Received: 4 May 2022 | Accepted: 17 August 2022
DOI: 10.1111/jfb.15200

REGULAR PAPER

JOURNAL OF FISH BIOLOGY fsbi

Investigating the behaviour of Atlantic salmon (*Salmo salar* L.) post-smolts during their early marine migration through the Clyde Marine Region

Jessie Lilly[1] | Hannele M. Honkanen[1] | David M. Bailey[2] | Colin W. Bean[3] | Ruaidhri Forrester[1] | Jessica R. Rodger[1] | Colin E. Adams[1]

[1]Scottish Centre for Ecology and the Natural Environment, IBAHCM, University of Glasgow, Glasgow, UK

[2]College of Medical, Veterinary & Life Sciences, Graham Kerr Building, University of Glasgow, Glasgow, UK

[3]NatureScot, Clydebank Business Park, Clydebank, UK

Correspondence
Jessie Lilly, Scottish Centre for Ecology and the Natural Environment, IBAHCM, University of Glasgow, Rowardennan, Loch Lomond, Glasgow G63 0AW, UK.
Email: j.lilly.1@research.gla.ac.uk

Funding information
Atlantic Salmon Trust; Interreg, Grant/Award Number: IVA5060; NatureScot

Abstract

It is thought that survival during migration is particularly poor for Atlantic salmon post-smolts immediately after entry into sea and particularly in the estuarine environment. Nonetheless, there is currently a lack of information on Atlantic salmon post-smolt movement behaviour in estuaries in the UK. This study used acoustic tagging to estimate loss rates and compare the behaviour of Atlantic salmon post-smolts migrating from two distinctly different rivers draining into the Clyde Estuary, the River Endrick ($n = 145$) and the Gryffe ($n = 102$). Contrary to most literature, post-smolts undertook rapid migrations through the estuary, potentially decreasing their exposure to predators/anthropogenic stressors and reducing their estimated loss rates (river: 1%–3% km^{-1}; estuary: 0.20%–0.60% km^{-1}). The low loss rates in the estuary occurred despite post-smolts engaging in passive reversal movements with the tide upon entering the estuary, possibly allowing them more time to adapt to the increased salinity. Atlantic salmon post-smolts from both the rivers used similar migration pathways exiting into the coastal marine zone during ebbing tide. This study provides novel information on the timing and migratory routes of Atlantic salmon post-smolts in the Clyde Estuary that can ultimately be used to inform management decisions on how to assess and reduce the potential impacts of current natural and anthropogenic stressors. Temporal repeatability of this study over multiple years is required to determine if there is variation in the factors driving the migratory patterns and loss rates of smolts in this system.

KEYWORDS
acoustic tags, Atlantic salmon, early marine migration, post-smolts, telemetry

1 | INTRODUCTION

Migration is the movement of animals between different habitats to reproduce and forage (Hendry *et al*., 2004). Diadromy is a migratory strategy that involves the predictable migration of fishes between freshwater and marine environments during certain life stages (Delgado & Ruzzante, 2020; McDowall, 2008). Anadromy is a form of diadromy where individuals spawn in fresh water and often return to the sea to feed (Quinn & Myers, 2004). The process of anadromy is costly as it requires both physiological and behavioural adaptations that increase the amount of stress experienced by a fish and ultimately their risk of exposure to both natural and anthropogenic threats (Crozier *et al*., 2004; Delgado & Ruzzante, 2020; Zydlewski *et al*., 2005).

The Atlantic salmon (*Salmo salar* L.) is a charismatic anadromous salmonid that in Northern Europe undergoes long-distance migrations during its first year at sea from its natal river to feeding grounds in the North-East Atlantic (Holm, 2000; Jacobsen *et al*., 2012; Mork *et al*., 2012; Ounsley *et al*., 2019). Currently, the Atlantic salmon is of high conservation interest due to diminishing numbers throughout their range (Gilbey *et al*., 2021; ICES, 2021). This decline has ultimately led to the categorization of Atlantic salmon as an Annex II species under the EU Habitats and Species Directive while in their freshwater habitat (Crozier *et al*., 2004; McLeod *et al*., 2005). This directive establishes a network of locations for conservation of threatened or at-risk species throughout Europe (McLeod *et al*., 2005). Despite considerable research aimed at understanding the freshwater migration of Atlantic salmon, the global decrease in Atlantic salmon is thought to be attributed to losses during marine migration (Parrish *et al*., 1998; Thorstad *et al*., 2012a).

A smolt can be defined as a salmonid that has undergone physiological changes in preparation for seawater entry (ICES, 2020; McCormick *et al*., 2013; Stich *et al*., 2015). In Scottish waters, the seaward migration of smolts is largely nocturnal and tends to coincide with periods of high-water discharge and water temperatures of *c*. 8°C. Smolt migration can be divided into passive and active movement. Passive movement can be defined as the displacement of an individual that is driven solely by water flow (Hedger *et al*., 2008). In contrast, smolts may engage in active movement by swimming which can influence the direction and rate of displacement (Finstad *et al*., 2005; Hedger *et al*., 2008). During their downstream riverine migration smolts have been reported to orientate towards and migrate at similar speeds to the prevailing current, suggesting that migration towards the estuarine environment is a passive process (Martin *et al*., 2009; Davidsen *et al*., 2005). Once smolts transition from their natal river to the estuary they are then referred to as post-smolts (Chaput *et al*., 2019).

In general, the estimated mortality rates of post-smolts in the estuarine environment have been reported to be higher than those during both their freshwater and early marine migration (Kocik *et al*., 2009; Lacroix, 2008; Thorstad *et al*., 2012b). The few studies that have estimated estuarine mortality have reported that the highest losses occur as smolts enter the estuary (Jepsen *et al*., 2006; Davidsen *et al*., 2009; Shephard & Gargan, 2021). This may be attributed to smolts not being physiologically prepared to avoid novel anthropogenic and natural stressors, such as fisheries (Holm *et al*., 2006), aquaculture farms (Shephard & Gargan, 2021) and predators (Dieperink *et al*., 2002; Handeland *et al*., 1996). Upon entering the estuary, post-smolts may require an acclimatization period to adapt to the increased salinity (Dempson *et al*., 2011; Handeland *et al*., 1996; Kocik *et al*., 2009). This acclimatization period is particularly evident for smaller post-smolts, as they have reduced osmoregulatory capabilities (Handeland *et al*., 1996; Hedger *et al*., 2011). This acclimatization period has been reported to last between 4 and 6 days and is characterized by passive downstream-upstream movements (defined as reversals) with the tide near the freshwater outlet (Halfyard *et al*., 2013; Kocik *et al*., 2009).

After this period, post-smolts transition to more saline environments where they have been reported to shift from passive to active swimming towards the estuarine outlet (Davidsen *et al*., 2009; Hedger *et al*., 2008; Lacroix & McCurdy, 1996; Martin *et al*., 2009). Some studies have reported that during this active migration period, post-smolts remain relatively stationary during the day, then shift to active migration during the night, leaving the estuary on an ebb tide (Hedger *et al*., 2008; Martin *et al*., 2009; Moore *et al*., 1998). The variation in diurnal behaviour may be related to foraging and predator avoidance (Fiske *et al*., 2020; Hedger *et al*., 2008). Post-smolts are visual predators that feed throughout their early marine migration and may use the light during the day to detect prey (Andreassen *et al*., 2001; Hedger *et al*., 2008; Kadri *et al*.,1997). Furthermore, migrating towards the marine environment during the night is thought to reduce the risk of being detected by predators (Lefévre *et al*., 2011).

Research investigating the specific components of their migration pathway where post-smolts are most vulnerable is essential to determine the potential mechanisms of population decline, and thus aid management decisions for the species (ICES, 2020). In this study the authors used acoustic tracking technology to monitor the movement of Atlantic salmon post-smolts from two distinctly different river systems draining into the Inner Clyde Estuary: the River Endrick and the River Gryffe in west-central Scotland. The Inner Clyde Estuary is part of the Clyde Marine Region, which also consists of the Outer Clyde Estuary and the Firth of Clyde (Marine Scotland, 2015; Figure 1; see Methods).

The River Endrick is of particular interest as it has been classified as a special area of conservation (SAC) due to important populations of brook lamprey [*Lampetra planeri* (Bloch, 1784)], river lamprey [*Lampetra fluviatillis (Linnaeus, 1758)*] and Atlantic salmon (JNCC/Joint Nature Conservation Committee, 2019). Prior to reaching the Inner Clyde Estuary, smolts migrating out of the River Endrick must travel a minimum total distance of *c*. 30 km through the Loch Lomond catchment (Honkanen *et al*., 2018), navigating through the largest freshwater body in Britain (Loch Lomond) and the River Leven (Maitland *et al*., 2000). Acoustic telemetry studies conducted in the Loch Lomond catchment have reported that smolts undertake very indirect migration routes, and survival rates during migration through the loch are extremely low (50%–57%; Honkanen *et al*., 2018; Lilly *et al*., 2021). The low survival rates are thought to be attributed to the increased energy expended while navigating through this region, which may increase the risk of predation (Honkanen *et al*., 2018). Previous studies have indicated that transporting salmonid smolts around migratory barriers increases their likelihood of reaching the estuary (Rechisky *et al*., 2012). To test whether high loss rates in the River Endrick and Loch Lomond could be mitigated, in this study, a small proportion of Atlantic salmon smolts captured and tagged from the River Endrick were transported and released in the upper River Leven, the river which connects Loch Lomond and the estuary (Figure 1). Lastly, in comparison to the Loch Lomond catchment,

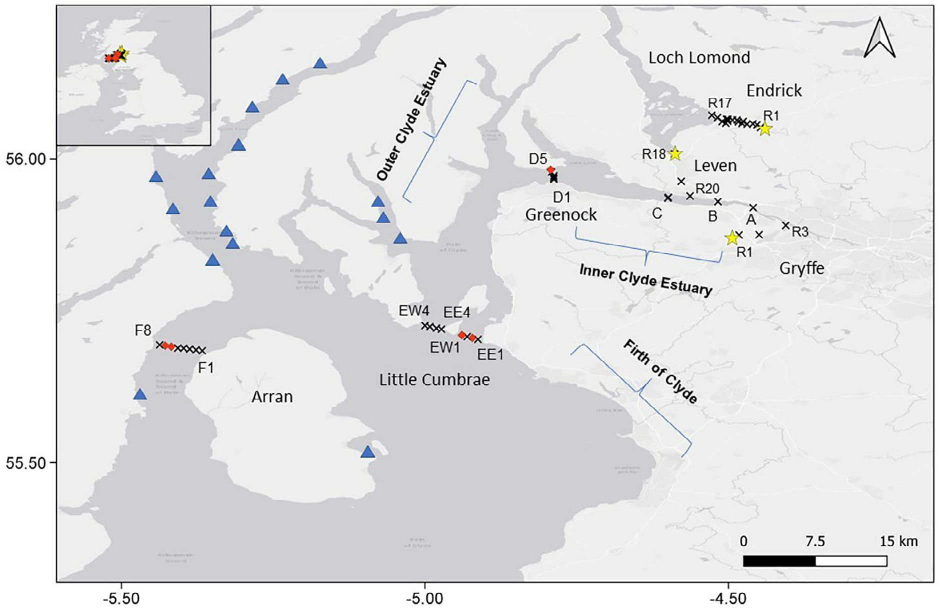

FIGURE 1 Map of acoustic receivers deployed (black crosses) within the Clyde Marine Region (Inner Clyde Estuary, Outer Clyde Estuary, Firth of Clyde), and rivers draining into Loch Lomond (River Endrick) as well as the Clyde Estuary (River Leven, River Gryffe). The red diamonds represent receivers that were not retrieved, and the yellow stars represent locations where Atlantic salmon smolts were released in this study (River Endrick: $n = 98$, lat. 56.0492, long. -4.43991; River Leven: $n = 47$, lat. 56.00761°, long. -4.58749°; River Gryffe: $n = 102$; 55.8693°, long. -4.49366°). The blue triangles depict the locations of operational fish farms ($n = 16$) in the Clyde Marine Region (Marine Scotland, 2022)

the River Gryffe has limited obstructions to smolt migration. The abundance of Atlantic salmon smolts in the River Gryffe is currently unknown. However, due to the absence of a lake it was hypothesized that the freshwater mortality rate of migrating River Gryffe smolts would be lower than for River Endrick smolts.

The main contemporary threats to Atlantic salmon migrating through the Clyde Marine Region include the development of fish farms and predation. Scotland is the second-largest producer of farmed salmon in Europe, with net pen production occurring along the western coast of Scotland (Tett *et al*., 2018; Whitmarsh & Wattage, 2006). Currently, in the Clyde Marine Region (Figure 1) there are active fish farms sites ($n = 16$), located on the east and west coasts of Arran ($n = 2$) as well in two adjoining sea lochs ($n = 14$), with plans to develop more in the coming years (Marine Scotland, 2022; Figure 1). One of the main concerns with fish farms is that the high density of farmed salmon contained in pens can enhance local populations of parasitic sea lice (*Lepeophtheirus salmonis* (Kroyer, 1837) (Todd *et al*., 2006), which are known to cause osmotic stress and mortality in post-smolts migrating in coastal zones (Finstad *et al*., 2000; Shephard & Gargan, 2021; Susdorf *et al*., 2018).

Another concern is that there are a number of predators of salmon smolts in the Clyde Estuary, including grey seals (*Halichoerus grypus* Fabricius, 1791), common seals (*Phoca vitulina* Linnaeus, 1758), common dolphin (*Delphinus delphis* Linnaeus, 1758) and dogfishes (spurdog (*Squalus acanthias* Linnaeus, 1758); lesser spotted dogfish (*Scyliorhinus canicula* Linnaeus, 1758) as well as a variety of seabird species including cormorants (*Phalacrocorax carbo sinensis*) and herring gulls (*Larus argentatus*) that migrate to the region each spring to breed (Dieperink *et al*., 2002; Gosch *et al*., 2014; Halls-Spencer, 2001; Morgan *et al*., 1986). However the extent to which these predators impact populations of Atlantic salmon in Scottish estuaries remains unknown.

The overall purpose of this study was to elucidate the behaviour of Atlantic salmon post-smolts in the Inner and Outer Clyde Estuary (Figure 1). This study had three main objectives; the first objective was to compare the freshwater and estuarine loss rates of Atlantic salmon smolts emigrating from the Rivers Endrick and Gryffe and to test whether individual characteristics of the fish influenced survival. We had two main hypotheses regarding estuarine loss: (a) estuarine loss rate would be higher than that of fresh water, and within the estuary the loss rate would be highest in the inner reaches, and (b) estuarine loss would be dependent on post-smolt size with larger post-smolts having a higher likelihood of completing a successful migration.

The second main objective of this study was to examine the environmental drivers of the movement of smolts through the Inner and Outer Clyde Estuary. Our two main pathway hypothesis were: (a) that, consistent with previous estuarine studies, post-smolts would engage in passive reversal movements with the tide in the Inner Clyde Estuary (Halfyard *et al*., 2017; Martin *et al*., 2009) and (b) as their migration progresses towards the Outer Clyde Estuary (Figure 1) post-smolts would engage in faster more unidirectional migrations towards the estuarine outlet, travelling primarily during the night (Hedger *et al*., 2008). The last and third objective of this study was to determine the main migratory pathways of post-smolts in the Clyde Marine Region and compare the migratory patterns of smolts from two different river systems. This information will inform management of the potential overlap between Atlantic salmon post-smolts and anthropogenic stressors during their spring migration.

2 | MATERIALS AND METHODS

2.1 | Description of study area

2.1.1 | Clyde Marine Region

The Clyde Marine Region is located on the west coast of Scotland and is composed of the Clyde Estuary (Inner and Outer Clyde Estuary) and

Firth of Clyde (Marine Scotland, 2015). The Firth of Clyde is the most southerly fjord in the North Atlantic, and it extends *c.* 100 km into the Scottish coast (Karunarathna, 2010; Thurstan & Roberts, 2010; Figure 1). The Firth of Clyde system is heavily influenced by semidiurnal tides of up to 3 m (Bekic *et al.*, 2006). Draining into the Firth of Clyde is the Clyde Estuary, where the inner estuary extends for *c.* 40 km between the town of Greenock and the tidal weir in Glasgow, whereas the outer estuary extends *c.* 30 km between Greenock and Cumbrae (Figure 1). The Inner Clyde Estuary has been extensively modified through dredging over the past few centuries to allow for shipping and navigation: modifying it from a relatively shallow and narrow estuary in the 17th century to a more open fjordic embayment (Bekic *et al.*, 2006; Karunarathna, 2010; Pye & Blott, 2014; Sabatino *et al.*, 2017). Six rivers (Rivers Clyde, Kelvin, White Cart, Black Cart, Gryffe and Leven) supply the main freshwater input to the Clyde Estuary, and the long-term average river inflow is *c.* 110 m^3 s^{-1} (Bekic *et al.*, 2006; Karunarathna, 2010).

2.2 | Fish capture and tagging

Between 15 April and 4 May 2021, 145 Atlantic salmon smolts were captured in a rotary screw trap in the River Endrick located 12.7 km upstream of its confluence with Loch Lomond, and a minimum distance of *c.* 30 km from the Inner Clyde Estuary (lat. 56.0492°, long. –4.43991°; Figure 1; Honkanen *et al.*, 2018). Similarly, between 12 and 19 April 2021, 102 Atlantic salmon smolts were captured in a rotary screw trap in the River Gryffe located 8.4 km upstream of its confluence with the Inner Clyde Estuary (lat. 55.8693°, long. −4.49366°; Figure 1). Only smolts greater than 130 mm fork length (FL) and 20 g mass were tagged with V7-2L acoustic tags (Innovasea). These tags have a length of 20 mm and weight of 1.6 g in air. Tags were programmed to emit a signal of 69 kHz at 137 dB every 18–38 s giving tags a lifespan of 75 days. Prior to tagging, smolts were anaesthetized in 0.1 g l^{-1} of tricaine methanesulfonate (MS222) buffered with 0.1 g l^{-1} of sodium bicarbonate. Once smolts entered stage three of anaesthesia (loss of equilibrium), they were measured for weight (g) and length (FL, mm). Using a scalpel, an incision of *c.*10 mm was made in the ventral abdominal wall, anterior to the pelvic girdle and the V7-2L–coded transmitter inserted into the peritoneal cavity. During surgery the smolts' gills were washed with a low dose of MS222 and river water to ensure they were supplied with oxygen and remained sedated. Sutures were closed using two interrupted surgeon knots with 4/0 Ethilon nylon sutures. Smolts were then placed into a recovery tank until they retained equilibrium and exhibited normal swimming behaviour, and then transferred into a container in the river with free-flowing water for *c.* 45 min before being released.

Atlantic salmon smolts from the River Endrick were released at two locations: 99 were released 10 m below the River Endrick trap (dates: 15 April–4 May 2021; lat. 56.0492, long. -4.43991), whereas 46 were transported and released into the upper reaches of the River Leven (*c.* 170 m downstream from the first deployed receiver) into which Loch Lomond discharges (dates: 23–30 April; lat. 56.00761°, long. −4.58749°). A maximum of five smolts were placed into a single fish transport bag containing *c.* 5 l of water infused with pure oxygen and sealed using cable ties. The transport bags were then placed in a large black bucket and secured at the back of the transport vehicle. The average travel duration from the River Endrick smolt trap to the River Leven release site was *c.* 30 min. Once at the River Leven release site, the smolts were placed into an in-river recovery container for *c.* 45 min prior to release. For this paper, smolts released from the River Endrick and River Leven are referred to as River Endrick release, and River Leven release smolts, respectively. Both release groups combined are referred to as River Endrick combined smolts. Data from River Endrick and Leven smolts were combined for estuarine analyses as they originated from the same population and displayed similar rates of survival and migratory behaviour within the estuary. Atlantic salmon smolts from the River Gryffe were released at only one location, 10 m below the River Gryffe trap (dates: 12 April–24 May 2021; lat. 55.86952°, long. −4.49497°).

2.3 | Acoustic receiver deployment

For the purpose of analysing smolt movement through different habitats, the authors divided the study area into three separate ecological zones: the freshwater zone, estuarine zone and coastal marine zone (Kocik *et al.*, 2009). The freshwater zone included all freshwater habitats; the estuarine zone (Clyde Estuary) was divided into two subzones: the inner (Inner Clyde Estuary) and outer estuary (Outer Clyde Estuary); and lastly, the coastal marine zone consisted of the Firth of Clyde (Figure 1). Receivers deployed in the freshwater zone ($n = 23$) included those deployed in the Loch Lomond catchment [River Endrick ($n = 17$; VR2W, $n = 4$ and VR2Tx, $n = 13$; Figure 1 R1–R17) and Leven ($n = 3$; VR2W, $n = 2$ and VR2Tx, $n = 1$; Figure 1, R18–R20)] and River Gryffe ($n = 3$; VR2W, $n = 2$, VR2Tx, $n = 1$; Figure 1, R1–R3), and comprised VR2W and VR2Tx receivers [Figure 1; see Lilly *et al.* (2021) for a description of acoustic receiver types]. Acoustic receivers used in this study have been reported to have a detection efficiency of *c.* 80%–90% at distances of up to 200 m in riverine and estuarine environments (Honkanen *et al.*, 2020). Receivers deployed at the entrance and exit of each section of the freshwater zone spanned distances ranging from 52 m at the exit of the River Endrick to 153 m at the exit of the River Gryffe, suggesting that receiver range would cover the full width of the river. Acoustic receivers were deployed in the River Endrick, River Leven and River Gryffe during 1 April to 5 July, 16 March to 5 July and 16 March to 20 July, respectively.

In the estuarine and coastal marine zones receiver sites were labelled in alphabetical order based on decreasing longitude (Figure 1). Receivers located adjacent to one another at the same site, providing full shore-to-shore coverage, were referred to as monitoring lines, whereas sites with a single receiver were referred to as monitoring nodes (Kocik *et al.*, 2009). In the estuarine zone, 18 acoustic receivers (VR2W, $n = 1$; VR2Tx, $n = 7$ and VR2Ar, $n = 10$) were deployed in the inner and outer estuary, during 10 April to 30 July. This consisted of a monitoring line of five receivers deployed off the coast of

Greenock, excluding D5 which could not be retrieved at the end of the study (Figure 1, D1–D5), which allowed the authors to estimate the number of smolts transitioning from the inner to the outer estuary. Furthermore, to estimate the number of post-smolts transitioning from the estuarine zone (Outer Clyde Estuary) to the coastal marine zone (Firth of Clyde), four VR2Ars were deployed on the east and west coasts of Little Cumbrae (line E), forming monitoring lines EE (EE1–EE4) and EW (EW1–EW4), respectively (Figure 1). The authors were unable to retrieve two VR2ARs on the east coast of Little Cumbrae (EE4, EE2). Lastly, in the coastal marine zone, eight VR2ARs were deployed during 10 April to 30 July 2021 in Kilbrannan Sound located off the west coast of Arran, forming monitoring line F (Figure 1). They were unable to retrieve two VR2ARs in Kilbrannan Sound (F6, F7).

2.4 | Statistical analysis

2.4.1 | False detections

All analyses in this study were conducted using R version 3.5.3 (R Core Team, 2019). Prior to data analysis, false detections were removed. Detection data were filtered for false detections using the short-interval criterion in the R package GLATOS (Holbrook *et al*., 2018; Pincock, 2012). The short interval criterion was defined as a single detection that occurred at one receiver within a duration greater than 30 times the average signal delay (14 min) of the tag (Hayden *et al*., 2016; Kneebone *et al*., 2014; Lilly *et al*., 2021). In addition, consecutive detections that occurred during a duration less than the tag's minimum signal delay (18 s) were removed from the data set (Hanssen *et al*., 2021). In total, 0.16% (n = 2151) of detections (n = 1,332,256) were considered false. Therefore, 1,330,095 detections were used for analyses.

2.5 | Loss estimates

To determine regions that may pose the most risk to migrating salmonids, the authors assessed the likelihood of smolts migrating through receiver regions in the freshwater zone and past monitoring nodes/points in the estuarine zone. In this study a successful migrant was considered as a smolt that migrated through the freshwater and/or the estuarine zone. Receiver regions in the freshwater zone included the River Endrick, River Leven and the River Gryffe. Monitoring points and nodes in the estuary included nodes and lines A, B and C, D, E (EW, EE combined; Figure 1), respectively. Nonetheless, the detection efficiency of acoustic telemetry is not always 100%, and therefore it must be assessed when providing estimates of survival (Halfyard *et al*., 2013). Receiver efficiency in the freshwater zone was assessed for the final River Endrick receiver (Figure 1, R17) as well as for the receivers deployed in the River Leven (Figure 1, R18–R19) and Gryffe (Figure 1, R1–R2; excluding the final freshwater receivers) by calculating the proportion of smolts detected at a downstream receiver that were not detected at the prior upstream receiver (Chavarie *et al*., 2021). Lastly, receiver efficiency in the estuarine zone was calculated using a mark-recapture model as discussed next (Halfyard *et al*., 2013).

2.6 | Mark-recapture model

Cormack Jolly Seber mark-recapture models (CJS) for live recaptures (Cormack, 1964; Jolly, 1965; Larocque *et al*., 2020; Seber, 1965) have been used in acoustic telemetry to estimate both migration success (S) of the target species and the detection efficiency of acoustic receivers (p) (Halfyard *et al*., 2013; Kocik *et al*., 2009; Larocque *et al*., 2020). Here CJS models (logit-link) were fitted, using maximum likelihood estimation, to determine the apparent success of River Endrick combined and River Gryffe post-smolts past monitoring lines in the estuarine zone using the RMark package (Laake, 2013) in R, which is based on the MARK programme (White & Burnham, 1999). Detection efficiency (p) is calculated as the percentage of post-smolts detected at a monitoring line that were missed on the previous. Sites used for this analysis included the last freshwater receiver (release site), as well as monitoring lines C, D and E (EW and EE combined) (Figure 1). Unfortunately, p could not be estimated at monitoring line E (Figure 1) as there were no monitoring lines beyond this point. CJS models were fitted separately for River Endrick combined and Gryffe post-smolts as River Gryffe post-smolts had a farther distance to travel to reach the first monitoring line (Figure 1, D) in comparison to River Endrick combined post-smolts.

The additional covariates included in the model assessing the probability of migration success included release site (for River Endrick combined only), monitoring line (C,D,E), FL and to test for potential tagging effects on survival tag burden was included (Halfyard *et al*., 2013). Monitoring line (C,D,E) was the only covariate tested against detection efficiency (p) (Larocque *et al*., 2020).

Goodness of fit of the global model ($\hat{c}$) was tested prior to model selection using the bootstrapping method (n = 1000 simulations) to calculate the overdispersion parameter of the global model as discussed in Laroque *et al*. (2020). For the River Endrick combined model, the estimated quasi-likelihood overdispersion parameter was greater than one (1.13); therefore, overdispersion parameters were adjusted and the quasi-likelihood AIC was calculated for each candidate model (Halfyard *et al*., 2013). Models were then ranked according to their QAIC values, and the optimal model was identified as the model that had the lowest QAIC value and the highest model weight (Gibson *et al*., 2015).

2.7 | Estuarine movement

2.7.1 | Space use

The number of Atlantic salmon post-smolts detected at each receiver in the estuarine zone was overlaid on a map to determine if they exhibited preferred migratory routes through this region. χ^2 tests were then used to (a) determine if the distribution of post-smolts detected at monitoring lines D and E (Figure 1) differed between the River Endrick combined and River Gryffe post-smolts and (b) determine if there was a significant difference between the number of post-smolts from each river detected at each receiver on monitoring lines D and E (Figure 1).

2.8 | Non-residency events

To determine the number of movements of post-smolts between monitoring points and lines in the estuarine zone, non-residency events were calculated using the RunResidenceExtraction function in the VTrack package in R (Campbell, 2012). A non-residency event is the movement of a post-smolt from one monitoring point/line to the next. For the purposes of this analysis, monitoring locations in the estuarine zone included points A and B as well as lines C, D and E. (Figure 1). In addition, monitoring line F in the coastal marine zone was included to determine the amount of post-smolts migrating to the west of Arran (Figure 1, F). Westward movements between monitoring points/lines were categorized as forward, and eastward as reversals. Reversal movements were minimum estimates and ranged in distance from 3.66 (Figue 1, B to A) to 32.50 km (Figure 1, E to D).

2.9 | Environmental factors influencing non-resident events

Circular statistics were used to assess whether the hour of the day or tidal cycle influenced initiation of movements by post-smolts within and out of the estuarine zone. To determine if post-smolt movements were influenced by the time of day, the timing of backward and forward movements was converted to degrees using R packages circular (Lund & Agostinelli, 2018) with 0° reflecting midnight and 180° reflecting noon (Murray *et al*., 2018). The Rayleigh test of uniformity was used to test whether the timing of movements within, and exit from, the estuarine zone was random or directed towards a specific time of day (Murray *et al*., 2018). Lastly, movements during each hour of the day were visualized using circular rose diagrams (Murray *et al*., 2018). The variation in sunrise and sunset periods for the duration of forward and backward movements was calculated using the getSunlightTimes function in the R package suncalc (time zone: Europe/London; Thieurmel & Elmarhraoui, 2019) and plotted on the rose diagrams to help depict daytime and night-time hours.

Water-level data from the inner and outer estuary was obtained (1 April to 1 August; 15-min increments) from the Greenock (lat. 55.95, long. −4.77) and Millport (lat. 55.74, long. −4.93) stations, respectively [UK Hydrographic Office (UKHO)]. The function TidalCharacteristics in the R package Tides (Cox & Schepers, 2018) was used to calculate the characteristics of the tidal water levels observed at each station, including the tide maxima and minima that occurred once in each tidal period. To enable the use of circular statistics, each tidal period was converted to degrees, with low tide represented as 0° and high tide as 180°. Because the tidal height data were represented in 15-min periods, the timestamps when post-smolts engaged in forward or backward movements were also rounded to the nearest 15-min period. These were then converted to degrees based on their time difference from low (0°) or high (180°) tide for the specific tidal period in which they occurred. Consistent with the time of day analysis, Rayleigh's test of uniformity was then used to test whether the timing of forward and backward movements was directed towards a specific tidal state, and movements during each tidal state were visualized using circular rose diagrams (Murray *et al*., 2018).

2.10 | Ethical statement

The care and tagging of Atlantic salmon smolts complied with UK Home Office regulated procedures as approved by UK Home Office licence number PP0483054.

3 | RESULTS

3.1 | Tagging summary

In total, 247 Atlantic salmon smolts were tagged in two river systems draining into the Clyde Estuary, the River Endrick and Gryffe. The average FL and weight of Atlantic salmon smolts tagged in the River Endrick ($n = 145$) were 143.31 ± 0.80 mm (range: 130–174) and 29.80 ± 0.51 g (range: 21.60–49.20), respectively. The average FL and weight of Atlantic salmon smolts tagged in the River Gryffe were 149.20 ± 1.00 mm (range: 132–183) and 34.05 ± 0.66 g (range: 22.70–54.50), respectively.

3.2 | Freshwater zone loss

The final River Endrick receiver successfully detected all smolts detected on the initial River Leven receiver (Table A1, A17; 100% efficiency). However, the efficiency of the initial River Leven receiver (Figure 1, R18) was low, only detecting 70% ($n = 23$) of River Endrick release smolts that were detected on the nearest downstream receiver. Efficiency estimates for the final River Leven (Table A1, R20) and Gryffe receiver (Table A1, R3) could not be estimated.

Of the 99 smolts tagged and released in the River Endrick, 78% ($n = 77$) were estimated to have failed to complete a successful migration through the freshwater zone. In addition, despite accounting for the reduced detection efficiency of the initial River Leven receiver (Table A1), smolts that were transported and released at the River Leven still had a higher overall estimated loss rate through the River Leven ($n = 18$; 3.32% km^{-1}; Table 1) than those released from the River Endrick ($n = 11$; 2.83% km^{-1}). Lastly, the overall loss rate of smolts in the River Gryffe (1.08% km^{-1}) migrating through the

TABLE 1 The percentage of Atlantic salmon smolts captured and tagged in the River Endrick and River Gryffe that were detected at key regions (freshwater zone) and monitoring points/lines (estuarine zone) in this study (Figure 1)

			Endrick (total = 99)		Leven (total = 46)		Combined (total = 145)		Gryffe (total = 102)	
Receiver loc.	**Dist Endrick (km)**	**Dist Gryffe (km)**	**Loss rate % (n)**	**Loss km^{-1} (%)**	**Loss rate % (n)**	**Loss km^{-1} (%)**	**Loss rate % (n)**	**Loss km^{-1} (%)**	**Loss rate % (n)**	**Loss km^{-1} (%)**
Endrick	12.70	-	24 (24)	1.91	-		-	-	-	-
Lomond	9.75	-	69 (52)	7.11	-	-	-	-	-	-
Leven	11.77	-	4 (1)	0.37	39 (18)	3.32	28 (19)	2.34	-	-
LL catchment	34.22	-	78 (77)	2.27	-	-	-	-	-	-
Gryffe	-	8.14	-		-		-		9 (9)	1.08
A	-	4.87	-	-	-	-	-	-	2(2)	0.41
B	-	4.04	-	-	-	-	-	-	1(1)	0.27
C	2.30	5.22	14 (3)	5.93	25 (7)	10.87	20 (10)	8.70	15(16)	3.07
D	12.26	12.26	21 (4)	1.72	0 (0)	0	10 (4)	0.82	6 (5)	0.49
E	33.43	33.43	15(15)	0	0 (0)	0	0 (0)	0 (0)	0(0)	0(0)
Clyde Estuary	47.99	60.59	32(7)	0.67	21(6)	0.45	28(14)	0.58	11 (10)	0.18

Notes. For assessing freshwater zone loss rates, the Loch Lomond catchment was subdivided into three sections (River Endrick, Loch Lomond, River Leven). The freshwater zone loss of River Gryffe smolts was assessed based on whether they were detected on the final River Gryffe receiver. Early estuarine zone loss was based on the number of post-smolts detected at monitoring points/lines in the Clyde Estuary (Figure 1, A–E). Lastly, an overall minimum estimate of loss was given for the freshwater zone (Loch Lomond Catchment; River Endrick release only) and estuarine zone (Est; Clyde Estuary; see Methods for zone descriptions).

freshwater environment was substantially lower than both River Endrick and River Leven release smolts (Table 1).

3.3 | Estuarine zone loss

In contrast to the freshwater zone, the overall difference in loss rate between River Endrick (0.67% km^{-1}) and River Leven smolts (0.45% km^{-1}) was small (0.22% km^{-1}), and slightly lower for River Leven smolts (Table 1). After the data from both groups were combined, the total proportion of unsuccessful River Endrick combined migrants in the estuarine zone (28%) was lower than that in the freshwater zone (66%; Table 1) In addition, although the overall loss rate of River Endrick and Leven smolts in the freshwater zone was 2.27 and 3.32% km^{-1}, respectively, it did not exceed 1% km^{-1} in the estuarine zone (Table 1). Loss rate appeared to decline with the distance River Endrick combined post-smolts travelled in the estuarine zone (Table 1). Mortality estimates were initially high, at 8.70% km^{-1} during the first few kilometres of their estuarine migration but then drastically declined as their migration progressed reaching 0% km^{-1} between monitoring lines D and E (Figures 1 and 2; Table 1).

For River Gryffe smolts there was little difference between overall freshwater (9%) and estuarine zone loss (11%; Table 1). However, as the two zones are vastly different in terms of migration travel distance, the loss rate in the estuarine zone (0.18% km^{-1}) was six times lower than that in the freshwater zone (1.08% km^{-1}; Table 1). Consistent with River Endrick combined post-smolts, the highest rate of loss for River Gryffe post-smolts occurred within a few kilometres prior to monitoring line C (Table 1; B to C: 5.22 km, 3.07% smolts km^{-1}) and then declined to 0% smolts km^{-1} between monitoring lines D and E (Table 1).

3.4 | Capture-mark-recapture model

For River Endrick combined and Gryffe post-smolts, migration success through the estuarine zone was not dependent on FL, tag burden, release site or receiver location. The best fitting model for both rivers suggested that there was no difference in survival between monitoring lines and that detection probability was similar among consecutive monitoring lines (Table 2). The model-averaged migration success of post-smolts from the River Endrick and Gryffe between monitoring lines in the estuarine zone was estimated to be 96% (CI: 88%–99%) and 98% (CI: 94%–99%), respectively; and the average detection probability of post-smolts from the River Endrick combined and River Gryffe at monitoring lines in the estuarine zone was estimated to be 82% (CI: 73%–89%) and 85% (CI: 80%–90%), respectively (Table 2).

3.5 | Migratory speed

On average it took River Endrick release smolts 15.99 ± 7.07 (± S.D.) days to migrate through the entire freshwater zone (minimum distance: 34.22 km). Loch migration was substantially slower than riverine migration for River Endrick release smolts. Migratory speed was calculated by dividing the minimum distance a smolt could travel to migrate downstream, divided by the duration of migration. Therefore, successful Loch migrants (n = 23) travelled at an estimated speed 0.03 ± 0.02 m s^{-1} over 9.17 ± 7.52 days (distance: 9.75 km; Table 3) through Loch Lomond. There was no substantial difference between the estimated migration speed of River Endrick release and River Gryffe release smolts in the riverine environment.

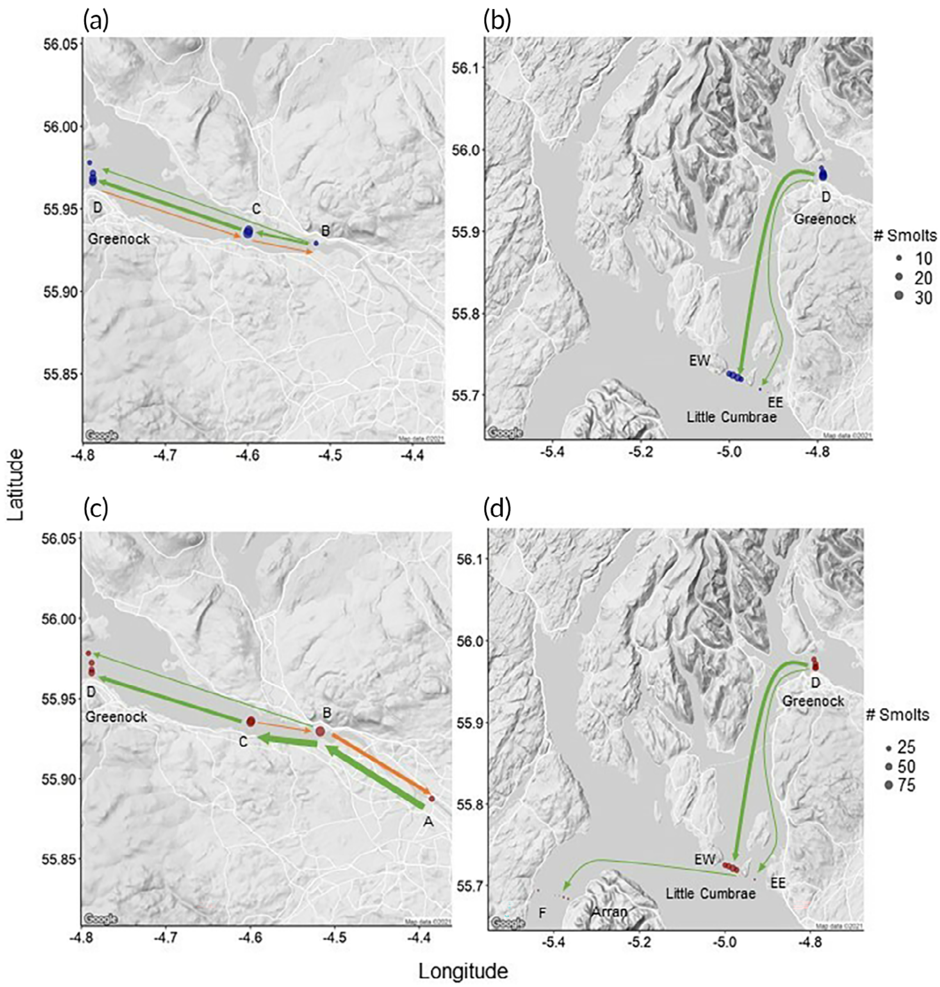

FIGURE 2 Maps representing the number of River Endrick combined (a,b) and River Gryffe (c,d) salmon post-smolts that were detected at monitoring points/lines in the estuarine and coastal marine zones [see methods; Figure 1; A,B,C,D,E (EW,EE),F] and their movement pathways between monitoring points/lines. The size of the circles in the maps reflects the number of post-smolts detected at a receiver. The total number of forward movements between monitoring points/lines is represented by the thickness of the green lines, and that of backward movements is represented by the thickness of the orange lines. # Smolts ∘ 10. ● 20. ● 30. # Smolts ∘ 25. ● 50. ● 75

On average Endrick release smolts travelled through the River Endrick (12.70 km; $n = 75$) and River Leven (11.78 km; $n = 22$) at *c.* 0.2 m s^{-1}, over 2.40 ± 3.29 and 3.92 ± 5.12 days, respectively (Table 2). In comparison, River Gryffe smolts (8.14 km, $n = 93$) migrated through the River Gryffe at *c.* 0.2 m s^{-1} over 5.06 ± 3.75 days (Table 2). The duration of the riverine migration of River Leven release smolts was *c.* 2–3 times longer compared to River Endrick and Gryffe smolts, taking *c.* 10 days to migrate *c.* 12 km, respectively (Table 3).

River Endrick combined and River Gryffe smolts were first detected entering the estuarine zone during 27 April 2021 and 15 April 2021, respectively, and were last detected in the estuarine zone on 31 May and 15 May (final detection monitoring point E; Figure 1), respectively. Based on the approximate distance from the River Leven/Gryffe exit and monitoring line E (River Leven: 47.46 km; River Gryffe: 59.32 km) the estimated speed of post-smolts through the estuarine zone was *c.* 0.16 m s^{-1} for River Endrick combined (0.16 ± 0.09 m s^{-1}) and (0.16 ± 0.06 m s^{-1}) for River Gryffe post-smolts. Speeds of post-smolts through the outer estuary [$n = 95$; D-E (Figure 1), 0.28 m s^{-1} ± 0.14 m s^{-1}] were found to be significantly faster than speeds through the inner estuary [release – D (Figure 1), $n = 107$, 0.15 ± 0.12 m s^{-1}; independent sample *t*-test, $t_{188} = -7.23$, $P < 0.01$; Table 3].

3.6 | Migration pathways

Upon entering the inner estuary, 37% ($n = 44$) of post-smolts that completed a successful migration into the Firth of Clyde ($n = 118$) were detected making a mean number of 1.75 ± 1.16 reversal movements (movements in the upstream direction) prior to exiting to the Firth of Clyde (Figure 2). On average reversals were found to occur 1.55 ± 1.43 days (range: 0.04–5.91) after exiting the freshwater zone. The mean number of reversals per individual was similar between both River Endrick combined and River Gryffe post-smolts (River Endrick combined, $n = 7$; 1.14 ± 0.38; River Gryffe, $n = 37$; 1.86 ± 1.23). The remaining 62% ($n = 72$) post-smolts that completed a successful migration through the estuary were not detected making reversal movements.

The highest proportion of detected reversals in the inner estuary for both successful River Endrick combined and River Gryffe post-smolts were detected between the receivers located closest to the freshwater outlet (Figure 2). For River Endrick combined post-smolts and River Gryffe post-smolts 78% ($n = 7$) and 72% ($n = 63$) of backward movements were detected between monitoring line C and point B and points B to A, respectively (Figures 1 and 2).

There was no significant difference between the number of detected River Endrick combined and River Gryffe post-smolts at each receiver at monitoring line D (Figures 1 and 2; $\chi^2_3 = 3.32$,

TABLE 2 Pool of the top five tested Cormack-Jolly-Seber models for River Endrick combined and River Gryffe salmon post-smolt migration success (*S*) in the estuarine zone (Figure 1, Clyde Estuary) and detection probability (*p*)

Location	Model	QAIC	Delta AIC	QAIC weights	No. of parameters	QDeviance
Endrick	S(.) p(.)	143.62	0	0.40	2	11.14
	S(FL) p(.)	144.67	1.05	0.24	3	138.47
	S(Release) p(.)	145.68	2.06	0.14	3	11.10
	S(Location) p(.)	147.0	3.38	0.07	4	10.28
	S(.) p(Location)	147.47	3.85	0.06	4	10.75
Gryffe	S(.) p(.)	133.12	0	0.29	2	5.89
	S(.) p(Location)	133.86	0.75	0.20	4	2.51
	S(TMR) p(.)	134.80	1.68	0.13	3	128.70
	S(FL) p(.)	135.04	1.92	0.11	3	128.94
	S(TMR) p(Location)	135.45	2.34	0.09	5	125.20

Notes. Covariates as predictors of *S* included release site (only for River Endrick combined post-smolts), monitoring line (Figure 1, C,D,E) (EW and EE combined), fork length and tag to body mass ratio (TMR). Monitoring line was the only covariate tested against *p*. Models were ordered based on quasi-likelihood QAIC.

TABLE 3 Mean migration speed (m s^{-1}) of smolts released from the River Endrick (End), Leven (Lev) and Gryffe (Gry) as well as the Endrick and Leven combined (Combo) as they migrate through the freshwater zone [Loch Lomond catchment (End, Lev, Combo; Figure 1, R1–R20), River Gryffe (Gry; Figure 1, R1–R3)] and the estuarine zone (Combo/Gry; Figure 1 A-E)

Zone	Location	Release site	No.	Start	End	Distance (km)	Speed (m s^{-1}) ± SD	Time (days) ± S.D.
Fresh	Endrick	End	75	R1	R17	12.7	0.23 ± 0.25	2.40 ± 3.29
	Lomond	End	23	R17	R18	9.7	0.03 ± 0.02	9.17 ± 7.52
	Leven	End	22	R18	R20	11.78	0.23 ± 0.15	3.92 ± 5.12
		Lev	28	R18	R20	11.78	0.03 ± 0.04	10.64 ± 11.57
	LL Catchment	End	22	R1	R20	34.22	0.03 ± 0.01	15.99 ± 7.07
	Gryffe	Gry	93	R1	R3	8.14	0.22 ± 0.16	5.06 ± 3.75
Est	Inner Estuary	Combo	37	A	D	14.84	0.19 ± 0.17	1.60 ± 1.21
		Gry	70	A	D	26.30	0.13 ± 0.07	3.23 ± 1.87
	Outer Estuary	Combo	31	D	E	33.12	0.25 ± 0.16	2.22 ± 1.57
		Gry	64	D	E	33.12	0.29 ± 0.12	1.76 ± 1.55
	Estuary	Combo	36	A	E	47.99	0.16 ± 0.09	4.75 ± 3.30
		Gry	80	A	E	60.59	0.16 ± 0.06	5.18 ± 2.66

Note. The total number of smolts used in this estimate (No.) is based on the number of smolts detected at both the start and end points of each measurement (Figure 1).

$P = 0.35$). In addition, the number of post-smolts from both groups detected at each receiver was found to not differ significantly from the expected distribution (River Endrick combined: $\chi^2_3 = 7$, $P = 0.07$; River Gryffe: $\chi^2_3 = 4.32$, $P = 0.23$; Figure 2).

On monitoring line E (Figure 1), a higher proportion of River Endrick combined and River Gryffe post-smolts were detected on the west side (EW) of Little Cumbrae (Figures 1 and 2; River Endrick combined: $n = 36$, 25%; River Gryffe: $n = 78$, 75%); *vs.* the east side (EE) (River Endrick combined: $n = 3$, 2%; River Gryffe: $n = 2$, 2%). For River Endrick combined post-smolts, there was a significant difference ($\chi^2_3 = 14.61$, $P = 2.18 \times 10^{-3}$) between the proportion of post-smolts detected at each receiver to the east of Little Cumbae (Figures 1 and 2b), but not for River Gryffe post-smolts ($\chi^2_3 = 1.67$, $P = 0.64$, Figure 2d). The highest proportion of River Endrick combined post-smolts ($n = 29$, 81%) were detected at the EW2 receiver (Figures 1 and 2b).

3.7 | Environmental predictors of movements and exit

3.7.1 | Tidal state

The timing of forward and reversal movements in the estuarine zone (monitoring lines A–E) was found to be dependent on the tidal state (forward: $z = 0.36$, $P < 0.001$; backward: $z = 0.83$, $P < 0.001$). The circular mean degree of forward movements occurred at 241.54 ± 1.43°, indicating that post-smolts engaged in forward movements during ebb tide (Figure 3a). The circular mean degree of reversal movements occurred at 24.04 ± 0.61°, indicating that post-smolts engaged in reversal movements during the beginning of flood tide (Figure 3b). The mean duration of half the tidal range for dates when successful post-smolts were detected in the estuarine zone ($n = 16$) was 6.22 ± 0.62 h; by converting the circular mean degree to hours this assumes that on average forward and reversal movements occurred at *c.* 2.13 h after high tide and 0.82 h after low tide, respectively.

The average range of sunrise and sunset times (hh:mm) when successful post-smolts ($n = 108$) engaged in forward movements ($n = 381$) in the estuarine zone (20 April 2021 to 28 May 2021) ranged from 04:47 to 05:43 and from 20:52 to 21:48, respectively (Figure 3d). Furthermore, the average range of sunset times when successful post-smolts ($n = 40$) engaged in reversal movements ($n = 67$) in the estuarine zone (23 April 2021 to 27 May 2021) ranged from 04:48 to 05:54 and from 20:42 to 21:46, respectively (Figure 3e). The timing of forward (Figure 3d) movements was dependent on the time of day (forward: $z = 0.26$, $P = 0$). On average post-smolts engaged in forward movements during the night, the mean time (hh:mm) they initiated a forward movement occurred at 23:47 ± 01:38 (Figure 3d). Contrary to forward movements, the timing of reversal movements was not dependent on the time of day (reversal: $z = 0.21$, $P = 0.06$; Figure 3e).

3.8 | Final movements

The final detection of post-smolts in the outer estuary (Figure 1; monitoring line E) was also found to be dependent on tide state with successful post-smolts migrating out of the outer estuary during ebb tide ($z = 0.35$, $P < 0.001$; Figure 3c). The mean circular degree of post-smolts' final detection at monitoring line E (Figure 1) was 290.07 ± 1.44° (Figure 3c). Based on the mean duration of half the tidal cycle when post-smolts were present in the estuarine zone (indicated above), this assumes that they migrated out of the outer estuary at *c.* 3.8 h after high tide. However, final detections were found to be not dependent on time of day ($z = 0.06$, $P = 0.62$; Figure 3f).

4 | DISCUSSION

This study has provided new insights into the freshwater and estuarine migration of Atlantic salmon post-smolts moving through the Clyde Estuary. Consistent with the authors' hypothesis, the freshwater loss rates of post-smolts migrating from the River Gryffe (1.08% km^{-1}) were found to be approximately half than for fish released from the River Endrick (2.27% km^{-1}; Table 1). Previous studies have indicated that freshwater mortality is positively associated with the total length of a system, as well as the presence of anthropogenic barriers and lakes (Chaput *et al*., 2019; Lilly *et al*., 2021; Stitch *et al*., 2015). Lilly *et al*. (2021) assessed the movement of smolts through the Loch Lomond catchment and reported high travel times (*c.* 5 days) and high overall freshwater mortality in the loch (43%). Consistent with this study, here the authors report that smolts also experienced long travel times (*c.*9 days) and, after accounting for the detection efficiency of receivers (Table A1), still experienced high overall mortality (56%) in Loch Lomond.

In comparison to smolts that had to navigate through the entire Loch Lomond catchment (nominally River Endrick release smolts in this study), transporting smolts around Loch Lomond (nominally River Leven release smolts) did appear to increase the overall likelihood and absolute number of smolts surviving to the Clyde Estuary. However, the rate of loss defined as the rate per distance travelled (% per kilometre) of smolt movement through the freshwater environment (all habitat types combined) was lower for River Endrick released smolts. This high rate of loss near the release site for River Leven release smolts may be related to the stress induced by transport. In hatchery-reared salmonid smolts this effect has been reported to last up until 48 h after transport and increases the likelihood of mortality (Iversen *et al*., 1998, 1998; Rechisky *et al*., 2012; Schreck *et al*., 1989). Furthermore, transported smolts have been reported to have reduced overall marine survival, which is potentially related to impaired homing abilities (Keefer *et al*., 2008). Therefore, before transporting smolts is implemented by managers as a management technique, more research is needed to determine: (a) how transport-induced stress can be mitigated and (b) whether transporting smolts increases the overall adult return rate.

Successful estuarine migrants in this study (River Endrick combined, $n = 36$; River Gryffe, $n = 80$) were found to be present in the Clyde Estuary only for a relatively short period (the last week in April to the second week of May). Contrary to the authors' hypothesis, here they show that estuarine zone loss rates for both River Endrick combined and River Gryffe smolts were lower than those for the freshwater zone loss rates and this difference was greatest for River Endrick released smolts.

Contrary to some estuarine studies, the authors did not find a significant effect of fish FL on migration success (Dieperink *et al*., 2002; Halfyard *et al*., 2017; Lacroix, 2008). Larger post-smolts are thought to be better able to evade predation because of increased swimming and osmoregulatory capacities (Dieperink *et al*., 2002; Fuiman & Magurran, 1994). Smolts with reduced osmoregulatory capacities are more likely to be physiologically stressed which may ultimately reduce their oxygen-carrying capacity and decrease their swimming ability (Handeland *et al*., 1996; Heisler, 1980). In this study, the size of smolts tagged was limited to fork length and weight greater than 130 mm and 20 g, respectively, and therefore there was a bias towards the larger individuals from the cohort. This ensured that the tag burden did not exceed *c.* 7% (mean TMR; River Endrick: 5.6 ± 0.8%; River Gryffe: 4.9 ± 0.09%), the ratio at which tag burdens have been reported to negatively affect survival in salmonids (Brown *et al*., 2010; Smircich & Kelly, 2014). Therefore, the smolts tagged in this study may not accurately reflect the wider population of Atlantic salmon post-smolts migrating through the Clyde Estuary, and future studies should use smaller tags to test this hypothesis.

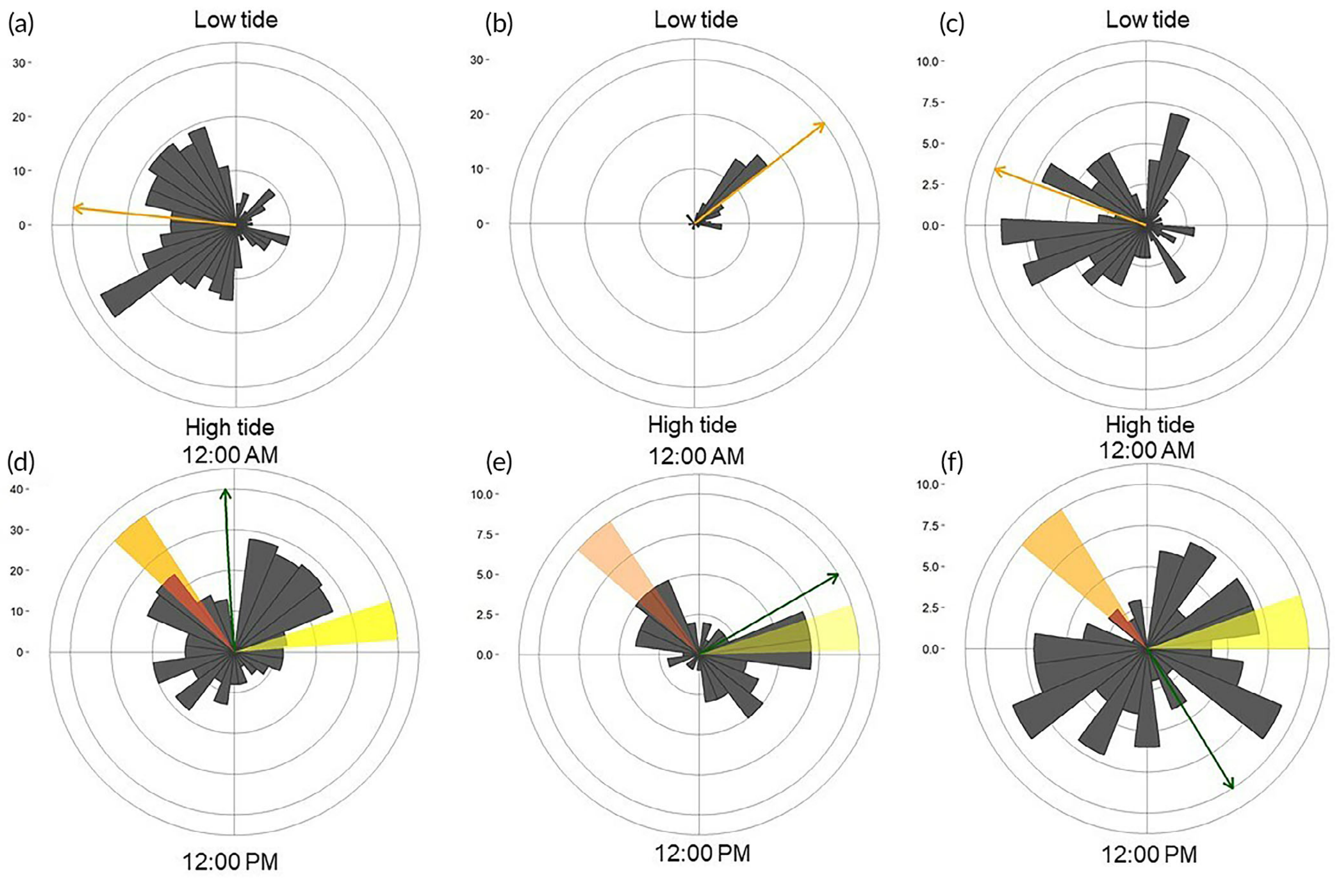

FIGURE 3 Rose diagram depicting the influence of tidal phase (a,b,c) and time of day (hours; d,e,f) when Atlantic salmon post-smolts engaged in forward (a,d) and reversal (b,e) movements and exited the estuarine zone (c,f), respectively. The orange and green arrows reflect the mean circular degree in the tidal phase (a,b,c), and mean time of day (d,e,f) when these movements occurred. In the time-of-day plots (d,e,f) the yellow and orange shaded bars reflect the variation in times when sunrise and sunset occurred throughout the time period when forward (20 April 2021 to 28 May 2021) and reversal movements (23 April 2021 to 27 April 2021) were initiated as well as exit movements (22 April 2021 to 31 May 2021)

Furthermore, loss rates of post-smolts in estuaries are thought to be positively associated with the complexity of the system, as predators of Atlantic salmon are known to utilize the tide to predict when fishes will migrate past constriction points (Hastie *et al*., 2016; Zamon, 2001). This pattern was shown by Chaput *et al*. (2019) who assessed post-smolt movement through two estuaries on the east coast of Canada and reported that loss rates were lower for post-smolts migrating through a wide-open bay (5%–33% loss rate) in comparison to the semi-enclosed constricted estuary (18%–72%) (Chaput *et al*., 2019). However, this pattern was not consistent among other studies that have reported relatively low levels of loss for post-smolts migrating through complex fjord systems (Dempson *et al*., 2011; Halfyard *et al*., 2012). This suggests that loss rates of post-smolts in estuaries may be the result of a complex combination of local stressors as well as the physical and geographic nature of the system (Chaput *et al*., 2019).

The unexpectedly low overall mortality rates of post-smolts in the Clyde Estuary may be a combination of the low complexity of the estuary and low abundance of predators. The highest loss rates of post-smolts in this study occurred as they migrated past monitoring line C (Figure 1; Table 1). This region served as the main migratory constriction point in the estuarine zone for both River Endrick combined and Gryffe post-smolts. At this location, River Endrick combined post-smolts had just exited from the River Leven, whereas River Gryffe post-smolts would have migrated *c*. 9 km from their river outlet through a narrow channel that has a maximum width of 200 m at high tide (Bekic *et al*., 2006).

In addition, during their first few days in the estuarine zone, 37% ($n = 44$) of successful estuarine migrants from both the River Endrick combined and River Gryffe fish were found to engage in around two reversal movements (movements upstream) in the inner estuary, and these were paired with tidal movements. These reversal movements are common among estuarine studies of smolt migration and are thought to be driven by a need to acclimatize to the increased salinity (Dempson *et al*., 2011; Halfyard *et al*., 2013; Hawkes *et al*., 2017; Kocik *et al*., 2009). Therefore, in this study, the high loss rate of post-smolts near monitoring line C may be due to the longer duration some post-smolts spent in the inner, as opposed to the outer, estuary. However, in this study the authors were unable to accurately decipher the behaviour of unsuccessful migrants from predators, and determine whether their behaviour differed significantly from that of successful estuarine migrants (Daniels *et al*., 2018).

Unlike the inner estuary, once post-smolts from both river systems successfully migrated past monitoring line D (Figure 1), there were no observed mortalities or reversal movements. Nonetheless, the reduction in observed reversal movements may be due to reduced receiver infrastructure in this region and thus poor detection of such movements. Forward movements out of the estuary were found to occur mainly during the night. The underlying reason for nocturnal movement of post-smolts in the Clyde Estuary is not known. However, some studies have hypothesized that post-smolts migrate during the night to decrease the chance of being spotted by predators and that they utilize daylight hours to feed during their estuarine migration (Andreassen *et al*., 2001; Fiske, 2020; Kadri, 1997).

Previous studies have reported that in estuaries with weak salinity gradients and tidally driven currents, smolts appear to actively migrate towards the estuarine outlet regardless of the direction of current (Økland *et al*., 2006; Thorstad *et al*., 2004). In contrast, the ground speed and number of net-seaward movements of smolts in estuaries with strong salinity gradients and tidally driven currents appear to be positively correlated with salinity and the outflowing tide (Martin *et al*., 2009). The salinity of the water near monitoring line C (Figure 1) where most reversal movements were recorded ranges from *c*. 20 to 25 ppm during low to high water, respectively (Allen, 1966) and is heavily influenced by freshwater input mainly from the Rivers Clyde and Leven. In comparison, the salinity of the surface water near monitoring line D (Figure 1) ranges from 24 to 32 ppm during low to high water, respectively (Allen, 1966). The higher salinity at monitoring line D (Figure 1) is due to its proximity to the sea as well as the displacement of inflowing freshwater water into surrounding sea lochs during a flood tide (Allen, 1996). In addition, the geography of the plateau extending across from monitoring line D creates a strong seaward residual current in the surface layer (Allen, 1966).

In the study reported here, the authors were unable to measure salinity or current speed at monitoring points and lines in the Clyde Estuary, which prevented the authors from determining whether post-smolts were actively swimming with the current. Nonetheless, due to the higher survival rates and swim speeds of post-smolts in the inner compared with the outer estuary, we can hypothesize that post-smolts were using both salinity gradients and currents to efficiently navigate through the outer estuary. This hypothesis is further supported by the fact that most post-smolts were detected leaving the estuarine zone mainly on the west side of Little Cumbrae (Figure 1) where the principle ebb tide flow is orientated (Davies & Mofor, 1990; Sabatino *et al*., 2017).

Based on the findings of this study it appears that the risk to post-smolt salmon migrating from the Rivers Endrick and Gryffe in the Clyde Estuary may currently be low. In the Clyde Marine Region there are currently active salmon farms within two adjoining sea lochs and along the coast of Arran (Marine Scotland, 2022; Figure 1). Sea lice larvae are known to drift up to 30 km with local currents for *c*. 4 days prior to settling at new locations as adults (Adams *et al*., 2016; Rees *et al*., 2015). Therefore, lice from farms in the Outer Clyde Estuary could drift into the inner estuary (Adams *et al*., 2016; Krkošek *et al*., 2009; Rees *et al*., 2015). The likelihood of infestation has been positively correlated with the salinity in the region, and mortality is thought to occur when smolts spend greater than a few weeks near a site (Krkošek *et al*., 2009). Therefore, due to the large freshwater input into the Inner and Outer Clyde Estuary and short duration smolts spent in this region (*c*. 5 days) the risk of River Endrick and Gryffe post-smolts becoming exposed to sea lice is likely low. Nonetheless, once smolts enter the Firth of Clyde their risk of sea lice exposure may increase as salinities near the surface more closely resemble full-strength sea water (*c*. 33 ppt; Slesser & Turrell, 2005). Because few smolts were detected on line F, it is assumed that they migrate along the east coast of Arran to reach the Irish Sea. Future studies are required to determine the duration spent in this region and potential risk of fish farm exposure.

Fishing in the Clyde Estuary is now dominated by a *Nephrops* fishery primarily captured using benthic otter trawls (Thurstan & Roberts, 2010). In the estuarine environment, the risk of overlap between migrating salmon post-smolts and fisheries conducted on, or near, the seabed is likely low, as both post-smolt and adult migrant salmon have been consistently reported to spend over 95% of their time near the surface (1–3 m depth) (Davidsen *et al*., 2008; Hedger *et al*., 2009; Holm *et al*., 2006; Newton *et al*., 2021). It is important to note that although this study provides important baseline information on the loss rates and potential drivers of post-smolt migration through the Clyde Marine Region, results are limited to only 1 year. Therefore, temporal repeatability of this project over multiple years is required to determine whether migratory patterns and survival rates reported are consistent across time (Thorstad *et al*., 2012a, 2012b; Chaput *et al*., 2019). In addition, it is highly plausible that smolts migrating from other river systems draining into the Clyde Estuary may exhibit differing migratory patterns which may result in a very different risk of exposure to anthropogenic stressors than that reported here.

In conclusion, this study found that Atlantic salmon post-smolts migrating through the Clyde Estuary emanating from the River Endrick and Gryffe experience relatively low mortality rates, which may in part be attributed to the short period of time they spend in this region. This suggests that loss of salmon during migration from the River Endrick and Gryffe is thus more likely the result of mortality experienced during migration in the freshwater environment (for the River Endrick) or further out to sea (for the River Gryffe population) (Marine Scotland, 2021). More information concerning the drivers of loss of post-smolts in the Clyde Estuary is still needed as even low estuarine loss rates could have a population level effect (Davidsen *et al*., 2009).

AUTHOR CONTRIBUTIONS

C.E.A. designed the tagging programme, J.L, C.E.A., H.M.H., C.W.B. and R.F. executed the field work. J.L. analysed the data and wrote the draft manuscript with critical review and feedback from all authors.

ACKNOWLEDGEMENTS

We thank A.Green, M. Newton, N. McCallum, J. P. Koene and the Paisley and Abercorn Angling Club for providing field support; as well as the Loch Lomond Fisheries Trust for use of a rotary screw trap. We thank the Atlantic Salmon Trust for additional acoustic receivers and tags as well as NatureScot and Marine Scotland for providing additional acoustic receivers.

FUNDING INFORMATION

This work was part of the SeaMonitor project funded by the European Union INTERREG VA Programme award number IVA5060; additional funding was provided by NatureScot and the Atlantic Salmon Trust.

ORCID

Jessie Lilly https://orcid.org/0000-0001-7540-6214

REFERENCES

Adams, T. P., Aleynik, D., & Black, K. D. (2016). Temporal variability in sea lice population connectivity and implications for regional management protocols. *Aquaculture Environment Interactions*, *8*, 585–596.

Allen, J. H. (1966). On the hydrography of the Clyde. *Coastal Engineering Proceedings*, *10*, 1360–1374.

Andreassen, P. M. R., Martinussen, M. B., Hvidsten, N. A., & Stefansson, S. O. (2001). Feeding and prey-selection of wild Atlantic salmon post-smolts. *Journal of Fish Biology*, *58*, 1667–1679.

Bekic, D., Ervine, D. A., & Lardet, P. (2006). A comparison of one and two divisional model simulation of the Clyde estuary, Glasgow. *Proceedings of the Seventh International Conference on Hydroscience and Engineering* (pp. 1–15). Philadelphia, PA: Drexel University.

Brown, R. S., Harnish, R. A., Carter, K. M., Boyd, J. W., Deters, K. A., & Eppard, M. B. (2010). An evaluation of the maximum tag burden for implantation of acoustic transmitters in juvenile Chinook Salmon. *North American Journal of Fisheries Management*, *30*(499–505), 505. https://doi.org/10.1577/M09-038.1.

Campbell, H. A. (2012). V-track: Software for analysing and visualising animal movement from acoustic telemetry detections. *Marine and Freshwater Research*, *63*(99), 815–820. https://doi.org/10.1071/mf12194.

Chaput, G., Carr, J., Daniels, J., Tinker, S., Jonsen, I., & Whoriskey, F. (2019). Atlantic salmon (Salmo salar) smolt and early post-smolt migration and survival inferred from multi-year and multi-stock acoustic telemetry studies in the Gulf of St. Lawrence, Northwest Atlantic. *ICES Journal of Marine Science*, *76*, 1107–1121.

Chavarie, L., Honkanen, H. M., Newton, M., Lilly, J. M., Greetham, H. R., & Adams, C. E. (2021). The benefits of merging passive and active tracking approaches: New insights into riverine migration by salmonid smolts. *Ecosphere*, *34*, 1–15.

Cormack, R. M. (1964). Estimates of survival from the sighting of marked animals. *Biometrika*, *51*, 429–438.

Cox, T., & Schepers, L. (2018). Tides: Quasi-Periodic Time Series Characteristics. R package version 1.1.

Crozier, W. W., Schön, P.-J., Chaput, G., Potter, E. C. E., Maoiléidigh, N. Ó., & MacLean, J. C. (2004). Managing Atlantic salmon (*Salmo salar* L.) in the mixed stock environment: Challenges and considerations. *ICES Journal of Marine Science*, *61*, 1344–1358.

Daniels, J., Chaput, G., & Carr, J. (2018). Estimating consumption rate of Atlantic salmon smolts (Salmo salar) by striped bass (Morone saxatilis) in the Miramichi River estuary using acoustic telemetry. *Canadian Journal of Fisheries and Aquatic Sciences*, *75*, 1811–1822.

Davidsen, J., Svenning, M.-A., Orell, P., Yoccoz, N., Dempson, J. B., Niemelä, E., … Erkinaro, J. (2005). Spatial and temporal migration of wild Atlantic salmon smolts determined from a video camera array in the sub-Arctic River Tana. *Fisheries Research*, *74*, 210–222.

Davidsen, J. G., Rikardsen, A. H., Halttunen, E., Thorstad, E. B., Økland, F., Letcher, B. H., … Næsje, T. F. (2009). Migratory behaviour and survival rates of wild northern Atlantic salmon *Salmo salar* post-smolts: Effects of environmental factors. *Journal of Fish Biology*, *75*, 1700–1718.

Davidsen, J. G., Plantalech Manel-la, N., Økland, F., Diserud, O. H., Thorstad, E. B., Finstad, B., … Rikardsen, A. H. (2008). Changes in swimming depths of Atlantic salmon *Salmo salar* post-smolts relative to light intensity. *Journal of Fish Biology*, *73*, 1065–1074.

Davies, P. A., & Mofor, L. A. (1990). Observations of flow separation by an isolated Island. *International Journal of Remote Sensing*, *11*, 767–782.

Delgado, M. L., & Ruzzante, D. E. (2020). Investigating diadromy in fishes and its loss in an -omics era. *iScience*, *23*, 101837.

Dempson, J. B., Robertson, M. J., Pennell, C. J., Furey, G., Bloom, M., Shears, M., … Robertson, G. J. (2011). Residency time, migration route and survival of Atlantic salmon *Salmo salar* smolts in a Canadian fjord. *Journal of Fish Biology*, *78*, 1976–1992.

Dieperink, C., Bak, B. D., Pedersen, L.-F., Pedersen, M. I., & Pedersen, S. (2002). Predation on Atlantic salmon and sea trout during their first days as post smolts. *Journal of Fish Biology*, *61*, 848–852.

Finstad, B., Bjorn, P. A., Grimnes, A., & Hvidsten, N. A. (2000). Laboratory and field investigations of salmon lice (Lepeophtheirus) salmonis (Kroyer) infestation on Atlantic salmon (Salmo salar L.) post-smolts. *Aquaculture Research*, *31*, 795–803.

Finstad, B., Økland, F., Thorstad, E. B., Bjørn, P. A., & McKinley, R. S. (2005). Migration of hatchery-reared Atlantic salmon and wild anadromous brown trout post-smolts in a Norwegian fjord system. *Journal of Fish Biology*, *66*, 86–96. https://doi.org/10.1111/j.0022-1112.2005.00581.x.

Fiske, A. N. (2020). Migration pattern and fjord use of Atlantic salmon (Salmo salar) smolt from two watercourses in the Nordfjord system: effects form environmental driver (Masters thesis). Norwegian University of Life Sciences, Ås, Norway, 72. Available from NMBU library https://static02.nmbu.no/mina/studier/moppgaver/2020-Fiske.pdf.

Fuiman, L. A., & Magurran, A. E. (1994). Development of predator defences in fishes. *Reviews in Fish Biology and Fisheries*, *4*, 145–183.

Gilbey, J., Utne, K. R., Wennevik, V., Beck, A. C., Kausrud, K., Hindar, K., … Verspoor, E. (2021). The early marine post-smolt distribution of Atlantic salmon in the NE Atlantic: A genetically informed stock-specific synthesis. *Fish and Fisheries*, *22*, 1274–1306. https://doi.org/10.1111/faf.12587.

Gibson, A. J. F., Halfyard, E. A., Bradford, R. G., Stokesbury, M. J. W., & Redden, A. M. (2015). Effects of predation on telemetry-based survival estimates: Insights from a study on endangered Atlantic salmon smolts. *Canadian Journal of Fisheries and Aquatic Sciences*, *72*, 728–741.

Gosch, M., Hernandez-Milian, G., Rogan, E., Jessopp, M., & Cronin, M. (2014). Grey seal diet analysis in Ireland highlights the importance of using multiple diagnostic features. *Aquatic Biology*, *20*, 155–167. https://doi.org/10.3354/ab00553.

Halfyard, E. A., Webber, D., Del Papa, J., Leadley, T., Kessel, S. T., Colborne, S. F., & Fisk, A. T. (2017). Evaluation of an acoustic telemetry transmitter designed to identify predation events. *Methods in Ecology and Evolution*, *8*, 1063–1071. https://doi.org/10.1111/2041-210X.12726doi:10.1111/2041-210X.1272.

Halfyard, E. A., Gibson, A. J. F., Ruzzante, D. E., Stokesbury, M. J. W., & Whoriskey, F. G. (2012). Estuarine survival and migratory behaviour of Atlantic salmon *Salmo salar* smolts. *Journal of Fish Biology*, *81*, 1626–1645. https://doi.org/10.1111/j.1095-8649.2012.03419.xdoi:10.1111/j.1095-8649.2012.03419.x.

Halfyard, E. A., Gibson, A. J. F., Stokesbury, M. J. W., Ruzzante, D. E., & Whoriskey, F. G. (2013). Correlates of estuarine survival of Atlantic salmon post smolts from the southern upland, Nova Scotia, Canada. *Canadian Journal of Fisheries and Aquatic Sciences*, *70*, 452–460.

Halls-Spencer, J. M. (2001). Maerl – a spectacular firth of Clyde habitat. The ecology and management of the Firth of Clyde. *Conference on the Ecology and Management of the Firth of Clyde*, (pp. 43–44).

Handeland, S. O., Järvi, T., Fernö, A., & Stefansson, S. O. (1996). Osmotic stress, antipredator behaviour, and mortality of Atlantic salmon (*Salmo salar*) smolts. *Canadian Journal of Fisheries and Aquatic Sciences*, *53*, 2673–2680.

Hanssen, E. M., Vollset, K. W., Salvanes, A. G. V., Barlaup, B., Whoriskey, K., Isaken, T. E., … Lennox, R. J. (2021). Acoustic telemetry predation sensors reveal the tribulations of Atlantic salmon (*Salmo salar*) smolts migrating through lakes. *Ecology of Freshwater Fish*, *00*, 11–14.

Hastie, G. D., Russell, D. J. F., Benjamins, S., Moss, S., Wilson, B., & Thompson, D. (2016). Dynamic habitat corridors for marine predators; intensive use of a coastal channel by harbour seals is modulated by tidal currents. *Behavioural Ecology and Sociobiology*, *70*, 2161–2174.

Hawkes, J. P., Sheehan, T. F., & Stich, D. S. (2017). Assessment of early migration dynamics of river-specific hatchery Atlantic salmon smolts. *Transactions of the American Fisheries Society*, *146*, 1279–1290. https://doi.org/10.1080/00028487.2017.1370017.

Hayden, T. A., Holbrook, C. M., Binder, T. R., Dettmers, J. M., Cooke, S. J., Vandergoot, C. S., & Krueger, C. C. (2016). Probability of acoustic transmitter detections by receiver lines in Lake Huron: Results of multi-year field tests and simulations. *Animal Biotelemetry*, *4*, 19. https://doi.org/10.1186/s40317-016-0112-9.

Hedger, R. D., Uglem, I., Thorstad, E. B., Finstad, B., Chittenden, C. M., Arechavala-Lopez, P., … Økland, F. (2011). Behaviour of Atlantic cod, a marine fish predator, during Atlantic salmon post-smolt migration. *ICES Journal of Marine Science*, *68*, 2152–2162.

Hedger, R., Martin, F., Hatin, D., Caron, F., Whoriskey, F., & Dodson, J. (2008). Active migration of wild Atlantic salmon Salmo salar smolt through a coastal embayment. *Marine Ecology Progress Series*, *355*, 235–246.

Hedger, R., Hatin, D., Dodson, J., Martin, F., Fournier, D., Caron, F., & Whoriskey, F. (2009). Migration and swimming depth of Atlantic salmon kelts *Salmo salar* in coastal zone and marine habitats. *Marine Ecology Progress Series*, *392*, 179–192.

Heisler, B. (1980). Regulation of the acid-base status in fishes. In M. A. Ali (Ed.), *Environmental physiology of fishes* (pp. 123–162). New York: Plenum Press.

Hendry, A. P., Castric, V., Kinnison, M. T., & Quin, T. P. (2004). The evolution of philopatry and dispersal: Homing versus straying in salmonids. In A. P. Hendry & S. C. Stearns (Eds.), *Evolution illuminated: Salmon and their relatives* (pp. 52–59). Oxford, U.K: Oxford University Press.

Holbrook C., Hayden T., Pye J., Nunes A. (2018) glatos: A package for the Great Lakes acoustic telemetry observation system. R package version 0.4.2.

Holm, M. (2000). Spatial and temporal distribution of post-smolts of Atlantic salmon (*Salmo salar* L.) in the Norwegian Sea and adjacent areas. *ICES Journal of Marine Science*, *57*, 955–964.

Holm, M., Jacobsen, J. A., Sturlaugsson, J., & Holst, J. C. (2006). Behaviour of Atlantic salmon (*Salmo salar* L.) recorded by data storage tags in the NE Atlantic – implications for interception by pelagic trawls. ICES ASC CM 2006/Q: 12.

Honkanen, H. M., Rodger, J. R., Stephen, A., Adams, K., Freeman, J., & Adams, C. E. (2018). Counterintuitive migration patterns by Atlantic salmon *Salmo salar* smolts in a large lake. *Journal of Fish Biology*, *93*, 159–162.

Honakanen, H. M., Rodger, J. R., Stephen, A., Adams, K., Freeman, J., & Adams, C. E. (2000). Summer survival and activity patterns of estuary feeding anadromous *Salmo trutta*. *Ecology of Freshwater Fish*, *29*, 31–39. https://doi.org/10.1111/eff.12485.

ICES. (2020). NASCO workshop for North Atlantic salmon at-sea mortality (WK Salmon, outputs from 2019 meeting). *ICES Scientific Reports*, *2*, 69, 1–175. https://doi.org/10.17895/ices.pub.5979.

ICES. (2021). Working group on North Atlantic Salmon (WGNAS). *ICES Scientific Reports*, *3*, 407. https://doi.org/10.17895/ices.pub.7923.

Iversen, M., Finstad, B., & Nilssen, K. J. (1998). Recovery from loading and transport stress in Atlantic salmon (*Salmo salar* L.) smolts. *Aquaculture*, *168*, 387–394.

Jacobsen, J. A., Hansen, L. P., Bakkestuen, V., Halvorsen, R., Reddin, D. G., White, J., … Pedersen, S. (2012). Distribution by origin and sea age of Atlantic salmon (*Salmo salar*) in the sea around The Faroe Islands based on analysis of historical tag recoveries. *ICES Journal of Marine Science*, *69*, 1598–1608.

Jepsen, N., Holthe, E., & Økland, F. (2006). Observations of predation on salmon and trout smolts in a river mouth. *Fisheries Management and Ecology*, *13*, 341–343.

JNCC/Joint Nature Conservation Committee. (2019). Endrick Water. Special Areas of Conservation (SAC). Available at: https://sac.jncc.gov.uk/site/UK0019840

Jolly, G. M. (1965). Explicit estimates from capture-recapture data with both death and immigration-stochastic model. *Biometrika*, *52*, 225–247.

Kadri, S., Metcalfe, N. B., Huntingford, F. A., & Thorpe, J. E. (1997). Daily feeding rhythms in Atlantic salmon II: Size-related variation in feeding patterns of post-smolts under constant environmental conditions. *Journal of Fish Biology*, *50*, 273–279.

Karunarathna, H. (2010). Modelling the long-term morphological evolution of the Clyde estuary, Scotland, UK. *Journal of Coastal Conservation*, *15*, 499–507.

Keefer, M. L., Caudill, C. C., Peery, C. A., & Lee, S. R. (2008). Transporting juvenile salmonids around dams impairs adult migration. *Ecological Applications*, *18*, 1888–1900.

Kneebone, J., Hoffman, W. S., Dean, M. J., & Armstrong, M. P. (2014). Movements of striped bass between the exclusive economic zone and Massachusetts state waters. *North American Journal of Fisheries Management*, *34*, 524–532.

Kocik, J. F., Hawkes, J. P., & Sheehan, T. F. (2009). Assessing estuarine and coastal migration and survival of wild Atlantic salmon smolts from the Narraguagus River, Maine using ultrasonic telemetry. *American Fisheries Society Symposium*, *69*, 293–310.

Krkošek, M., Morton, A., Volpe, J. P., & Lewis, M. A. (2009). Sea lice and salmon population dynamics: Effects of exposure time for migratory fish. *Proceedings of the Royal Society B: Biological Sciences*, *276*, 2819–2828.

Laake, J. L. (2013). RMark: An R Interface for Analysis of Capture-Recapture Data with MARK. Available at: https://cran.r-project.org/web/packages/RMark/index.html

Lacroix, G. L. (2008). Influence of origin on migration and survival of Atlantic salmon (*Salmo salar*) in the bay of Fundy, Canada. *Canadian Journal of Fisheries and Aquatic Sciences*, *65*, 2063–2079.

Lacroix, G. L., & McCurdy, P. (1996). Migratory behaviour of post-smolt Atlantic salmon during initial stages of seaward migration. *Journal of Fish Biology*, *49*, 1086–1101.

Larocque, S. M., Johnson, T. B., & Fisk, A. T. (2020). Survival and migration patterns of naturally and hatchery-reared Atlantic salmon (*Salmo salar*) smolts in a Lake Ontario tributary using acoustic telemetry. *Freshwater Biology*, *65*, 835–848.

Lefèvre, M. A., Stokesbury, M. J. W., Whoriskey, F. G., & Dadswell, M. J. (2011). Migration of Atlantic salmon smolts and post-smolts in the Rivière saint-Jean, QC north shore from riverine to marine ecosystems. *Environmental Biology of Fishes*, *96*, 1017–1028.

Lilly, J., Honkanen, H. M., McCallum, J. M., Newton, M., Bailey, D. M., & Adams, C. E. (2021). Combining acoustic telemetry with a mechanistic model to investigate characteristics unique to successful Atlantic salmon smolt migrants through a standing body of water. *Environmental Biology of Fishes*. https://doi.org/10.1007/s10641-021-01172-x.

Lund, U., & Agostinelli, C. (2018). CircStats: Circular Statistics, from 'Topics in Circular Statistics'. R Package version 0.2–6. Available at: https://cran.r-project.org/web/packages/CircStats/CircStats.pdf

Maitland, P. S., Adams, C. E., & Mitchell, J. (2000). The natural heritage of Loch Lomond: Its importance in a national and international context. *Scottish Geographical Journal*, *116*, 181–196.

Marine Scotland. (2015). Illustrative map referred to in the explanatory note to the Scottish marine regions order 2015. Available at: https://www.gov.scot/binaries/content/documents/govscot/publications/factsheet/2020/10/marine-planning-regional-boundaries/documents/map-of-marine-regions/map-of-marine-regions/govscot%3Adocument/map%2Bmarine%2Bregions.pdf

Marine Scotland. (2021). Salmon fishing: proposed river gradings for 2022 season. Available at: https://www.gov.scot/publications/salmon-fishing-proposed-river-gradings-for-2022-season/

Marine Scotland. (2022). Aquaculture - Active finfish sites (28.2.2022). Available at: https://marinescotland.atkinsgeospatial.com/nmpi/default.aspx?layers=1586

Martin, F., Hedger, R. D., Dodson, J. J., Fernandes, L., Hatin, D., Caron, F., & Whoriskey, F. G. (2009). Behavioural transition during the estuarine migration of wild Atlantic salmon (*Salmo salar* L.) smolt. *Ecology of Freshwater Fish*, *18*, 406–417.

McCormick, S. D., Regish, A. M., Christensen, A. K., & Björnsson, B. T. (2013). Differential regulation of sodium–potassium pump isoforms during smolt development and seawater exposure of Atlantic salmon. *Journal of Experimental Biology*, *216*, 1142–1151.

McDowall, R. M. (2008). Diadromy, history and ecology: A question of scale. *Hydrobiologia*, *602*, 5–14.

McLeod, C. R., Yeo, M., Brown, A. E., Burn, A. J., Hopkins, J. J., & Way, S. F. (2005). *The habitats directive: Selection of special areas of conservation in the UK* (2nd ed.). Peterborough, UK: Joint Nature Conservation Committee Available at: https://hub.jncc.gov.uk/assets/5d20b480-9cc1-490f-9599-da6003928434.

Moore, A., Ives, S., Mead, T. A., & Talks, L. (1998). The migratory behaviour of wild Atlantic salmon (*Salmo salar* L.) smolts in the river test and Southampton water, southern England. *Hydrobiologia*, *372*, 295–304.

Morgan, R. I. G., Greenstreet, S. P. R., & Thorpe, J. E. (1986). First observations on distribution, food and fish predators of post-smolt Atlantic salmon, *Salmo Salar*, in the outer Firth of Clyde. ICES Document CM 1986/M: 27. 8 pp.

Mork, K. A., Gilbey, J., Hansen, L. P., Jensen, A. J., Jacobsen, J. A., Holm, M., … Wennevik, V. (2012). Modelling the migration of post-smolt Atlantic salmon (*Salmo salar*) in the Northeast Atlantic. *ICES Journal of Marine Science*, *69*, 1616–1624. https://doi.org/10.1093/icesjms/fss108.

Murray, T. S., Cowley, P. D., Bennett, R. H., & Childs, A.-R. (2018). Fish on the move: Connectivity of an estuary-dependent fishery species evaluated using a large-scale acoustic telemetry array. *Canadian Journal of Fisheries and Aquatic Sciences*, *75*, 2038–2052. https://doi.org/10.1139/cjfas-2017-0361.

Newton, M., Barry, J., Lothian, A., Main, R., Honkanen, H., Mckelvey, S., … Adams, C. (2021). Counterintuitive active directional swimming behaviour by Atlantic salmon during seaward migration in the coastal zone. *ICES Journal of Marine Science*, *78*, 1730–1743. https://doi.org/10.1093/icesjms/fsab024.

Økland, F., Thorstad, E. B., Finstad, B., Sivertsgård, R., Plantalech, N., Jepsen, N., & McKinley, R. S. (2006). Swimming speeds and orientation of wild Atlantic salmon post-smolts during the first stage of the marine migration. *Fisheries Management and Ecology*, *13*, 271–274. https://doi.org/10.1111/j.1365-2400.2006.00498.x.

Ounsley, J. P., Gallego, A., Morris, D. J., & Armstrong, J. D. (2019). Regional variation in directed swimming by Atlantic salmon smolts leaving Scottish waters for their oceanic feeding grounds—A modelling study. *ICES Journal of Marine Science*, *77*, 315–325. https://doi.org/10.1093/icesjms/fsz160.

Parrish, D. L., Behnke, R. J., Gephard, S. R., McCormick, S. D., & Reeves, G. H. (1998). Why aren't there more Atlantic salmon (*Salmo salar*). *Canadian Journal of Fisheries and Aquatic Science*, *55*, 281–287. https://doi.org/10.1139/d98-012.

Pincock, D. G. (2012). *False detections: What they are and how to remove them from detection data*. Halifax: VEMCO.

Pye, K., & Blott, S. J. (2014). The geomorphology of UK estuaries: The role of geological controls, antecedent conditions and human activities. *Estuarine, Coastal and Shelf Science*, *150*, 196–214. https://doi.org/10.1016/j.ecss.2014.05.014.

Quinn, T. P., & Myers, K. W. (2004). Anadromy and the marine migrations of Pacific salmon and trout: Rounsefell revisited. *Reviews in Fish Biology and Fisheries*, *14*, 421–442.

R Core Team. (2019). *R: A language and environment for statistical computing Vienna*. Vienna, Austria: R Foundation for Statistical Computing.

Rees, E. E., St-Hilaire, S., Jones, S. R., Krkšsek, M., DeDominicis, S., Foreman, M. G. G., … Revie, C. W. (2015). Spatial patterns of sea lice infection among wild and captive salmon in western Canada. *Landscape Ecology*, *30*, 989–1004. https://doi.org/10.1007/s10980-015-0188-2.

Rechisky, E. L., Welch, D. W., Porter, A. D., Jacobs-Scott, M. C., Winchell, P. M., & McKern, J. L. (2012). Estuarine and early marine survival of transported and in-river migrant Snake River spring Chinook salmon smolts. *Scientific Reports*, *2*, 448.

Sabatino, A. D., O'Hara Murray, R. B., Hills, A., Speirs, D. C., & Heath, M. R. (2017). Modelling Sea level surges in the firth of Clyde, a fjordic embayment in south-West Scotland. *Natural Hazards*, *84*, 1601–1623.

Schreck, C. B., Solazzi, M. F., Johnson, S. L., & Nickelson, T. E. (1989). Transportation stress affects performance of coho salmon, Oncorhynchus kisutch. *Aquaculture*, *82*, 15–20. https://doi.org/10.1016/0044-8486(89)90391-8.

Seber, G. A. F. (1965). A note on the multiple-recapture census. *Biometrika*, *52*, 249–259.

Shephard, S., & Gargan, P. (2021). Wild Atlantic salmon exposed to sea lice from aquaculture show reduced marine survival and modified response to ocean climate. *ICES Journal of Marine Science*, *78*, 368–376. https://doi.org/10.1093/icesjms/fsaa079.

Slesser, G., Turrell, W. (2005). Annual cycles of physical, chemical and biological parameters in Scottish waters (2005 update). Fisheries Research Services Internal Report 19.

Smircich, M. G., & Kelly, J. T. (2014). Extending the 2% rule: The effects of heavy internal tags on stress, physiology, swimming performance, and growth in brook trout. *Animal Biotelemetry*, *2*, 1–7. https://doi.org/10.1111/eff.12564.

Stich, D. S., Zydlewski, G. B., Kocik, J. F., & Zydlewski, J. D. (2015). Linking behaviour, physiology, and survival of Atlantic salmon smolts during estuary migration. *Marine and Coastal Fisheries*, *7*, 68–86.

Susdorf, R., Salama, N., Todd, C., Hillman, R., Elsmere, P., & Lusseau, D. (2018). Context-dependent reduction in somatic condition of wild Atlantic salmon infested with sea lice. *Marine Ecology Progress Series*, *606*, 91–104.

Tett, P., Black, K., Hughes, A., & Wilding, T. (2018). Review of the environmental impacts of salmon farming in Scotland executive summary and main report. *The Scottish Parliament*, *1*, 197.

Thieurmel, B., & Elmarhraoui, A. (2019). Suncalc: Compute sun position, sunlight phases, moon position and lunar phase. R Package version 0.5.0. Available at: https://rdrr.io/cran/suncalc/.

Thorstad, E. V., Økland, F., Finstad, B., Sivertsgård, R., Bjørn, P. A., & McKinley, R. S. (2004). Migrtion speeds and orientation of Atlantic salmon and sea trout post-smolts in a Norwegian fjord system. *Environmental Biology of Fishes*, *71*, 305–311.

Thorstad, E. B., Whoriskey, F., Uglem, I., Moore, A., Rikardsen, A. H., & Finstad, B. (2012a). A critical life stage of the Atlantic salmon *Salmo salar*: Behaviour and survival during the smolt and initial post-smolt migration. *Journal of Fish Biology*, *81*, 500–542.

Thorstad, E. B., Uglem, I., Finstad, B., Chittenden, C. M., Nilsen, R., Økland, F., & Bjørn, P. A. (2012b). Stocking location and predation by marine fishes affect survival of hatchery-reared Atlantic salmon smolts. *Fisheries Management and Ecology*, *19*, 400–409.

Thurstan, R. H., & Roberts, C. M. (2010). Ecological meltdown in the firth of Clyde, Scotland: Two centuries of change in a coastal marine ecosystem. *PLoS One*, *5*, e11767.

Todd, C., Whyte, B., MacLean, J., & Walker, A. (2006). Ectoparasitic Sea lice (*Lepeophtheirus salmonis* and *Caligus elongatus*) infestations of wild, adult, one sea-winter Atlantic salmon *Salmo salar* returning to Scotland. *Marine Ecology Progress Series*, *328*, 183–193.

White, G. C., & Burnham, K. P. (1999). Program MARK: Survival estimation from populations of marked animals. *Bird Study*, *46*, S120–S139.

Whitmarsh, D., & Wattage, P. (2006). Public attitudes towards the environmental impact of salmon aquaculture in Scotland. *European Environment*, *16*, 108–121.

Zamon, J. E. (2001). Seal predation on salmon and forage fish schools as a function of tidal currents in the San Juan Islands, Washington, USA: Seal predation on salmon and forage fish. *Fisheries Oceanography*, *10*, 353–366. https://doi.org/10.1046/j.1365-2419.2001.00180.x.

Zydlewski, G. B., Haro, A., & McCormick, S. D. (2005). Evidence for cumulative temperature as an initiating and terminating factor in downstream migratory behaviour of Atlantic salmon (Salmo salar) smolts. *Canadian Journal of Fisheries and Aquatic Sciences*, *62*, 68–78. https://doi.org/10.1139/f04-179.

SUPPORTING INFORMATION

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

How to cite this article: Lilly, J., Honkanen, H. M., Bailey, D. M., Bean, C. W., Forrester, R., Rodger, J. R., & Adams, C. E. (2022). Investigating the behaviour of Atlantic salmon (*Salmo salar* L.) post-smolts during their early marine migration through the Clyde Marine Region. *Journal of Fish Biology*, *101*(5), 1285–1300. https://doi.org/10.1111/jfb.15200

APPENDIX A

TABLE A1 Total number of Atlantic salmon smolts (No.) tagged and released (Rel) in the River Endrick (End), Leven (Lev) and Gryffe (Gry) that were detected at the exit of the River Endrick (Figure 1, R17), and within the River Leven (Figure 1, R18–R20) and Gryffe (Figure 1, R1–R3), respectively

Region	Rel.	No.	R1	R2	R3	R17	R18	R19	R20
LL	End	99	-	-	-	75 (0)	23 (10)	19 (3)	22 (–)
Leven	Lev	46	-	-	-	-	-	13 (15)	28 (–)
Leven	End com	145	-	-	-	-	-	32 (18)	50 (–)
Gryffe	Gry	102	99 (0)	93 (0)	93 (–)	-	-	-	-

Note. Receivers are labelled in sequential order towards the exit of the Clyde estuary. Receiver efficiency for River Leven release smolts was not estimated for the first River Leven receiver, as smolts were released a ~170 m downstream of the receiver. The number of salmon smolts that were not detected at a receiver but were detected at the subsequent downstream receiver is indicated by brackets.