 | Entry time by Atlantic salmon (*Salmo salar*) smolts into the estuary of Killary Fjord (a) and tidal stage at the time of entry into the estuary of Killary Fjord (b), Republic of Ireland, 2017 and 2018. The shaded portion of the circle shows average sunset-to-sunrise hours. Coloured lines on the outer circle indicate the mean number of salmon smolts in 2017 (blue) and 2018 (green), with ranges indicating the standard error of the mean (too small to be visible). Group bars sum to 100%. Blue circles and green triangles on the outer circle represent the exact point of entry by smolts in 2017 and 2018.

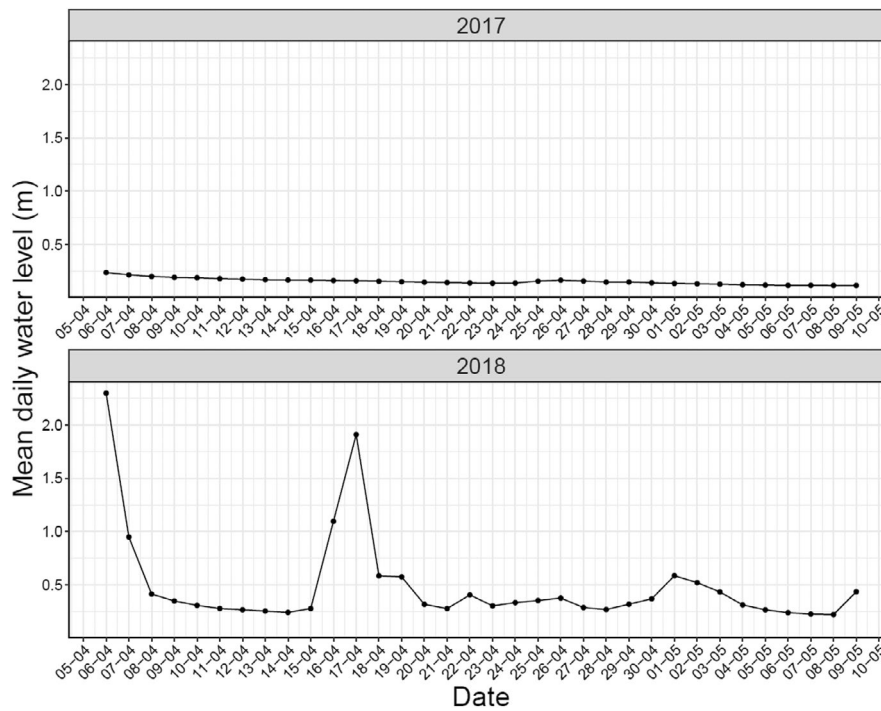


FIGURE 6 | Mean daily water levels (m) at the Derrinkee–Sandpit station in the River Erriff, Republic of Ireland, during April–May, 2017 and 2018.

Brown et al. 2010). However, tag burdens of acoustic-tagged smolts were similar in 2017 and 2018, so tag burden did not likely explain different survival between years. Additionally, radio-tagged smolts, which exhibited the lowest river survival, also had the lowest tag burden. Several other studies also reported no effect of higher tag burden on smolt survival (e.g., Lothian et al. 2024; Newton et al. 2016; Sortland, Jepsen et al. 2024), even up to 12.7% tag burden (Newton et al. 2016).

We found that most mortalities were due to terrestrial or avian predation, although acoustic telemetry could not identify specific predators. Radiotelemetry suggested otter or mink and herons were the most common predators. Herons and mink were frequently observed in the area, and otter spraints were scattered along the riparian zone, supporting our findings. This evidence aligns with previous research that found avian predators and mustelids consumed significant numbers of smolts (Aarestrup et al. 1999; Dolloff 1993; Flávio et al. 2020; Harris et al. 2008; Heggenes and Borgstrøm 1988; Jepsen, Flávio, and Koed 2019; Koed et al. 2002; Koed, Baktoft, and Bak 2006; Ruggles 1980). Our study highlights the benefits of using multiple tracking methods to identify factors limiting Atlantic salmon smolt survival (Chavarie et al. 2022; Flávio et al. 2021; Lennox et al. 2023; Sortland et al. 2023).

Smolts migrated during day and night in the river, unlike earlier studies that found smolts moved predominantly at night, likely to reduce predation risk (Flávio et al. 2020; Martin et al. 2009; Moore et al. 1995, 1998; Sortland, Jepsen et al. 2024). However, daytime migration can increase with higher temperatures and later in the season (Haraldstad et al. 2017; Ibbotson et al. 2006; Moore et al. 1995). The River Erriff has little riverbank vegetation to provide shade, so smolts in our study may have experienced

higher temperatures on bright days that prompted daytime migration. Smolts released in the morning could encourage daytime migration, although this was unlikely to have affected their behaviour beyond the initial river stretches. River spates prompted hatchery-reared salmon smolts to migrate regardless of light intensity or water temperature (Greenstreet 1992), so the observed variation in diel patterns may reflect smolts adaptively choosing to migrate during day or night, depending on a combination of factors, including predation risk, temperature, water flow and river topography (Thorstad et al. 2012).

Nocturnal migration was more prevalent in the estuary and fjord than in the river, with most acoustic-tagged smolts entering the estuary at night. The observed nocturnal migration might have been a strategy to avoid visual predators (Jepsen, Holthe, and Økland 2006; Solomon 1982), as smolts often suffer high mortality in estuaries due to predation (Halfyard et al. 2013; Hvidsten and Møkkelgjerd 1987; Jepsen, Holthe, and Økland 2006; Jepsen, Flávio, and Koed 2019; Koed, Baktoft, and Bak 2006; Thorstad et al. 2012; Vollset et al. 2016). Similarly, survival of smolts exiting the River Bush in Northern Ireland at night was significantly higher in a coastal bay than for smolts departing during the day (Flávio et al. 2020). In our study, daytime migration increased at the two most seaward arrays, which was consistent with previous findings that daytime migration tends to increase as smolts approach the sea and later in the migration season (Lacroix and McCurdy 1996; Moore et al. 1995; Sortland, Aarestrup and Birnie-Gauvin 2024). Increased daytime migration at fjord arrays in our study could have been due to (1) tidal influences facilitating or impeding migration at certain times of the day and night (ebb tide transport pattern; Moore et al. 1995, 1998); (2) foraging behaviour by salmonids that use visual cues to locate prey (Hansen et al. 2013); (3) smolts arriving later in

the year than in the river and estuary where increased photoperiod or higher temperatures could have prompted more daytime movements (Haraldstad et al. 2017; Sortland, Aarestrup and Birnie-Gauvin. 2024); or (4) smolts were more silvery, which potentially made daytime migration safer (Ibbotson et al. 2006).

Smolts entered the estuary during the last quarter of the ebb tide in our study, a pattern also documented in other studies (Lacroix, McCurdy, and Knox 2004; Lacroix and McCurdy 1996; Lefèvre et al. 2013; Lilly et al. 2022; Moore et al. 1995, 1998; Stich, Zydlewski, and Zydlewski 2016). Using ebb tide transportation may increase smolt survival by reducing energy expenditure and time spent in the estuary where predation rates can be high (Jepsen, Holthe, and Økland 2006; Mather 1998; Serrano et al. 2009; Thorstad et al. 2012). Moreover, the estuary likely had the highest amount of freshwater during the last quarter of the ebb tide, which could indicate that smolts preferred to migrate in low-salinity waters (Stich, Zydlewski, and Zydlewski 2016). Entering the estuary in low-salinity waters may have helped smolts to adjust to saltwater and decrease osmoregulatory stress, thereby improving survival (Gudjonsson, Jonsson, and Antonsson 2005; Halfyard et al. 2013). Therefore, smolts migrating at night and using ebb tide transportation could have contributed to the high estuary survival observed in this study.

Water levels were significantly lower in 2017 than in 2018 in our study, which could have made it easier for predators to capture smolts in shallow areas, because high water levels and turbidity reduce predator hunting success (Dodrill 2016; Martínez-Abraín et al. 2020; Wolff et al. 2016). Therefore, low survival of acoustic-tagged smolts in 2017 could have been due to low water levels that resulted in increased predation rates in the river. Despite higher water levels in 2018, radio-tagged smolts had lower river survival than acoustic-tagged smolts. Behavioural differences, such as nocturnal migration to avoid visual predators, can influence smolt survival (e.g., Ibbotson, Beaumont, and Pinder 2011; Vollset, Barlaup, and Normann 2017). However, we found no differences in diel patterns of smolts in the river to explain lower survival of acoustic-tagged smolts in 2017 and radio-tagged smolts in 2018 than acoustic-tagged in 2018. Low survival of radio-tagged smolts may be linked to later tagging and release than acoustic-tagged smolts in 2018. For example, fewer smolts may have migrated later in the season, which could have reduced predator swamping and increased individual predation risk (Furey et al. 2021). Overall, while acoustic-tagged smolts had higher survival in 2018 with higher water levels, radio-tagged smolts did not, which suggests that water levels alone did not influence survival.

In our study, most smolt mortalities were in the initial river stretch below the release point, where smolts could still have been affected by capturing, handling and tagging (Brown et al. 2006, 2010; Lacroix, Knox, and McCurdy 2004; Lennox et al. 2023). Predators typically target prey that are easier to catch, such as weak, injured or stressed individuals (Dallas et al. 2010; Jenkins, Mullen, and Brand 2004). Consequently, fish still recovering from handling and tagging could be more vulnerable to predation (e.g., Adams et al. 1998). Handling

and tagging do not always affect fish behaviour, survival or predation risk (e.g., Anglea et al. 2004; Jepsen, Christoffersen, and Munksgaard 2008; Lothian et al. 2024), and tagging procedures we used followed strict EU animal welfare guidelines, where smolts were allowed to fully recover before being released. Nevertheless, the potential impact of handling and tagging cannot be excluded, and our mortality estimates should be considered on the higher end of a likely range. To determine if high mortality rates were predominantly due to tagging or the bottleneck, future research should explore if bypassing the bottleneck improves smolt survival. Moreover, smolts are typically counted and released from the trap in the River Black in the morning, thereby exposing normally nocturnal migrating smolts to higher predation risks. Future studies should investigate if night-time releases improve survival of migrating smolts through high-risk areas (e.g., Vollset, Barlaup, and Normann 2017).

Telemetry is a valuable tool to track fish migrations, but not without certain risks. A primary concern is the possibility that a predator consumes a tagged fish, thereby leading to overestimating survival if such smolts are erroneously assigned as survivors (Daniels et al. 2019; Gibson et al. 2015; Klinard and Matley 2020). To mitigate this risk, we checked data for abnormality, such as upstream movement or smolts skipping arrays. However, if predator behaviour is not distinguishable from smolt behaviour, we could have incorrectly assigned fate of some smolts. In addition, tag shedding by smolts can lead to wrongly assigning live smolts as mortalities (Chavarie et al. 2022). This could have been the case for tags found on the river bottom, which were assigned as unknown river mortalities. However, tags are usually shed after a longer period (> 25 days; Brunson et al. 2019; Lacroix, Knox, and McCurdy 2004; Lawrence et al. 2023), and most smolts in our study completed their migration within a few weeks, so the impact of tag shedding on our results was likely minimal.

4.1 | Management Implications

Index rivers, like the River Erriff, play a central role in estimating marine survival by monitoring smolt output and subsequent adult returns, typically at the regional or national level. Smolt traps in many index rivers are located 100 m–40 km upstream from river mouths (Flávio et al. 2020). If unaccounted smolt mortalities occur between a trap and river mouth, as in our study, marine mortality will be overestimated (Flávio et al. 2020). Hence, addressing freshwater bottlenecks, which is often more feasible than challenges at sea, can benefit salmon populations by increasing the number of smolts reaching the sea (Thorstad et al. 2021) and improving the accuracy of marine survival estimates. Mortality at sea is generally considered density-independent, so increasing smolt output will likely result in increased numbers of returning adult (Crozier and Kennedy 1993; Jonsson, Jonsson, and Hansen 1998; Thorstad et al. 2012).

Potential management options to reduce predation pressure on migrating smolts in the River Black include scaring predators using visual or audible measures (Marsh et al. 1992; Vercauteren et al. 2010), predator exclusion by screening

(Gorenzel et al. 1994) and transporting smolts past the bottleneck (McCarthy et al. 2008; Park 1980). Predator removal has been used to preserve prey species (e.g., Hervieux et al. 2014; Makhado et al. 2009; Schultz et al. 2013). However, like salmon, several of the main predators in our study are protected species (the European otter is protected under the Habitats Directive; Council Directive 92/43/EEC, and all birds are protected under the Wildlife Act, 1976), and predator removal is often costly and ineffective (Lennox et al. 2018). Moreover, the bedrock cascade is a natural bottleneck supporting multiple species and complex predator–prey interactions. Understanding these predator–prey dynamics is essential to develop informed management strategies that account for predatory impact on prey species, like the Atlantic salmon, and wider ecosystem considerations.

Our findings demonstrated that trap-site selection needs to be considered in the context of local physical and ecological factors to maximise the accuracy of fish counts. To that end, in similar rivers, relocating a trap below a bottleneck could be beneficial by (1) preventing smolts from being handled before traversing the high-risk area and (2) providing more accurate smolt counts that improve estimates of marine survival. Determining the number of smolts that die before reaching the sea is vital to refine marine survival estimates and inform management of salmon populations.

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Ethics Statement

Project approved by Inland Fisheries ethics committee. Project tagging licence granted by Health Products Regulatory Authority Licence No. AE19118/P001

Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section.