Received: 20 March 2023 | Revised: 7 October 2023 | Accepted: 13 October 2023
DOI: 10.1111/jfb.15591

REGULAR ARTICLE

JOURNAL OF FISH BIOLOGY fsbi

Migration patterns and navigation cues of Atlantic salmon post-smolts migrating from 12 rivers through the coastal zones around the Irish Sea

Jessie Lilly[1] | Hannele H. Honkanen[1] | Jessica R. Rodger[1,2] | Diego del Villar[3] | Patrick Boylan[1] | Amy Green[1] | Diego Pereiro[4] | Lorna Wilkie[2] | Richard Kennedy[5] | Andrea Barkley[5] | Robert Rosell[5] | Niall Ó. Maoiléidigh[4] | Ross O'Neill[4] | Catherine Waters[4] | Deirdre Cotter[4] | David Bailey[6] | William Roche[7] | Ross McGill[3] | James Barry[7] | Samantha V. Beck[8,9] | Jim Henderson[10] | Debbie Parke[10] | Frederick G. Whoriskey[11] | Brian Shields[12] | Philip Ramsden[12] | Silas Walton[13] | Melanie Fletcher[13] | Ken Whelan[2] | Colin W. Bean[1,14] | Sophie Elliott[15] | Adrian Bowman[16] | Colin E. Adams[1]

[1]Scottish Centre for Ecology and the Natural Environment, School of Biodiversity, One Health and Veterinary Medicine, University of Glasgow, Glasgow, UK

[2]Atlantic Salmon Trust, Perth, UK

[3]Loughs Agency, Londonderry, UK

[4]Marine Institute, Newport, Ireland

[5]Agri-food and Biosciences Institute, Hillsborough, UK

[6]School of Biodiversity, One Health and Veterinary Medicine, University of Glasgow, Glasgow, UK

[7]Inland Fisheries Ireland, Dublin, Ireland

[8]Galloway Fisheries Trust, Newton Stewart, UK

[9]Institute for Biodiversity and Freshwater Conservation, UHI Inverness, Inverness, UK

[10]The Nith Catchment Fishery Trust and Nith District Salmon Fishery Board, Dumfries, UK

[11]Ocean Tracking Network, Dalhousie University, Halifax, Nova Scotia, Canada

[12]Environment Agency, Penrith, UK

[13]Natural England, Penrith, UK

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

[15]Game & Wildlife Conservation Trust, Salmon & Trout Research Centre, Wareham, UK

Abstract

The freshwater phase of the first seaward migration of juvenile Atlantic salmon (*Salmo salar*) is relatively well understood when compared with our understanding of the marine phase of their migration. In 2021, 1008 wild and 60 ranched Atlantic salmon smolts were tagged with acoustic transmitters in 12 rivers in England, Scotland, Northern Ireland and Ireland. Large marine receiver arrays were deployed in the Irish Sea at two locations: at the transition of the Irish Sea into the North Atlantic between Ireland and Scotland, and between southern Scotland and Northern Ireland, to examine the early phase of the marine migration of Atlantic salmon smolts. After leaving their natal rivers' post-smolt migration through the Irish Sea was rapid with minimum speeds ranging from 14.03 to 38.56 km.day^{-1} for Atlantic salmon smolts that entered the Irish Sea directly from their natal river, to 9.69–39.94 km.day^{-1} for Atlantic salmon smolts that entered the Irish Sea directly from their natal estuary. Population minimum migration success through the study area was strongly correlated with the distance of travel, populations further away from the point of entry to the open North Atlantic exhibited lower migration success. Post-smolts from different populations experienced different water temperatures on entering the North Atlantic. This was largely driven by the timing of their migration and may have significant consequences for feeding and ultimately survivorship. The influence of water currents on post-smolt movement was investigated using data from previously constructed numerical hydrodynamic models. Modeled water current data in the northern Irish Sea showed that post-smolts had a strong preference for migrating when

[16]School of Mathematics & Statistics, University of Glasgow, Glasgow, UK

Correspondence
Jessie Lilly, Scottish Centre for Ecology and the Natural Environment, School of Biodiversity, One Health and Veterinary Medicine, University of Glasgow, Rowardennan, Glasgow, UK.
Email: jessiemlilly@gmail.com

Present address
Jessie Lilly, Northwest Atlantic Fisheries Centre, St.Johns, Newfoundland, Canada.

Funding information
Atlantic Salmon Trust; Department of Agriculture, Environment and Rural Affairs, Northern Ireland; Derwent Owners Association; Dumfries and Galloway Council; Environment Agency; EU INTERREG VA Programme (Environment Theme), Grant/Award Number: IVA5060; Holywood Trust; Maritime Fisheries Fund; Natural England; NatureScot; Nith District Salmon Fishery Board; Salmon Scotland; United Utilities PLC

the current direction was at around 283° (west-north-west) but did not migrate when exposed to strong currents in other directions. This is the most favorable direction for onward passage from the Irish Sea to the continental shelf edge current, a known accumulation point for migrating post-smolts. These results strongly indicate that post-smolts migrating through the coastal marine environment are: (1) not simply migrating by current following (2) engage in active directional swimming (3) have an intrinsic sense of their migration direction and (4) can use cues other than water current direction to orientate during this part of their migration.

KEYWORDS
acoustic tags, coastal zone, current following, marine migration, migration cues, post-smolts, slope current, telemetry

1 | INTRODUCTION

Migration is common in both aquatic and terrestrial organisms and involves population-level directed seasonal movements amongst habitats (Avgar et al., 2014; Dingle & Drake, 2007). These movements often occur over long distances and can evolve if the fitness benefits, such as increasing the likelihood of acquiring resources, outweigh the costs of migration (Avgar et al., 2014; Mueller & Fagan, 2008; Tamario et al., 2019). The costs associated with long distance migration can include increased exposure to natural and anthropogenic stressors, predators, diseases, and parasites (Altizer et al., 2011; Dieperink et al., 2002; Holm et al., 2006; Shephard & Gargan, 2021). In addition, there is potential for navigational error, which may increase the likelihood of mortality (Furey et al., 2015; Lilly et al., 2021). Understanding the navigational cues that guide the timing and direction of movement involved in migrations will help to uncover the ecological processes involved (Minkoff et al., 2020; Nathan et al., 2008). There is still very little known about the cues that marine organisms use to navigate through the open sea. The lack of visual landmarks in pelagic environments (Luschi, 2013) have driven interest in investigating the use of magnetic fields, localized water currents, and salinity and temperature gradients as navigation aids in this environment (Dadswell et al., 2010; Lohmann et al., 2022; Minkoff et al., 2020).

One species that undergoes long distance marine migrations is the Atlantic salmon (*Salmo salar*). The Atlantic salmon is an anadromous salmonid that spawns in fresh water and migrates to sea to access better feeding opportunities (Limburg & Waldman, 2009). The main assumed benefits of migration to sea are higher fecundity in females and greater mating success in males, that result from a larger body size from faster growth at sea compared with freshwater (Adams et al., 2022). However, there are costs associated with this migratory strategy including increased energy expenditure and exposure to anthropogenic and natural stressors in the marine environment (Alerstam et al., 2003; Limburg & Waldman, 2009).

After 1–7 years in their natal river, Atlantic salmon smolts begin to migrate downstream towards the estuarine environment (Milner et al., 2003; Thorstad, Uglem, et al., 2012; Zydlewski et al., 2014). This downstream migration tends to occur during the night and is rapid, with migration more likely during periods of high river discharge (Bjerck et al., 2021; Lothian et al., 2018). Nocturnal migration is thought to be a tactic that decreases the risk from visual predators (Lefèvre et al., 2012). Larger smolts are thought to be better able to evade predators due to their faster swimming speeds (Flávio et al., 2021). Atlantic salmon smolts from rivers in the UK and Ireland enter the estuarine environment during late April and May. Following entry to sea water they are referred to as post-smolts until December 31st of the same year (Gilbey et al., 2021; ICES, 2020). Once in the estuary, post-smolts have been reported to rely on tidal currents to rapidly transit this habitat, mainly moving during the night at ebb tide (Lacroix et al., 2004; Lothian et al., 2018). Studies have shown a positive relationship between sea entry date and subsequent marine survival, however, the mechanism through which this occurs is uncertain (although for discussion of possibilities see Friedland et al., 1998; Kennedy & Crozier, 2010).

Until recently, knowledge of the distribution of post-smolts in the offshore marine environment has largely been limited to research directed surface trawls and the allocation of captured post-smolts to river of origin by genetics or tagging (Gilbey et al., 2021; Holst et al., 2000; SALSEA-Merge, 2012). For post-smolts migrating from rivers in the UK and Ireland, trawl data have shown that post-smolts from multiple river systems overlap temporally (in May and June) and spatially in the continental slope current which flows approximately north to the west of the coasts of Ireland and Scotland (Gilbey et al., 2021; Holm, 2000; SALSEA-Merge, 2012). The slope current ultimately flows towards known salmon feeding grounds in the Norwegian Sea and the Vøring plateau, where post-smolts from the UK, Ireland and elsewhere in Europe, have been captured during the month of August (Gilbey et al., 2021; Holm, 2000; Shelton et al., 1997). In addition, post-smolts are present in the slope current and Vøring plateau when water temperatures range between 6 and 12°C (Gilbey et al., 2021; Hindar et al., 2020; Holm, 2000; Holm et al., 2003).

Whilst there is a reasonable body of literature on the navigational cues used by smolts in fresh water and some data on the location of fish of known origin in the offshore marine environment, there is currently a knowledge gap in our understanding of how they navigate through the coastal marine environment (Crozier et al., 2018; Mork et al., 2012). Information on the environmental cues that post-smolts may use in coastal marine regions is mostly limited to inferences from the results of particle tracking studies. These studies suggest that how salmonid post-smolts use the navigational cues available to migrate in coastal areas is likely to be dependent on the geographic location of the river system (Furey et al., 2015; Mork et al., 2012; Ounsley et al., 2020). Thus, post-smolts may adopt strategies that increase their metabolic costs by actively swimming in a direction different from local current patterns, if such tactics increase their chances of arriving at feeding grounds during periods of high prey abundance and/or decrease their exposure to predators (Ounsley et al., 2020). For example, Mork et al. (2012) predicted from simulations that post-smolts emigrating from rivers along the western coast of Ireland could gain a migration cost advantage on their migration towards their northern feeding grounds by migrating with the continental slope current early in their marine migration. In contrast, Ounsley et al. (2020) used simulated post-smolt movements from rivers that drain to the west coast of Scotland to note that for post-smolt migration to coincide with the temporal and spatial patterns of post-smolts in the continental shelf edge current shown by scientific trawling surveys, considerably more active swimming in directions that frequently deviate from local current patterns was necessary.

An understanding of the migratory pathways and cues used for navigation by Atlantic salmon is important information for management of anthropogenic coastal activity on this important species (Furey et al., 2015; Gilbey et al., 2017). Acoustic telemetry has developed sufficiently in the last few years to allow for the tracking of relatively small Atlantic salmon smolts and post-smolts as they make the transition from river to the sea. The technique involves inserting a small transmitting tag into a study animal. The tag emits a sound signal, coded with a unique identification number that can be detected by acoustic receivers often placed in a fixed position in the marine environment (Crossin et al., 2017). In this study we used acoustic telemetry to describe the migration of salmon from 14 sites in 12 rivers around the Irish Sea.

This study had three main objectives:

1. To compare the relative migration success of post-smolts amongst populations migrating through the Irish Sea from different river systems.
2. To identify some underlying drivers of variation in migration success.
3. Identify the environmental cues which best predict the migration of Atlantic salmon through the transitional zone from the Irish Sea into the North Atlantic.

2 | MATERIALS AND METHODS

This study was made possible by an extensive collaboration between six projects (SeaMonitor; the West Coast Tracking Project; COMPASS, the Nith, Derwent and AFBI Salmon Tracking Projects) involving 14 different research groups who shared tasks and data to address the regional scale questions addressed here.

2.1 | Study area

The Irish Sea (51.9° to 56° N; 2.9 to 7.0 °W) is a channel that extends around 350 km roughly orientated along a north–south axis. It connects to the North Atlantic Ocean in the north via the North Channel and to the Celtic Sea in the south (Figure 1; Dabrowski et al., 2010; Howarth, 2005). For the purpose of this paper, the North Channel is included as part of the Irish Sea. The main drivers of the current in the Irish Sea are the M2 (the gravitational effect of the moon) and S2 (the gravitational effect of the sun) tidal constituents with the dominant flow directed northwards (2.50 $km^3.day^{-1}$; Olbert et al., 2012; Olbert & Hartnett, 2010).

2.2 | Fish capture and tagging

In this study, 1008 wild and 60 ranched (River Burrishoole) Atlantic salmon were captured as migrating smolts from 14 sites in 12 separate rivers (in the UK and Ireland) during April and May 2021. Wild smolts were captured using either a 1.2 m diameter rotary screw trap, a fyke net or a wolf trap (River Burrishoole only). Ranched smolts from the River Burrishoole were reared in ponds adjacent to their natal river and released at the same location as wild smolts (see Cotter et al. 2022 for more information). Smolts were tagged in one river in England (River Derwent), four rivers in Scotland (the Rivers Gryffe, Endrick, Nith, Bladnoch,) plus one tributary of the River Nith (the River Crawick), six rivers in Northern Ireland (Rivers Glendun, Carey, Bush, Bann, Roe, $n = 11$,) and one tributary of the River Bann (Agivey) and one river in Ireland (River Burrishoole; Figure 1; Table 1). Tagged fish were released at the capture site except for those from the River Endrick and River Derwent where a proportion of fish were also transported downstream before release (Figure 1; Table 1). Data on fish tagged from each of the two tributaries of the Nith catchment (River Nith & Crawick) were combined (henceforth called the River Nith). Similarly, data from the River Bann and Agivey River were combined as the River Bann (Figure 1). Salmon smolts were tagged with five models of acoustic tags (V7-2x, V7-4x, V8-4x, V7D-2x; InnovaSea, Bedford, Nova Scotia, Canada). All models emit a coded acoustic signal on 69 kHz, the signal being emitted with a

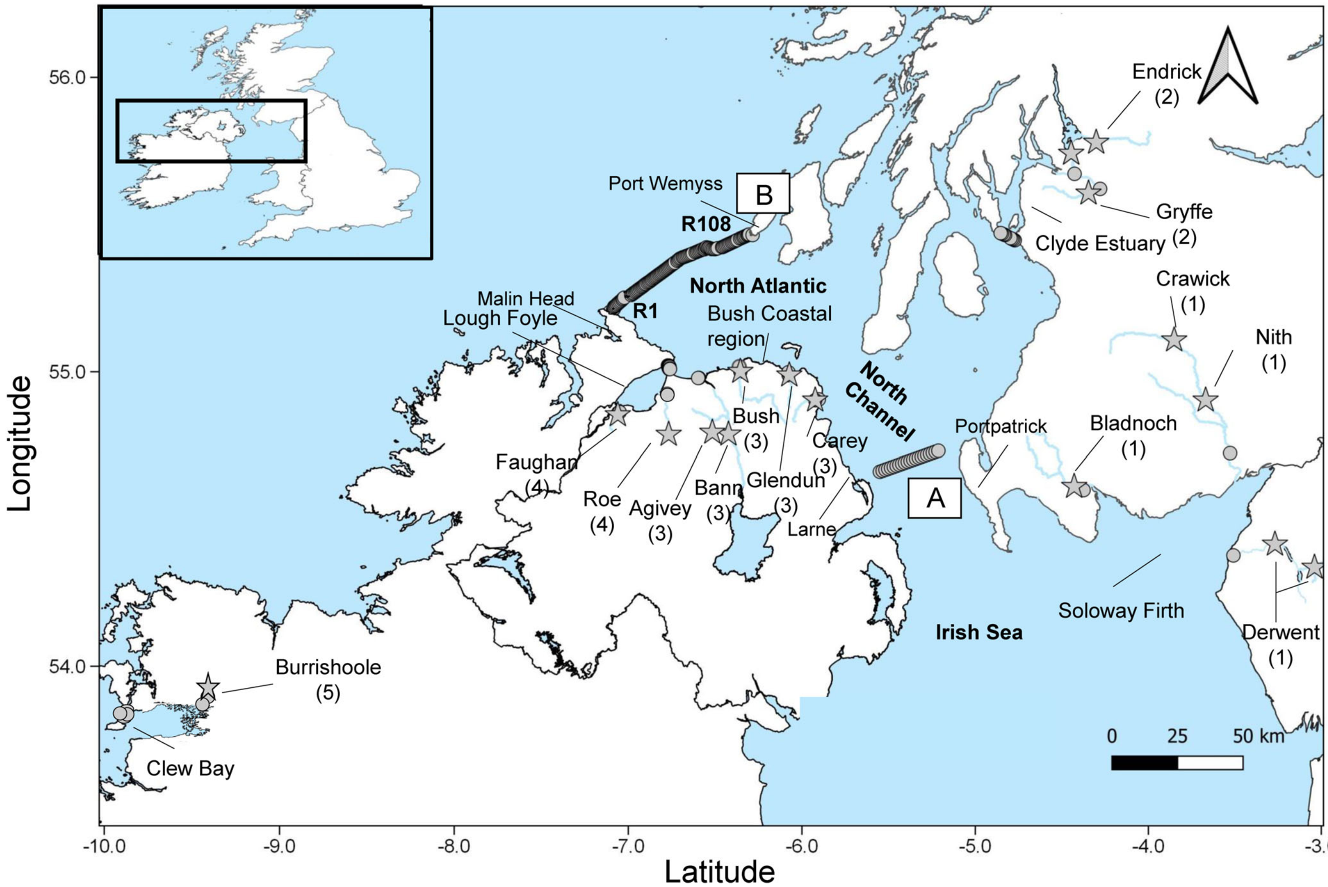

FIGURE 1 Map displaying the 14 capture sites in 12 rivers where Atlantic salmon smolts ($n = 1008$) were captured for tagging in England, Scotland, Northern Ireland and the Republic of Ireland for this study. In addition, 60 hatchery origin smolts were tagged and released in the River Burrishoole. The coastal region each river belongs to is referenced in brackets next to the river name. Where Region one (1) refers to the Solway Firth (Rivers Derwent, Nith, Bladnoch); Region two (2) refers to the Clyde Estuary (Rivers Endrick and Gryffe); Region three (3) refers to the Bush Coastal region (rivers Bann, Bush, Carey and Glendun); Region four (4), refers to Lough Foyle (rivers Roe and Faughan); Region five (5), refers to Clew Bay (River Burrishoole). Tagged fish release sites are represented by stars, and acoustic receivers ($n = 183$) are represented by gray dots. Marine monitoring lines (A and B) in the Irish Sea are labeled in alphabetical order from south to north. Twenty-two acoustic receivers were initially deployed at monitoring line A. One hundred and eight acoustic receivers were deployed at monitoring line B and are labeled in numerical order from the furthest west receiver (R1) on the monitoring line to the furthest east (R108). Refer to Figure S2 for the locations of acoustic receivers that were not retrieved from marine monitoring line A ($n = 2$) and B ($n = 9$).

pre-determined mean delay (with variation around that delay) from the last signal; the nominal delay of tags in this study are shown in Table 1. The minimum fork length and weight of smolts tagged with V7-2x, and V7-4x was 130 mm and 20 g, respectively. Tag models used differed in their dimensions. The mass and length of tags were: V7-2x, 1.5 g and 19.5 mm, V7-4x 1.8 g and 21.5 mm, V8-4x 2.0 g and 20.5 mm, and V7D-2x 1.7 g and 22.0 mm. The tags were programmed with differing transmission rates and had expected battery life durations of 99 to 522 days dependent on tag model and tagging location (Table 1).

2.3 | Fish tagging

Tagging followed standard surgical tagging methods. In general, once anesthetized with MS222, smolts were measured for fork length (±0.1 cm) and mass (±0.1 g). The tag was then inserted into the abdominal cavity through a ca. 9–10 mm anterior to posterior incision made lateral to the ventral midline, anterior to the pelvic girdle. One or two interrupted surgeon knots were then used to close the incision using veterinary sutures. The fish were placed in aerated water to recover and released once fully recovered (see Lilly et al., 2021 for details). In the River Burrishoole, fish were held overnight in covered flow-through tanks before release the following day, elsewhere fish were released on the same day as tagging during daylight hours. The care and tagging of Atlantic salmon smolts was conducted under license from national authorities (UK Home Office license PP0483054 (England/Scotland); UK Home Office license PPL2869 (N. Ireland); HPRA License AE19121/P003 Case No. 7028960 (Ireland).

2.4 | Acoustic receiver deployment

In total 183 acoustic receivers operating at a frequency of 69 kHz were deployed in this study (Table S1; Figure 1). This included VR2W/

TABLE 1 Details of the salmon smolts fitted with acoustic tags during 2021 in England (Eng), Scotland (Scot), Northern Ireland (NI) and the Republic of Ireland (I) for this study.

Loc.	River	Release site (lat, long °)	Tag type	Tag life (days)	No. (*n*)	Nom. delay (s)	Date tagged (day-month, 2021)	Tag expiry date (day-month, all 2021 except*)	FL (mm)	Mass (g)	Tag burden (by mass)
Eng.	Derwent	54.6105, −3.0616 54.6876, −3.2978	V7-2x	75	41 (150)	18–38	29-04 to 03-05	13-07 to 17-07	141 ± 7.3	30.0 ± 5.02	0.05 ± 0.01
Scot	Bladnoch	54.8672, −4.4989	V7-2x	75	54 (130)	18–38	20-04 to 14-05	04-07 to 28-07	142 ± 7.9	30.0 ± 5.05	0.06 ± 0.01
	Nith	55.3783, −3.9313	V7-2x	75	66 (130)	18–38	23-04 to 06-05	07-07 to 20-07	148 ± 10.9	33.2 ± 7.20	0.05 ± 0.01
	Crawick (Nith tributary)	55.3783, −3.9313	V7-2x	75	23 (49)	18–38	16-04 to 23-04	30-06 to 07-07	138 ± 5.2	27.0 ± 2.33	0.06 ± 0.01
	Endrick	56.0492, −4.4399, 56.0085, −4.5897	V7-2x	75	50 (145)	18–38	15-04 to 03-05	29-06 to 17-07	143 ± 8.8	29.7 ± 5.61	0.06 ± 0.01
	Gryffe	55.8693, −4.4942	V7-2x	75	93 (102)	18–38	12-04 to 24-04	26-06 to 08-07	149 ± 10.1	34.2 ± 6.66	0.05 ± 0.01
NI	Bann	54.9841, −6.5618	V7-2x	99	18 (59)	20–40	07-05 to 25-05	14-08 to 01-09	163 ± 15.5	44.8 ± 13.90	0.04 ± 0.01
	Agivey (Bann tributary)	54.9879, −6.6661	V7-2x	99	16 (41)	20–40	20-04	28-07	153 ± 9.3	37.7 ± 7.1	0.04 ± 0.01
	Bush	55.2029, −6.5233	V7-4x	522	73 (80)	30–60	13-04 to 26-04	*17-09 to 30-09-22	168 ± 8.6	48.0 ± 7.99	0.04 ± 0.01
	Carey	55.2010, −6.2292	V7-2x	99	6 (9)	20–40	29-04 to 05-05	06-08 to 12-08	165 ± 6.2	45.3 ± 4.18	0.03 ± 0.0
	Glendun	55.1215, −6.0663	V7-2x	99	21 (24)	20–40	16-04 to 30-04	07-24 to 07-08	142 ± 7.5	31.1 ± 4.55	0.05 ± 0.01
	Roe	54.9710, −6.9253	V7-2x	94	9 (11)	30–60	29-04	01-08	152 ± 3.9	36.4 ± 3.32	0.04 ± 0.01
	Faughan	55.0251, −7.2359	V7-2x	94	38 (53)	30–60	07-05 to 15-05	09-08 to 17-08	143 ± 4.2	-	-
I	Burrishoole	53.9137, −9.5713	V8-4x	173	46 (50)	40–80	05-05 to 07-05	25-10 to 27-10	195 ± 9.6	84.5 ± 13.50	0.02 ± 0.004
			V7D-2x	100	9 (10)	30–90	07-05	15-08	205 ± 17.8	101.8 ± 28.50	0.02 ± 0.01
			V7-2x	120	19 (25)	40–80	05-05 to 11-05	04-09 to 08-09	150 ± 7.1	32.0 ± 4.04	0.05 ± 0.01

Note: No. is the number that successfully migrated from their natal river or estuary into the Irish Sea from *n*, the total number tagged. The tag model (Tag type), the tag life (Tag life), the nominal tag signal delay (Nom. Delay; the range of time over which the tag emits a signal), the date range that they were tagged (Date tagged), the tag expiry date (Tag expiry date; all tags expired during 2021, excluding River Bush smolts tagged with V7-4x tags which expired during 2022 [*]), fork length (FL, mean ± SD), mass (Mass, mean ± SD) and tag burden (Tag Burden, mean ± SD) are presented. All smolts were wild, excluding River Burrishoole smolts tagged with V8-4x and V7-2x tags that were of hatchery origin. For a summary of the distribution of the length (FL) of Atlantic salmon smolts tagged in each river system see Figure S1.

Tx receivers (InnovaSea Ltd., Nova Scotia, Canada) deployed at the exit of the rivers where smolts were tagged ($n = 11$; Figure 1; Table S1). Only smolts that were detected on the final riverine receiver were included in the analysis. In addition, three monitoring lines were deployed at the exit of estuaries and embayments including: the Clyde Estuary ($n = 8$; Figure 1; Table S1), Lough Foyle ($n = 10$; Figure 1; Table S1) and Clew Bay ($n = 10$; Figure 1; Table S1). Here an estuary was defined as "*a basin where river and ocean forcing (being both tides and waves) interact to determine* [its] *physical properties*" (Hume et al., 2007) and a coastal embayment as "*an extension of the sea into an indentation of the coast*" (Schwartz, 1982).

Lastly, two monitoring lines consisting of VR2AR receivers (see Lilly et al. (2021) for a description of acoustic receiver types) were deployed in the Irish Sea; this included a line of 22 acoustic receivers extending from Larne, Northern Ireland to Portpatrick, Scotland (54.83° N 5.71° W to 54.89° N 5.14° W) deployed by the COMPASS project (Figure 1; monitoring line A; distance ca. 36 km; mean receiver spacing [± SD] = 1.13 km ± 1.83 $\times 10^{-3}$ km; mean depth of receivers = 0.14 ± 0.02 km) and a line of 108 acoustic receivers extending from Malin Head, Ireland to Port Weymss, Scotland deployed by the SeaMonitor project (Figure 1; monitoring line B; distance ca. 63 km; mean receiver spacing = 0.58 ± 0.20 km; mean depth of receivers = 0.04 ± 0.02 km). The combination of V7 tags and VR2AR acoustic receivers has been reported in three studies to have a raw detection efficiency of 75% and 90% at 200 m in coastal conditions in Scotland similar to those of this study (Main, 2021; Newton et al., 2021; Honkanen et al., 2018). In our study, 19 acoustic receivers could not be retrieved at the end of the study and were presumed lost. This included four at the exit of the Clyde Estuary, three at the exit of Lough Foyle, one at the exit of Clew Bay, two from monitoring line A, and nine from monitoring line B (Table S1; Figure S2).

2.5 | Environmental data

Modeled water current data for the study area were derived from the Marine Institute's Northeast Atlantic Model, or NEA-ROMS (Dabrowski et al., 2016). The model is based on the Regional Ocean Modeling System (ROMS), a free-surface, hydrostatic, primitive equation ocean model (Shchepetkin & McWilliams, 2005). The model domain covers a significant portion of the North-West European continental shelf with a horizontal and vertical resolution of about 4 km and 40 sigma levels (total number of vertical layers), respectively. It is one-way nested within the high- resolution (1/12°) Mercator Ocean PSY2V4R2 operational model of the North Atlantic, whereby daily values for potential temperature, sea surface height and velocity are linearly interpolated at the open ocean boundaries (Nagy et al., 2020).

Seawater temperature was derived from the WeStCOMS model (Aleynik et al., 2016). This model resolves the circulation over an area extending from the Isle of Man to the North Minch, and from the Scottish mainland to the Outer Hebrides archipelago, with a varying horizontal resolution of 0.1–2.3 km. WeStCOMS has a terrain-following coordinate system (Chen et al., 2006), meaning that the depths of the vertical layers change depending on the bathymetry and the fluctuations of the sea level. Temperature was derived from the layer closest to the surface, with a depth range from zero to two meters below the surface. This depth was chosen as post-smolts have been reported to migrate primarily in the top three meters of the water column during their early marine migration (Davidsen et al., 2008; Holm et al., 2006; Newton et al., 2021). In a tidally mixed area like the Irish Sea, the vertical gradients of temperature are minimal. Therefore, the temperature in the WeStCOMS surface layer is representative of the temperature at the depth where post-smolts migrate.

WeStCOMS is restarted every week from a resting state, introducing a discontinuity in the circulation series. Nevertheless, the distribution of temperature and salinity is retained. As a result, the model restart does not affect the continuity of the temperature series. Lastly, in this study, hourly ocean currents and temperatures were derived from the closest NEA-ROMS and WeStCOMS nodes to each acoustic receiver deployment location.

2.6 | Statistical analysis

All analyses in this study were conducted using R versions 3.5.3 and 4.1.1 (R Core Team, 2021).

2.7 | False detection filtering

Detection data was filtered for false detections using the short-interval criterion in the R package *Glatos* and by removing consecutive detections at a single receiver that occurred within the period that was less than the minimum nominal delay of that tag (Table 1; Holbrook et al., 2018; Pincock, 2012 (for a detailed description of false detection filtering see Lilly et al. (2022)). Post-smolts that were detected at monitoring lines A and B for multiple days beyond the date when 75% of post-smolts had left the Irish Sea were removed from the analysis, as such detections were likely either a fish mortality, or a tag that was consumed by a predator. In this study only one detection met this criterion; that of a tag implanted into an Atlantic salmon post-smolt from the River Bann (ID: 46806) detected on monitoring line B from June 30th – July 6th. All other tags detected at lines A and B in this study were assumed to be indicative of the presence of a passing post-smolt.

2.8 | Migration success

Minimum migration success was defined as the number of post-smolts detected at a monitoring line expressed as a proportion of all detections of tags that entered the Irish Sea either from their natal river, or estuary (Clyde Estuary (River Endrick, River Gryffe), Lough Faughan (River Roe, River Faughan) (Figure 1). The *minimum migration success rate* for a river or group of rivers migrating northward through the Irish Sea, is the minimum migration success rate for that group expressed proportionate to the distance traveled in km (%.km^{-1}). Minimum migration success rates calculated for post-smolts entering the Solway Firth (from the rivers Derwent, Nith and Bladnoch) should be interpreted with caution as there was no acoustic receiver array deployed south of monitoring line A which prevented us from determining if these post-smolts were engaging in southerly migrations (Green et al., 2022). Therefore, while results are reported for these rivers in subsequent tables, their minimum migration success to monitoring line B is not directly compared to other populations.

2.9 | Biotic factors influencing migration success

To examine the effects of biotic factors on minimum migration success through the Irish sea, fork length (fl), mass, tag burden (fraction of tag mass to body mass), condition factor (k) (calculated according to Barnham and Baxter (1998)), date of sea entry and minimum distance traveled to monitoring line B were used as factors in a General Linear Mixed Model (GLMM) with a binomial error structure and logit link function that was fit using the R package lme4 stats (Bates et al., 2015).

$$\text{Logit}(\text{Migration success} \sim \text{FL} + \text{k} + \text{Date of sea entry} + \text{Minimum distance traveled} + (1|\text{River}). \quad (1)$$

River was included as a random effect (Kessel et al., 2016). The dependent variable (Irish Sea migration success) was coded as 1, if a post-smolt tag was detected on monitoring line B, and 0 if a post-smolt tag was detected entering the marine study area but not on monitoring line B. Smolts migrating from rivers draining into the Solway Firth were excluded from this analysis (rivers Derwent, Nith and Bladnoch) for the reason indicated above, as were smolts from the River Burrishoole as this river did not drain directly into the Irish Sea. River Faughan smolts were also removed from the analysis as mass measurements were not available. Smolts that were not detected leaving their natal river or estuary but were detected on monitoring line B ($n = 19$) were removed from the analysis. Date of sea entry was converted to a Julian day (decimal date) using the function 'decimal_date' in the R package lubridate (Grolemund & Wickham, 2011). Correlation between continuous variables was assessed using Spearman's Rank correlation tests. Fork length was highly correlated with mass ($r = 0.94$) and tag burden ($r = -0.90$), therefore the initial model only included fork length, k, Julian day and minimum distance traveled. Thus, 257 detections were included in the analysis ($1 = 101$, $0 = 156$). The 'glmulti' function in the glmulti package with a wrapper to incorporate the random effect was used to select the model that contained the best set of independent variables with the lowest Akaike Information Criterion (AIC) (Barry et al., 2016). The top three models that had a ΔAICc <2 were then compared with likelihood ratio tests using the function 'lrtest' in the R package lmtest (Zeileis, & Horthorn., T., 2002) to determine the significance of each explanatory variable in the final model. Lastly, once the final model was determined, McFaddens R^2 was used to assess the fit of the model.

2.10 | Migration duration and speed

The mean duration of the post-smolt migration through the Irish Sea was calculated as the time elapsed between the final tag detection at the point of entry to the marine study area and their first detection at monitoring line B. In addition, the mean speed of migrating post-smolts through the Irish Sea was calculated in kilometers per day (km. day^{-1}). To do this the minimum distance traveled to reach monitoring line B, calculated as a straight-line distance (excluding land) using the Google Earth "Ruler tool" between the point of entry to the study site and monitoring line B (sensu Barry et al., 2020), divided by the time elapsed between the two detection points.

2.11 | Post-smolt distribution

To assess the distribution of detections of Atlantic salmon post-smolts across monitoring lines A and B, post-smolt detections were grouped into regional clusters based on the proximity of neighboring rivers. Five regional clusters were identified. Region 1 was defined as the Solway Firth (Rivers Derwent, Nith and Bladnoch), Region 2 was the Clyde Estuary (Rivers Endrick & Gryffe), Region 3 was the Bush Coastal region (Rivers Bann, Bush, Carey & Glendun), Region 4 as Lough Foyle (Rivers Roe & Faughan) and Region 5 was Clew Bay (River Burrishole).

Pearson Chi-square tests (χ^2) were used to determine if the detection frequency of tags in post-smolts from each region was equally distributed amongst receivers on monitoring lines A and B. Due to the large number of receivers in each monitoring line, line A receivers were clustered into 11 groups comprising two adjacent receivers and monitoring line B was divided into 12 groups of nine adjacent receivers. To ensure that the number of post-smolts detected in a receiver group was not overestimated, duplicated detections of the same individual fish in the same receiver group were removed. Lastly, if post-smolt tags were detected in adjacent groups within a period of time less than the tag's nominal delay (Table 1) then only the initial detection was retained for analysis.

The distribution of post-smolt tag detections on monitoring lines A and B was visualized using the 'get_google_map' function in the R package *ggmap* (Kahle & Wickham, 2013). A heatmap of the number of post-smolt tag detections at each site was constructed using the 'stat_density_2d' function in the R package *ggplot2* (Wickham, 2016). Lastly, to determine where most post-smolts exited the Irish Sea, the interquartile range of the receivers where their initial detection occurred on monitoring line B was extracted for each population. The interquartile range represents the 25th – 75th percentile around the median of the receiver locations (ordered from 1 to 108), on which post-smolts were detected on monitoring line B. For this analysis and the analyses described below, the migration exit point from the Irish Sea was defined as the initial detection of tagged fish on monitoring line B, as at this point, we knew they were traveling in a broadly north westerly direction and assumed that entry into the North Atlantic followed.

2.12 | Migration timing

To determine the dates when the highest percentage of post-smolts were most likely to enter and exit the Irish Sea for the North Atlantic, the median and 25% quantiles of dates were calculated for the final detection of tagged post-smolts at the point of entry to the study area (either from their natal river (regions 1 and 3) or estuary (regions 2 and 4) and on initial detection on monitoring line B (Bjerck et al., 2021).

2.13 | Environmental correlates of transition into North Atlantic

2.13.1 | Temperature

To determine if most post-smolts exited from the Irish Sea into the North Atlantic during the temperatures reported for Atlantic salmon during their riverine and marine migration, the modeled average daily water temperature recorded across all receiver locations on monitoring line B on the median date when post-smolts from each river system had their initial detection on monitoring line B was extracted from the WeStCOMS model.

2.14 | Environmental cues of transition into North Atlantic

2.14.1 | Time of day

To determine if the exit of a post-smolt from the Irish Sea was dependent on time of day, the mean number of exits for each hour of the day and night were compared. Where day and night were defined as the hours between sunrise and sunset and between sunset and sunrise, respectively (Christoffersen et al., 2019). Sunset and sunrise times were calculated using the getSunlightTimes function in the R package *suncalc* (Thieurmel & Elmarhraoui, 2019). The initial detection of a post-smolt on monitoring line B during each hour was then converted to degrees (and to a circular object) using the R package *circular* and visualized using circular rose diagrams (Lund & Agostinelli, 2018), where 0° and 180° represented midnight and noon, respectively (Lilly et al., 2022).

2.14.2 | Current direction

Hourly current direction data for each receiver location on monitoring line B was obtained from the NEA-ROMS hydrodynamic model as described above, where currents traveling in the north to east, east to south, south to west and west to north were represented by compass bearings in the ranges from 1° to 89°, 90°–179°, 180°–269° and 270°–359°, respectively. Since the current direction data were averaged over hourly periods, the timestamps when post-smolts were initially detected on monitoring line B were also rounded to the nearest hour. Rayleigh's tests of uniformity were then used to test whether the initial detection of a post-smolt on monitoring line B coincided with a specific current direction. These movements were visualized using circular rose diagrams (Lilly et al., 2022; Murray et al., 2018).

To assess whether post-smolts were exiting the Irish Sea with the most frequent current direction, we used rose diagrams to plot the current direction when a post-smolt was initially detected on a receiver on monitoring line B versus the current directions available to them at the same receiver during the timespan they were present in the Irish Sea region. Rose diagrams were created for the five receivers where the highest number of initial detections of post-smolts occurred.

3 | RESULTS

3.1 | Tagged fish summary

In total, 582 Atlantic salmon smolts successfully migrated from their natal river into estuarine and marine waters and were included in this study. The mean fork length (mean mm ± SD, $n = 527$), mass (g, $n = 489$) and tag burden (tag to body mass ratio, $n = 489$) of wild smolts in this study were 149 ± 12.7 mm, 35.0 ± 9.3 g and 0.05 ± 0.01, respectively. The mean fork length, mass and tag burden of ranched smolts ($n = 55$) from the River Burrishoole in this study were 197.0 ± 11.8 mm, 87.3 ± 17.7 g and 0.02 ± 0.01, respectively.

3.2 | Migration metrics

For Atlantic salmon smolts that entered the Irish Sea directly from their natal river (regions 1 and 3) minimum migration success ranged from 6% for the River Nith post-smolts to 62% for River Bann post-smolts (Table S2). Atlantic salmon smolts from regions 1 and 4 had to migrate through their natal estuary prior to reaching the Irish Sea. The minimum migration success of post-smolts through the Irish Sea for fish from these rivers ranged from 24% for River Endrick post-smolts to 95% for River Faughan post-smolts (Table S2).

The minimum migration success rates in the Irish Sea (the number of fish that were detected at monitoring line B as a proportion of those entering the study area expressed as percentage per unit distance traveled) differed between rivers. Minimum migration success rate for Atlantic salmon smolts that entered the Irish sea directly from the exit of their natal river ranged from 0.02%.km^{-1} for River Nith smolts to 1.35%.km^{-1} for River Bann post-smolts (Table S2). Furthermore, minimum migration success rate for Atlantic salmon smolts that entered the Irish sea directly from the exit of their natal estuary ranged from 0.14%.km^{-1} for river Endrick post-smolts to 2.51%.km^{-1} for River Faughan post-smolts.

The first date of entry of post-smolts into the Irish sea was dependent on the date they exited either their natal river (smolts from regions 1 and 3) or estuary (regions 2 and 4). The period between the first date of entry of a tagged post-smolt into the Irish Sea and detection of the last individual leaving the study site was 63 days. Across all populations the median dates of entry and exit of post-smolts from the Irish Sea were May 6th ± 8.1 days (± SD; range: April 18th – June 2nd) and May 14th ± 13.4 days (range: April 21st to June 20th), respectively (Table S3). While most post-smolts entered the Irish Sea during the first two weeks in May, there appeared to be a difference between rivers based upon their total distance traveled through the Irish Sea (Tables S2 and S3; Figure 2). Most post-smolts from rivers in Northern Ireland exited the Irish Sea by the second week in May, whereas post-smolts from English and Scottish rivers left during the first week of June (Figure 2; Table S3). There were no post-smolts from the River Burrishoole detected in the Irish Sea receiver arrays (A and B), however, the median date of entry into the coastal zone, west of Ireland for post-smolts from this river in 2021 was May 11th ± 2.0 days (Figure 2; Table S3). However, it is important to note that smolts from the River Burrishoole were acoustically tagged later in the spring in comparison to all other rivers in this study (excluding the River Faughan; Table 1).

One consistent finding amongst all rivers is that post-smolts undertook rapid migrations through the Irish Sea. For smolts that

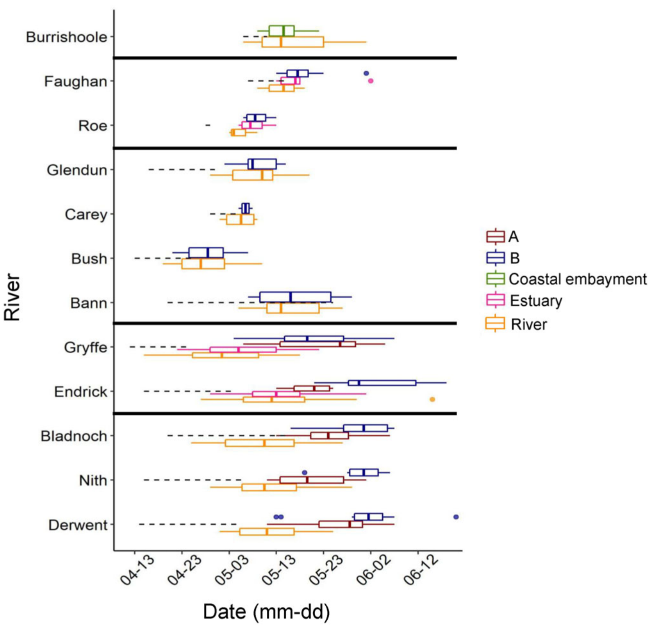

FIGURE 2 A boxplot plot displaying the dates (mm-dd) when Atlantic salmon (*Salmo salar*) post-smolts ($n = 582$) were last detected in their natal river/estuary (Rivers Endrick, Gryffe, Roe, Faughan) or coastal embayment (River Burrishoole) and entered the coastal zones of the Irish Sea or the west coast of Ireland (River Burrishoole; Figure 1: Clew Bay) and were detected on monitoring lines A and B (excluding the River Burrishoole Figure 1). In the boxplots, the centre line represents the median, the box encompasses the 25 to 75% quartiles, the bars are the values within 1.5 interquartile units and the dots represent outliers. It should be noted that the dates when smolts were tagged (represented by the dashed black line) differed in each river system. The thick black lines divide rivers into their coastal regions (see methods).

entered the Irish Sea directly from their natal river, their mean minimum migration speed (± SD) through Irish Sea (regions 1 and 3) ranged from 14.03 ± 7.32 km.day^{-1} for River Derwent post-smolts to 38.56 ± 12.86 km.day^{-1} for River Bann post-smolts (Table S2). In addition, for post-smolts that entered the Irish Sea from their natal estuary, their minimum migration speed through the Irish Sea ranged from 9.69 ± 1.71 km.day^{-1} for River Endrick post-smolts, to 39.94 ± 12.04 km.day^{-1} for River Roe post-smolts (Table S2).

3.3 | Predictors of minimum migration success

Modeling minimum migration success through the Irish Sea showed that only minimum migration distance successfully predicted the probability of a successful migration ($p = 0.005$; Table 2). K ($p = 0.50$) and Julian day ($p = 0.41$) did not significantly improve the model (Table 2). In addition, a General Linear Model (GLM) was used to fit the final model as there was not a significant difference between the final model with and without river location included as a random effect ($\chi^2 = 0$, $df = 2$, $p = 1$). However, only 4% of the variation in migration success was explained by minimum migration distance (Table 2: $R^2_M = 0.04$). The mean distance (± SD) for Atlantic salmon smolts which made a successful or unsuccessful migration through the Irish Sea was 87.6 ± 57.0 km (± SD) and 116.5 km ± 57.5 km, respectively. The model predicted the overall probability of a detected successful migration by a post-smolt through the Irish Sea at the minimum (38.0 km), mean (105.1 km) and maximum (168.0) distance traveled by fish in this study were 52.9, 38.6 and 26.8%, respectively (Table 2; Figure 3).

3.4 | Monitoring line passage

Post-smolts were detected on a mean number of 1.4 ± 0.9 (± SD; $n = 43$; range: 1–6) receivers on monitoring line A and 1.9 ± 1.1 ($n = 148$; range: 1–6) receivers on monitoring line B. Only post-smolts migrating from regions 1 (Rivers Derwent, Nith & Bladnoch) and 2 (Rivers Endrick & Gryffe) were detected at monitoring line A (Table S2; Figure 4). Post-smolts from all river systems in regions 1 to 4 were detected on monitoring line B (Table S2; Figure 4). There were no post-smolts from Region 5 (River Burrishoole) detected on either of monitoring line A or B.

In this study, post-smolts migrating from the same coastal region displayed similar passage positions on monitoring lines A and B (Figure A3). The total number of post-smolts detected at each receiver grouping on monitoring line A from regions 1 and 2 was evenly distributed across the line (Region 1: $\chi^2_{10} = 14.56$, $p = 0.149$; Region 2: $\chi^2_{10} = 12.71$, $p = 0.24$; Figure 4a,b). In contrast, the number of post-smolts detected at each receiver grouping on monitoring line B, where post-smolts transition from the Irish Sea to the North Atlantic was not evenly distributed across the monitoring line (Region 1: $\chi^2_{11} = 33.2$, $p = 4.9 \times 10^{-4}$; Region 2: $\chi^2_{11} = 35.4$, $p = 2.2 \times 10^{-4}$; Region 3: $\chi^2_{11} = 176.5$, $p = 2.2 \times 10^{-16}$; Region 4: $\chi^2_{11} = 40.5$, $p = 3.0 \times 10^{-5}$; Figure 4).

Model	Variable	Value	SE	z-value	*p*	R^2_M	R^2_C
Initial	Intercept	−1.14	3.90	−0.29	0.77	0.09	0.09
	FL	0.12	0.13	0.93	0.35		
	K	−1.37	1.35	−1.02	0.31		
	Julian day	2.88	6.24	0.46	0.64		
	Min.distance traveled	−7.30	2.73	−2.67	7.54×10^{-3}		
Final	Intercept	0.44	0.26	1.71	0.09	0.04	
	Min.distance	−8.63	2.27	−3.80	1.45×10^{-4}		

TABLE 2 Parameter values from the General Linear Mixed Model (GLMM) and General Linear Model (GLM) assessing the influence of the fork length (fl), condition factor (K), julian day and minimum distance traveled (min. distance; see methods) on the successful migration of Atlantic salmon post-smolts through the Irish Sea.

Note: River location was included as a random effect in the initial model (GLMM) and the final model (GLM) did not included river as a random effect. The last two columns show the variation explained by the fixed effects (R^2_M) and the full model (R^2_C; fixed effects and the random effect [River]).

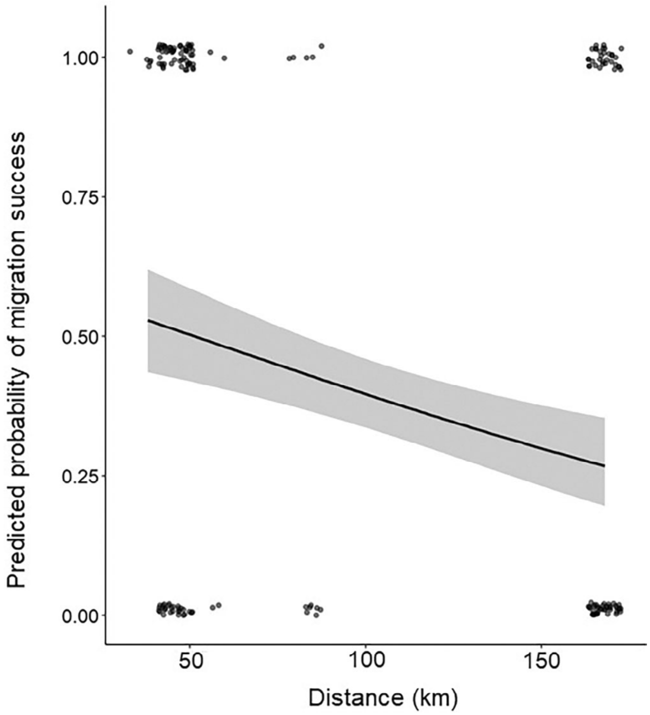

FIGURE 3 The binomial General Linear Model (GLM) model showing the effect of minimum migration distance (Distance [km]) from the exit of smolts natal river/estuary to monitoring line B on the probability of migration success (measured as minimum migration success) of Atlantic salmon (*Salmo salar*) post-smolt through the Irish Sea. The shaded region is the 95% confidence interval of the final model.

In general, there appeared to be a relationship between where on the line B a post-smolt was detected and the location of the river drainage into the Irish Sea. For example, post-smolts migrating through the Irish Sea from regions located along the west coast of Scotland (Figure 4a,b; Figure S3b–e) and England (Figure 4a; Figure S3a) appeared to have a higher likelihood of being detected near the centre of monitoring line B, with the highest concentration (interquartile range) of post-smolts migrating from regions 1 and 2 being detected over a distance of approximately 20 km between receivers 49 and 75 ($n_{smolts} = 11$) and 47–78 ($n_{smolts} = 20$), respectively (Table 3; Figure 4a,b; Figure S3a–e). By contrast, post-smolts migrating from rivers in Northern Ireland appeared to remain close to the Irish coast, with the highest concentration (interquartile range) of post-smolts migrating from regions 3 and 4 detected over a distance of approximately 15 km between receivers 31–44 ($n_{smolts} = 48$) and 24–39 ($n_{smolts} = 11$), respectively (Table 3; Figure 4c,d; Figure S3f–k).

3.5 | Environmental correlates of migration

3.5.1 | Temperature

In this study, most (median value; Table S3) Atlantic salmon post-smolts from rivers in Northern Ireland exited the Irish Sea during the period of April 24th (River Bush) to May 17th (River Faughan), when the daily water temperature across monitoring line B ranged from 9.1 to 9.9°C. In contrast, most (median value; Table S3) post-smolts from Scottish/English rivers exited the Irish Sea approximately two weeks later, during the period of May 29th (River Endrick) to June 4th (River Bladnoch) when the temperature ranged from 10.3 to 11.0°C.

3.6 | Environmental cues initiating migration

3.6.1 | Time of day

Atlantic salmon post-smolts were detected exiting the Irish Sea during all hours of the day. However, a higher mean number of post-smolts per hour were found to exit the Irish Sea during the day ($n_{hours} = 43$, 0.15 ± 0.11 post-smolts/hour (± SD)) compared with during the night ($n_{hours} = 25$, 0.11 ± 0.26 post-smolts/hour).

3.6.2 | Current direction

In this study, the timing of a post-smolt migrating from the Irish Sea into the wider North Atlantic (first detection on monitoring line B receiver) was highly dependent on current direction ($z = 0.49$,

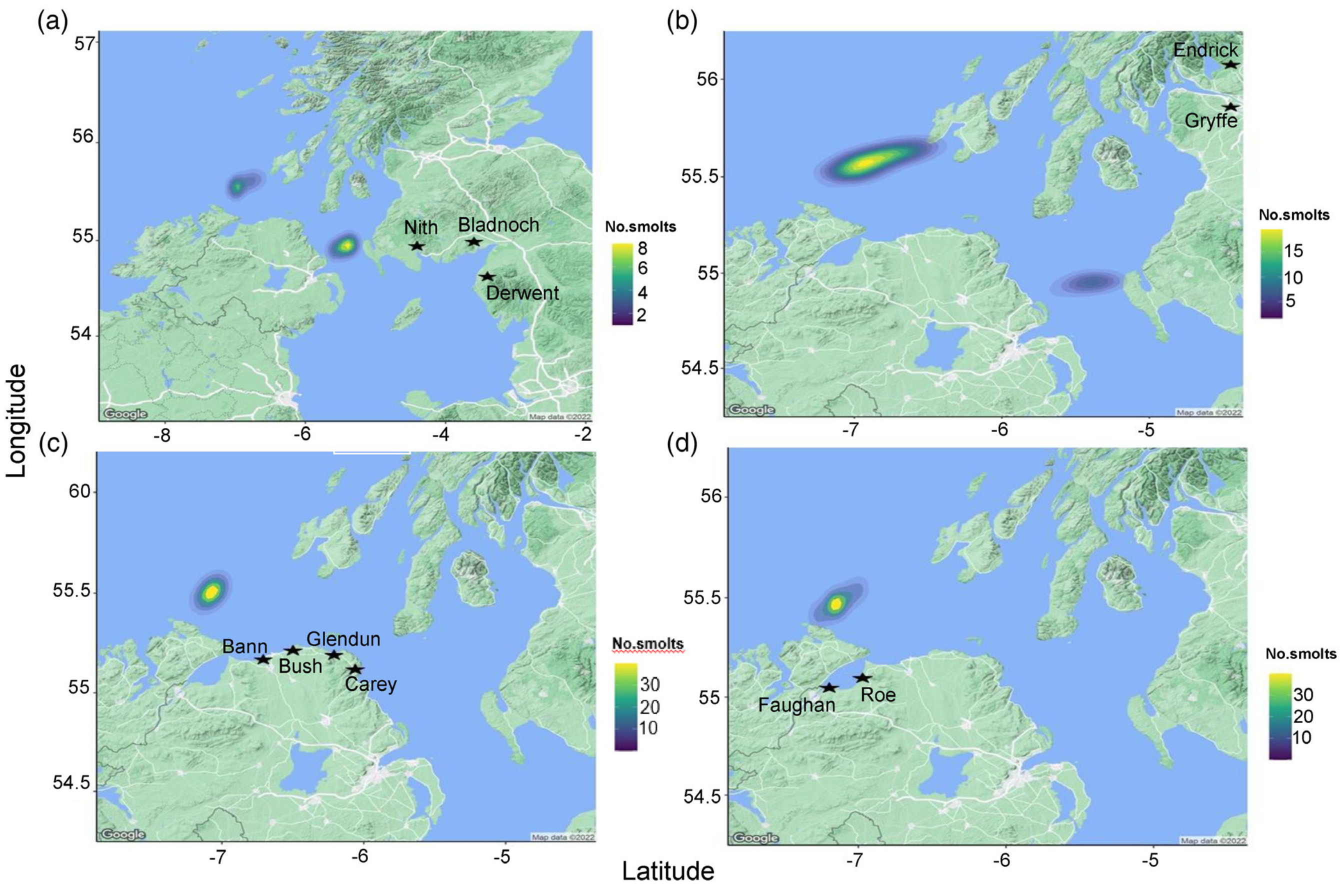

FIGURE 4 Heatmaps displaying the number of Atlantic salmon (*Salmo salar*) post-smolts detected at each acoustic receiver on monitoring lines A and B (Figure 1) during the period of this study. The black stars show the location of each river ($n = 11$) where Atlantic salmon post-smolts originated. Rivers are grouped by coastal region where they entered the Irish Sea (Figure 1, (a) Region 1: Rivers Derwent, Nith, Bladnoch; (b) Region 2: Rivers Endrick, Gryffe; (c) Region 3: Rivers Bann, Bush, Carey, Glendun; (d) Region 4: Rivers Roe, Faughan).

TABLE 3 The interquartile range of receiver locations on monitoring line B (Figure 1) where post-smolts from each coastal region (No. smolts) (rivers from each region combined in "Overall") and river had their initial detection in this study, as well as the length of the monitoring line (distance [km]) and % of line (% of interquartile range/distance of entire line [distance ~63 km]) over which the interquartile range occurred.

			Interquartile range of initial detections			
Region	River	No. smolts total	No smolts	Range	Distance (km)	% of line
1	Overall	22	11	49–75	15.30	24.36
	Derwent	11	6	47–74	15.10	24.04
	Nith	6	3	50–63	7.65	12.18
	Bladnoch	5	2	54–80	14.40	22.93
2	Overall	36	20	47–78	17.60	28.03
	Endrick	9	6	41–71	17.80	29.34
	Gryffe	27	15	49–79	16.90	22.77
3	Overall	68	48	31–44	6.13	11.26
	Bann	21	13	27–37	5.95	9.47
	Bush	39	29	33–44	6.61	10.53
	Carey	3	2	47–74	15.10	24.04
	Glendun	5	3	34–45	6.03	9.60
4	Overall	23	11	24–39	8.91	14.19
	Roe	5	3	24–34	6.08	9.68
	Faughan	18	10	22–40	10.80	17.20
5	Burrishoole	0	0	-	-	-

Note: The interquartile range represents the 25th–75th percentile around the median receiver location ($n_{locations} = 108$) on monitoring line B (ordered from 1 to 108) on which smolts were detected.

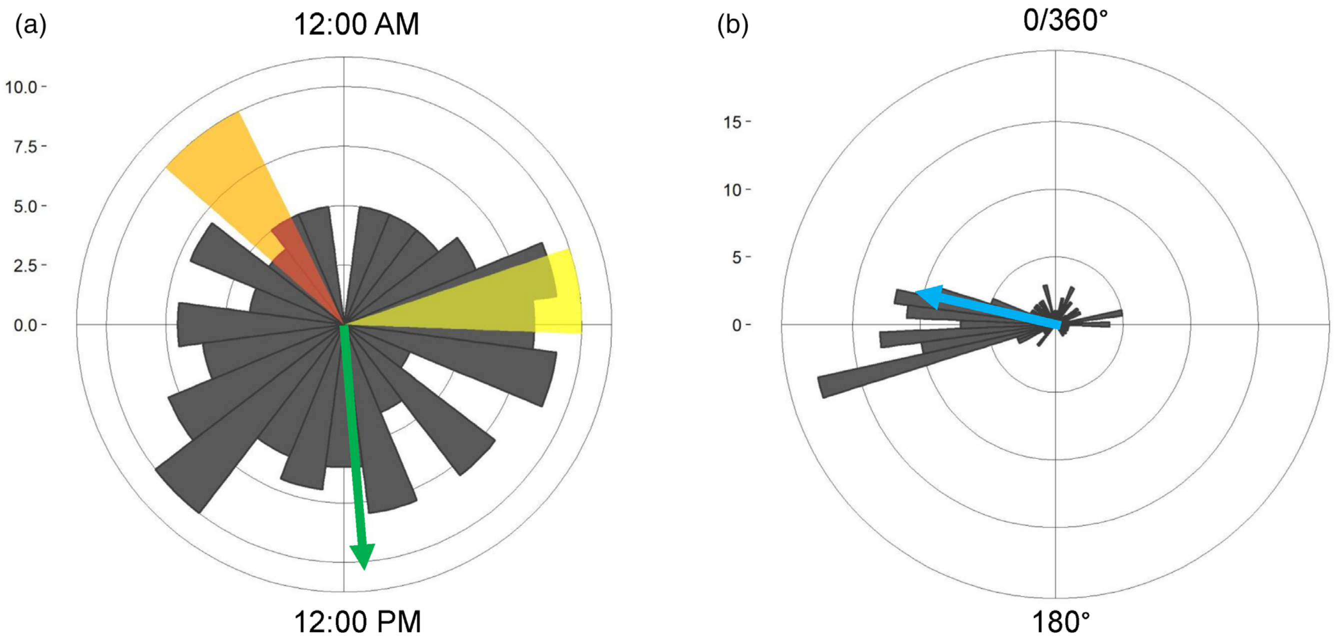

FIGURE 5 Rose diagrams depicting (a) the hour of the day and (b) the direction of currents (°) when Atlantic salmon (*Salmo salar*) post-smolts were initially detected at a unique acoustic receiver on monitoring line B. The green and blue arrows show the mean hour (a) and mean current direction (b) when post-smolts were initially detected respectively (Lilly et al., 2022). The orange and yellow bands (a) show the variation in sunrise and sunset times for the total period over which any post-smolts were detected on monitoring line B (ie. April 21st–June 20th).

TABLE 4 The proportion of Atlantic salmon (*Salmo salar*) post-smolts (%) initially detected on monitoring line B ($n = 148$) when mean current (averaged hourly, modeled values ± SD [range]) was orientated in a north-east (1–89°), south-east (90–179°), south-west (180–269°) and north-west (270–360°) direction.

Current direction	Degree range	% of smolts (n)	Mean direction (°)	Mean u (m/s)	Mean v (m/s)	Mean speed (m/s)
NE	1°–89°	18 (26)	53.60 ± 0.50 (0–89.0)	0.59 ± 0.45 (0–1.28)	0.28 ± 0.14 (0–0.46)	0.72 ± 0.36 (0.04–1.29)
SE	91°–179°	5 (8)	109.0 ± 0.33 (91.0–147.0)	0.82 ± 0.40 (0.13–1.30)	0.27 ± 0.30 (0–0.81)	0.89 ± 0.43 (0.24–1.42)
SW	181°–269	36 (54)	255.70 ± 0.18 (218.0–269.0)	1.04 ± 0.31 (0.49–1.75)	0.25 ± 0.15 (0.01–0.55)	1.09 ± 0.29 (0.57–1.77)
NW	271–359	40 (60)	291.40 ± 0.37 (271.0–353.0)	0.68 ± 0.41 (1.64–0.05)	0.17 ± 0.10 (0.01–0.48)	0.73 ± 0.37 (0.11–1.67)

Note: The horizontal (u; m/s) and vertical (v; m/s) components of the current speed for each directional grouping is provided as well as the absolute speed (Mean speed; m/s; sum of vertical and horizontal components).

$p < 0.001$). The mean current direction (circular mean degree) at the time of initial post-smolt detection (all rivers combined) occurred at 283.3° ± 1.11° (± SD; between west and north-west; range: 0–353°; Figure 5b). Furthermore, the highest proportion of post-smolts ($n = 60$; 40.3%; Table 4) were initially detected on monitoring line B during an ebb tide when currents were tracking westwards. During the period when these post-smolts were detected, the westward component of the current was approximately four times faster (0.68 ± 0.41 m/s) than the northward component (0.17 ± 0.10 m/s; Table 4). Lastly, most post-smolts exited the Irish Sea when currents were tracking in a westerly direction. Examination of the five receivers with the most post-smolt detections, showed that post-smolts would be exposed to considerable variation in current direction. For example, a high proportion of the currents tracked north-east on the ebbing tide (Figure S4). However, despite this most post-smolts exited the Irish Sea when currents were tracking in a westerly direction, indicating that they were responding to current direction when choosing to migrate.

4 | DISCUSSION

Prior to this study, our understanding of post-smolt migration through the Irish Sea was limited to a few studies with small sample sizes comprising post-smolts from one or two rivers from the same country conducted by a single research project (Barry et al., 2020; Green et al., 2022). While these provided valuable insights into the migratory patterns of post-smolts through the Irish Sea, our study highlights the importance of merging resources and disseminating results from projects conducted across jurisdictions to better understand the early marine migration and to improve conservation efforts of Atlantic salmon (Flye et al., 2021).

4.1 | Migration success

In this study we measured the minimum migration success of post-smolts through the coastal zones of the Irish Sea. The actual migration success is likely to be higher than the minimum reported here and the variation between minimum migration success and actual migration success may differ between rivers of origin for several reasons. The receiver locations where tags were detected along monitoring line B differed by river group and it is likely that detection probabilities would differ across the line due to the loss of a few receivers and differences in depth throughout the study area (Figure S2). Therefore, it is possible that some post-smolts were able to pass through monitoring line B without being detected. However, despite these caveats, the high density of receivers in this line (mean receiver spacing = 580 m) and previously measured detection efficiencies (75%–90% at 200 m) in coastal conditions in Scotland (Main, 2021; Newton et al., 2021; Honkanen et al., 2018) strongly point to relatively high detection probability for the monitoring line where post-smolts passed out of the Irish Sea and into the North Atlantic. Thus, it is assumed here that comparisons of between-river minimum migration success rate are likely to represent real between-population differences.

4.2 | Biotic predictors of Irish Sea passage

Here we report that there was a negative relationship between the minimum total distance traveled through the Irish Sea and the population-specific minimum migration success pointing to migration success being a function of migration distance. Overall minimum migration success for Atlantic salmon post-smolts that entered the Irish sea directly from their natal river ranged from 6% for River Nith smolts (278 km through the Irish Sea to the North Atlantic) to 62% for River Bann smolts (46 km). Furthermore, overall minimum migration success for Atlantic salmon post-smolts that entered the Irish sea from their natal estuary ranged from 24% for River Endrick post-smolts (168 km through the Irish Sea to the North Atlantic) to 95% for River Faughan post-smolts (38 km). Unsurprisingly post-smolts migrating a greater distance through the Irish Sea also spent more time migrating (e.g. from natal river exit: River Derwent: 256.0 km, 23.04 days versus River Bush: 47.1 km, 1.31 days; from estuarine exit: River Endrick: 168.0 km, 17.86 days versus River Roe: 14.8 km over 1.02 days).

The loss of Atlantic salmon post-smolts from the cohort of migrating post-smolts in this study is likely related in part at least, to natural threats. Predators such as Harbor seals (Allegue et al., 2020; Carter et al., 2001), cetaceans (e.g. the Bottlenose Dolphin [*Tursiops truncatus*]; Arso Civil et al., 2019; Wilson et al., 1997), piscivorous birds (e.g. the Cormorant [*Phalacrocorax carbo*]; Kennedy & Crozier, 2010), and fishes (e.g. Atlantic cod (*Gaadus morhua*), Saithe (*Pollachias virens*); Thorstad et al., 2011; Thorstad, Uglem, et al., 2012) have been reported as present in river mouths and estuaries during the period when salmonids are present, suggesting that they may prey on post-smolts. These species are also found in the Irish Sea; however, it is currently unknown what effects they may have on migrating post-smolts during their early marine migration (Brown et al., 2012; Flávio et al., 2020; Kennedy & Crozier, 2010; Kiely et al., 2000; Mackey et al., 2004; Righton et al., 2001). One assumption of our study is that all tag detections at monitoring line B (except for one that was removed) were those of post-smolts. Supporting this assumption is the observation of the similarity of swim speeds and directional passage reported by previous studies (Chaput et al., 2019; Green et al., 2022). However, we were unable with complete certainty to rule out the possibility that some detections were from tags inside a post-smolt predator. Future studies could utilize predation tags and/or acoustically tag potential predators of post-smolts to better quantify predator behavior (Gibson et al., 2015; Hanssen et al., 2022; Lennox et al., 2021; Nash et al., 2022).

Contrary to other estuarine and early marine migration studies suggesting that larger post-smolts have a higher likelihood of completing a successful migration, here we report that for post-smolts migrating through the Irish Sea, there was no size effect on successful Irish Sea passage (Gregory et al., 2018; Gregory et al., 2019). Larger smolts are thought to undertake more efficient, faster migrations due to their higher muscle mass, thus reducing their exposure to predators (Flávio et al., 2021; Kennedy et al., 2022). In this study, the smallest size of smolt tagged was constrained to limit tag burden. Here tag burden, the ratio of tag mass to fish body mass, did not exceed 0.07, the value at which negative effects of tag burden may manifest in some species (Brown et al., 2010). However, a result of this constraint is that the smaller smolts in the size range of migrants were not included in this study which may have prevented us from detecting a size effect on survival.

The date of sea entry is thought to be a key factor linked to post-smolt growth and survival, as it may dictate the likelihood of overlap of migrating fish with key prey items such as fish larvae and amphipods (Hvidsten et al., 2009; Thorstad, Uglem, et al., 2012; Utne, Pauli, et al., 2021). In this study we did not find any effect of Irish Sea entry date on marine migration success. While the timing of Irish Sea entry did vary by up to a month for fish from some populations (e.g. Table S3; River Endrick, 30 days) on average, post-smolts spent a relatively short period in the Irish Sea, ranging from 1.0 ± 0.71 to 22.8 ± 8.45 days (mean ± SD; Table S2) for River Roe and River Nith post-smolts, respectively. Scientific trawling surveys targeting post-smolts are required to determine if post-smolts are consuming significant amounts of prey while migrating through the Irish Sea and if prey abundance varies from early to late spring (SalSea Merge, 2012). Due to their relatively efficient migration through the Irish Sea, we speculate that post-smolts may not utilize the Irish Sea region for feeding but instead focus on making a rapid transition through the area to reduce the time taken to reach more northern feeding grounds (Table S2; Ounsley et al., 2020).

4.3 | Migratory pathways

Results from this study suggest that post-smolts migrating from the same coastal region exhibit similar migratory patterns when migrating through the Irish Sea. However, there is an apparent difference in migratory patterns between post-smolts migrating from Northern Irish and English/Scottish Rivers. Post-smolts from regions 1 and 2 appeared to exit the Irish Sea near the centre of monitoring line B, whereas very few post-smolts from rivers in Northern Ireland (regions 3 and 4) were detected exiting on the north eastern half of monitoring line B. There were no smolts from Ireland (Region 5) detected on monitoring line B. Based on the capture locations of coded wire tagged post-smolts collected by scientific surface trawling surveys in 2008 and 2009, smolts from the west of Ireland appear to travel in a northerly direction on a migratory path to meet the northerly current along the edge of the continental shelf of Scotland (Holst, 2012; Mork et al., 2012).

Consistent with the findings of Barry et al. (2020) and Green et al. (2022) it appears that most post-smolts migrate in a north, to north westerly direction through the Irish Sea. However, ten post-smolts that entered the Irish Sea from Region 2 (River Endrick, $n = 4$; River Gryffe, $n = 6$) were detected making a southerly migration towards monitoring line A, and two of these were subsequently detected migrating back to monitoring line B (Table S2). The largest freshwater input into the Irish Sea originates from the ClydeEstuary, which creates a southerly coastal current extending to the Mull of Galloway. This current is most notable during the ebb tide (Kasai et al., 1999; Young et al., 2000). The post-smolts from Region 2 may have been diverted south by this current. The remaining eight fish from Region 2 migrating south past monitoring line A remain unaccounted for. Although highly speculative, it is not impossible that these fish may have migrated further south around the coast of Ireland. This possibility requires further investigation.

Based upon their predicted migratory trajectories it appears that the risk of spatial overlap between migrating post-smolts and anthropogenic stressors in the Irish Sea is minimal (ICES, 2023). Most fisheries in this region operate nearshore, targeting invertebrates such as Norwegian lobster (*Nephrops norvegicus*) using demersal trawls (ICES, 2019). During their coastal migration, Atlantic salmon post-smolts have been reported to remain within the top six metres of the water column and results from our study suggest that a majority of post-smolts migrate away from nearshore coastal area (Davidsen et al., 2008).

While post-smolts from English and Scottish rivers did take between two and three weeks to migrate through the Irish Sea, all post-smolts were found to undergo relatively efficient migrations, moving rapidly (10–39 km.day^{-1};Table S2). Migration speeds in this study are similar to those reported by both Barry et al. (2020) and Green et al. (2022) who showed that post-smolts from rivers in Northern Ireland and England migrate quickly through the Irish Sea at rates of 7 and 26 km.day^{-1}, respectively.

4.4 | Environmental correlates of post-smolt transition

4.4.1 | Temperature

Across all populations the sea temperature ranged between 9 and 11°C as post-smolts migrated out of the Irish Sea into the wider North Atlantic. This is similar to temperatures reported during their offshore marine migration (Holm et al., 2006; Ounsley et al., 2020). Post-smolts from Northern Irish populations experienced sea water temperatures of around 9–10°C compared with fish from English and Scottish populations where the temperature was marginally higher (~10–11°C). This is almost certainly an effect of the differences in the timing of migration for these populations. However, the temperature experienced may have some consequences for migrating fish. Water temperatures experienced by post-smolts has been reported to be a critical factor associated with post-smolt growth and ultimately adult return rates (Friedland et al., 1998). Sea temperature in the coastal zone is also thought to be important in determining the likelihood of post-smolts overlapping with high abundances of key prey items once in marine waters (Thorstad, Whoriskey, et al., 2012; Utne, Paul, et al., 2021).

4.5 | Environmental cues of post-smolt transition

4.5.1 | Time of day

Contrary to our expectations, here Atlantic salmon post-smolts were found to exit the Irish Sea regardless of the time of day. Some studies have noted that as post-smolts transition from the riverine to early marine environment, they shift from a primarily nocturnal migration, to migrating both during the night and day (Davidsen et al., 2009; Dempson et al., 2011; Lacroix & McCurdy, 1996). The likelihood of diurnal migration is thought to be related to a trade off between the risk of encountering predators and the need to locate prey. Predators have been reported to aggregate near the outlets of rivers and estuaries during periods when large numbers of prey are present (Hastie et al., 2016; Zamon, 2001). Migrating during the night may be beneficial to smolts navigating through rivers and estuaries as they contain a higher number of migratory constriction points in comparison to the pelagic zone of the coastal marine environment (Lacroix et al., 2004). Post-smolts are visual predators that must feed during their early marine migration to fuel the energetic costs of migrating vast distances to reach their northern feeding grounds (Utne, Thomas, et al., 2021). Migrating during the day as well as at night may be a strategy that increases their chances of capturing prey along their migratory route (Andreassen et al., 2001; Hedger et al., 2008; Kadri et al., 1997).

4.5.2 | Current direction

To date there has been one acoustic telemetry study assessing the potential environmental drivers of post-smolt movement through the Irish Sea and results suggested that post-smolts were traveling with the outgoing current (Barry et al., 2020). However, this study was limited to a small sample size ($n = 3$) and was not able to determine the direction of the current, limiting the ability to generalize the findings to multiple rivers from the UK and Ireland.

By combining actual post-smolt movement data with detailed current data in the Irish Sea, here we show that Atlantic salmon post-smolts were exiting the Irish Sea with the outgoing tide when currents were tracking in a west-north-west direction towards the continental shelf slope current. The main driver of the current in the Irish Sea are the M2 and S2 tidal constituents with the dominant volume of water directed northwards during the spring and winter; however, during the summer months the dominant volume of water can reverse to southward (2.50 $km^3.day^{-1}$; Howarth, 2005; Olbert et al., 2012; Olbert & Hartnett, 2010). During the post-smolt migration period, currents at the point where the Irish Sea transitions into the wider North Atlantic were, at different times, flowing in almost all possible directions. In this study, migrating post-smolts showed a very strong preference for migrating when the current was on average 283° from north (approximately west-north-west) with remarkably little variation around that (standard deviation on the mean of 1.1°). There are a number of logical conclusions that flow from this finding. These results strongly indicate that post-smolts migrating through the coastal marine environment in the Irish Sea area: (1) are not simply migrating by current following (2) that they engage in active directional swimming (3) that they must have an intrinsic sense of the direction of their migration and (4) that they must use cues other than water current direction to orientate during this part of their migration. All of these provisional conclusions require to be specifically tested in future studies.

This study is the first to describe the early marine migration of post-smolts from a large number of rivers (12) in the UK and Ireland over the same migration season. While in this study we were able to obtain baseline information on the spatial variation in migration survival, timing, directionality and some drivers of post-smolt migration through the Irish Sea, results are limited to only one year. With warming oceanic conditions, which have been shown to modify local circulation patterns, these results may not adequately describe future migratory behavior of post-smolts migrating through the Irish Sea (Olbert et al., 2012; Thorstad et al., 2021; Thorstad, Whoriskey, et al., 2012). Rising water temperatures may cause post-smolts to transition to the Irish Sea when biotic and abiotic conditions are less conducive to survival (Hvidsten et al., 1998; Kennedy & Crozier, 2010). Therefore, temporal repeatability of this project over multiple years is required to quantify temporal variation and to examine whether changes in ocean circulation patterns could modify migratory patterns and post-smolts migration success through the Irish Sea (Chaput et al., 2019; Thorstad, Whoriskey, et al., 2012).

AUTHOR CONTRIBUTIONS

C.E.A, P.B, N.ÓM. D.M.B, R.M, D.dV., R.K, and K.W planned and designed the study, J.L, H.H, J.R.R, A.G, D.dV, R.K, B.A, R.R, R.O, C.W, D.C, J.B, S.B, J.H, D.P, B.S, P.R, S.W, M.F executed the field work and collected the telemetry data and D.P provided the oceanographic data. J.L analyzed the data. J.L wrote the draft manuscript with critical review and feedback from all authors.

ACKNOWLEDGMENTS

We thank the six projects: SeaMonitor; West Coast Tracking Project; COMPASS, the Nith, Derwent, and AFBI salmon Tracking Projects, and the scientists, administrative and technical personnel working on them that made this study possible. We also thank staff and volunteers from Fisheries Management Scotland, Marine Scotland, the Atlantic Salmon Trust, the Nith Catchment Fishery Trust, the Nith Fisheries Board, the Galloway Fisheries Trust, the Loch Lomond Fisheries Trust, the Paisley Abercorn Angling Club, the West Cumbria Rivers Trust, and Ocean Tracking Network. This paper was much improved by the considerable work of two excellent anonymous referees. Project SeaMonitor was funded by EU award IVA5060 from the Interreg 5A programme, the COMPASS project was funded by EU Interreg 5A, the West Coast Tracking project was funded by the Atlantic Salmon Trust, the Nith smolt tracking project was funded by the Nith District Salmon Fishery Board and the Holywood Trust and Dumfries and Galloway Council, the Derwent Salmon tracking project was funded by the Environment Agency, Natural England, the Derwent Owners Association, and the United Utilities PLC, and the AFBI salmon tracking projects were funded by the Department of Agriculture, Environment and Rural Affairs of Northern Ireland (DAERA NI).

FUNDING INFORMATION

This study was funded by EU INTERREG VA Programme (Environment Theme), the Maritime Fisheries Fund, Salmon Scotland, the Atlantic Salmon Trust, the Environment Agency, Natural England, The Derwent Owners Association, United Utilities PLC, NatureScot the Nith District Salmon Fishery Board, the Holywood Trust, Dumfries and Galloway Council and the Department of Agriculture, Environment and Rural Affairs of Northern Ireland.

ORCID

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

REFERENCES

Adams, C. E., Chavarie, L., Rodger, J. R., Honkanen, H. M., Thambithurai, D., & Newton, M. P. (2022). An opinion piece: the evolutionary and ecological consequences of changing selection pressures on marine migration in Atlantic salmon. *Journal of Fish Biology*, *100*(4), 860–867. Portico. https://doi.org/10.1111/jfb.15024

Alerstam, T., Hedenström, A., & Åkesson, S. (2003). Long-distance migration: Evolution and determinants. *Oikos*, *103*(2), 247–260. https://doi.org/10.1034/j.1600-0706.2003.12559.x

Aleynik, D., Dale, A. C., Porter, M., & Davidson, K. (2016). A high-resolution hydrodynamic model system suitable for novel harmful algal bloom modelling in areas of complex coastline and topography. *Harmful Algae*, *53*, 102–117. https://doi.org/10.1016/j.hal.2015.11.012

Allegue, H., Thomas, A., Liu, Y., & Trites, A. (2020). Harbour seals responded differently to pulses of out-migrating Coho and Chinook smolts. *Marine Ecology Progress Series*, *647*, 211–227. https://doi.org/10.3354/meps13389

Altizer, S., Bartel, R., & Han, B. A. (2011). Animal migration and infectious disease risk. *Science*, *331*(6015), 296–302. https://doi.org/10.1126/science.1194694

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*(6), 1667–1679. https://doi.org/10.1111/j.1095-8649.2001.tb02321.x

Arso Civil, M., Quick, N. J., Cheney, B., Pirotta, E., Thompson, P. M., & Hammond, P. S. (2019). Changing distribution of the east coast of

Scotland bottlenose dolphin population and the challenges of area-based management. *Marine and Fresh Water Ecosystems*, *29*(S1), 178–196. https://doi.org/10.1002/aqc.3102

Avgar, T., Street, G., & Fryxell, J. M. (2014). On the adaptive benefits of mammal migration. *Canadian Journal of Zoology*, *92*(6), 481–490. https://doi.org/10.1139/cjz-2013-0076

Barnham, C., & Baxter, A. (1998). *Condition factor, K, for salmonid fish, fisheries notes*. Victoria Department of Primary Industries. http://bamboorods.ca/Trout%20condition%20factor.pdf

Barry, J., Kennedy, R. J., Rosell, R., & Roche, W. K. (2020). Atlantic salmon smolts in the Irish Sea: First evidence of a northerly migration trajectory. *Fisheries Management and Ecology*, *27*(5), 517–522. https://doi.org/10.1111/fme.12433

Barry, J., Newton, M., Dodd, J. A., Hooker, O. E., Boylan, P., Lucas, M. C., & Adams, C. E. (2016). Foraging specialisms influence space use and movement patterns of the European eel *Anguilla Anguilla*. *Hydrobiologia*, *766*, 333–348. https://doi.org/10.1007/s10750-015-2466-z

Bates, D., Mächler, M., Bolker, B., & Walker, S. (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, *67*(1), 1–48. https://doi.org/10.48550/arXiv.1406.5823

Bjerck, H. B., Urke, H. A., Haugen, T. O., Alfredsen, J. A., Ulvund, J. B., & Kristensen, T. (2021). Synchrony and multimodality in the timing of Atlantic salmon smolt migration in two Norwegian fjords. *Scientific Reports*, *11*(1), 6504. https://doi.org/10.1038/s41598-021-85941-9

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*(2), 499–505. https://doi.org/10.1577/M09-038.1

Brown, S. L., Bearhop, S., Harrod, C., & McDonald, R. A. (2012). A review of spatial and temporal variation in grey and common seal diet in the United Kingdom and Ireland. *Journal of the Marine Biological Association of the United Kingdom*, *92*(8), 1711–1722. https://doi.org/10.1017/S0025315411002050

Carter, T. J., Pierce, G. J., Hislop, J. R. G., Houseman, J. A., & Boyle, P. R. (2001). Predation by seals on salmonids in two Scottish estuaries. *Fisheries Management and Ecology*, *8*(3), 207–255. https://doi.org/10.1046/j.1365-2400.2001.00247.x

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*(4), 1107–1121. https://doi.org/10.1093/icesjms/fsy156

Chen, C., Beardsley, R., & Cowles, G. (2006). An unstructured grid, finite-volume coastal ocean model (FVCOM) system. *Oceanography*, *19*(1), 78–89. https://doi.org/10.5670/oceanog.2006.92

Christoffersen, M., Svendsen, J. C., Behrens, J. W., Jepsen, N., & van Deurs, M. (2019). Using acoustic telemetry and snorkel surveys to study diel activity and seasonal migration of round goby (*Neogobius melanostomus*) in an estuary of the Western Baltic Sea. *Fisheries Management and Ecology*, *26*(2), 172–182. https://doi.org/10.1111/fme.12336

Crossin, G. T., Heupel, M. R., Holbrook, C. M., Hussey, N. E., Lowerre-Barbieri, S. K., Nguyen, V. M., Raby, G. D., & Cooke, S. J. (2017). Acoustic telemetry and fisheries management. *Ecological Applications*, *27*(4), 1031–1049. https://doi.org/10.1002/eap.1533

Crozier, W., Whelan, K., Buoro, M., Chaput, G., Grant, S., Hyatt, K., Irvine, J., Ó'Maoiléidigh, N., Prévost, E., Rivot, E., Russell, I., Schmidt, M., & Wells, B. (2018). *Atlantic salmon mortality at sea: Developing an evidence-based "Likely Suspects" Framework. Based on a workshop organized by the Atlantic Salmon trust, held in Edinburgh Tuesday 6th November – Thursday, 8th November 2017*. Atlantic Salmon Trust. https://atlanticsalmontrust.org/wp-content/uploads/2018/08/Blue-Journal-June-2018.pdf

Dabrowski, T., Hartnett, M., & Olbert, A. I. (2010). Influence of seasonal circulation on flushing of the Irish Sea. *Marine Pollution Bulletin*, *60*(5), 748–758. https://doi.org/10.1016/j.marpolbul.2009.11.018

Dabrowski, T., Lyons, K., Nolan, G., Berry, A., Cusack, C., & Silke, J. (2016). Harmful algal bloom forecast system for SW Ireland. Part I: Description and validation of an operational forecasting model. *Harmful Algae*, *53*, 64–76. https://doi.org/10.1016/j.hal.2015.11.015

Dadswell, M. J., Spares, A. D., Reader, J. M., & Stokesbury, M. J. W. (2010). The North Atlantic subpolar gyre and the marine migration of Atlantic salmon *Salmo salar*: The 'merry-go-round' hypothesis. *Journal of Fish Biology*, *77*(3), 435–467. https://doi.org/10.1111/j.1095-8649.2010.02673.x

Davidsen, J. G., Plantalech Manel-la, N., Økland, F., Diserud, O. H., Thorstad, E. B., Finstad, B., Sivertsgård, R., McKinley, R. S., & Rikardsen, A. H. (2008). Changes in swimming depths of Atlantic salmon *Salmo salar* post-smolts relative to light intensity. *Journal of Fish Biology*, *73*(4), 1065–1074. https://doi.org/10.1111/j.1095-8649.2008.02004.x

Davidsen, J. G., Rikardsen, A. H., Halttunen, E., Thorstad, E. B., Økland, F., Letcher, B. H., Skardhamar, J., & Naesje, 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*(7), 1700–1718. https://doi.org/10.1111/j.1095-8649.2009.02423.x PMID: 20738643.

Dempson, J. B., Robertson, M. J., Pennell, C. J., Furey, G., Bloom, M., Shears, M., Ollerhead, L. M. N., Clarke, K. D., Hinks, R., & 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*(7), 1976–1992. https://doi.org/10.1111/j.1095-8649.2011.02971.x

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*(3), 848–852. https://doi.org/10.1111/j.1095-8649.2002.tb00917.x

Dingle, H., & Drake, V. A. (2007). What is migration? *Bioscience*, *57*(2), 113–121. https://doi.org/10.1641/B570206

Flávio, H., Caballero, P., Jepsen, N., & Aarestrup, K. (2021). Atlantic salmon living on the edge: Smolt behaviour and survival during seaward migration in river Minho. *Ecology of Fresh Water Fish*, *30*(1), 61–72. https://doi.org/10.1111/eff.12564

Flávio, H., Kennedy, R., Ensing, D., Jepsen, N., & Aarestrup, K. (2020). Marine mortality in the river? Atlantic salmon smolts under high predation pressure in the last kilometres of a river monitored for stock assessment. *Fisheries Management and Ecology*, *27*(1), 92–101. https://doi.org/10.1111/fme.12405

Flye, M. E., Sponarski, C. C., Zydlewski, J. D., & McGreavy, B. (2021). Understanding collaborative governance from a communication network perspective: A case study of the Atlantic Salmon recovery framework. *Environmental Science & Policy*, *115*, 79–90. https://doi.org/10.1016/j.envsci.2020.10.001

Friedland, K. D., Hansen, L. P., & Dunkley, D. A. (1998). Marine temperatures experienced by post smolts and the survival of Atlantic salmon, *Salmo salar* L., in the North Sea area: Post smolt survival and marine conditions. *Fisheries Oceanography*, *7*(1), 22–34. https://doi.org/10.1046/j.1365-2419.1998.00047.x

Furey, N. B., Vincent, S. P., Hinch, S. G., & Welch, D. W. (2015). Variability in migration routes influences early marine survival of juvenile salmon smolts. *PLoS One*, *10*(10), e0139269. https://doi.org/10.1371/journal.pone.0139269

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*(5), 728–741. https://doi.org/10.1139/cjfas-2014-0245

Gilbey, J., Utne, K. R., Wennevik, V., Beck, A. C., Kausrud, K., Hindar, K., Garcia de Leaniz, C., Cherbonnel, C., Coughlan, J., Cross, T. F., Dillane, E., Ensing, D., García-Vázquez, E., Hole, L. R., Holm, M., Holst, J. C., Jacobsen, J. A., Jensen, A. J., Karlsson, S., … Verspoor, E. (2021). The early marine distribution of Atlantic salmon in the north-East Atlantic: A genetically informed stock-specific synthesis. *Fish and Fisheries*, *22*(6), 1274–1306. https://doi.org/10.1111/faf.12587

Gilbey, J., Wennevik, V., Bradbury, I. R., Fiske, P., Hansen, L. P., Jacobsen, J. A., & Potter, T. (2017). Genetic stock identification of Atlantic salmon caught in the Faroese fishery. *Fisheries Research*, *187*, 110–119. https://doi.org/10.1016/j.fishres.2016.11.020

Green, A., Honkanen, H. M., Ramsden, P., Shields, B., del Villar-Guerra, D., Fletcher, M., Walton, S., Kennedy, R., Rosell, R., O'Maoiléidigh, N., Barry, J., Roche, W., Whoriskey, F., Klimley, P., & Adams, C. E. (2022). Evidence of long-distance coastal sea migration of Atlantic salmon, Salmo salar, smolts from Northwest England (river Derwent). *Animal Biotelemetry*, *10*(3), 1–9. https://doi.org/10.1186/s40317-022-00274-2

Gregory, S. D., Armstrong, J. D., & Britton, J. R. (2018). Is bigger really better? Towards improved models for testing how Atlantic salmon *Salmo Salar* smolt size affects marine survival. *Journal of Fish Biology*, *92*(3), 578–592. https://doi.org/10.1111/jfb.13550

Gregory, S. D., Ibbotson, A. T., Riley, W. D., Nevoux, M., Lauridsen, R. B., Russell, I. C., Britton, J. R., Gillingham, P. K., Simmons, O. M., & Rivot, E. (2019). Atlantic salmon return rate increases with smolt length. *ICES Journal of Marine Science*, *76*(6), 1702–1712. https://doi.org/10.1093/icesjms/fsz066

Grolemund, G., & Wickham, H. (2011). Dates and times made easy with lurbidate. *Journal of Statistical Software*, *40*(3), 1–25. https://doi.org/10.18637/jss.v040.i03

Hanssen, E. M., Vollset, K. W., Salvanes, A. G. V., Barlaup, B., Whoriskey, K., Isaksen, T. E., Normann, E. S., Hulbak, M., & Lennox, R. J. (2022). Acoustic telemetry predation sensors reveal the tribulations of Atlantic salmon (*Salmo salar*) smolts migrating through lakes. *Ecology of Fresh Water Fish*, *31*(2), 424–437. https://doi.org/10.1111/eff.12641

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. *Behavioral Ecology and Sociobiology*, *70*, 2161–2174. https://doi.org/10.1007/s00265-016-2219-7

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. https://doi.org/10.3354/meps07239

Hindar, K., Hole, L., Kausrud, K., Malmstrom, M., Rimstad, E., Robertson, L., Sandlund, O. T., Thorstad, E. B., Vollset, K., de Boer, H., Eldegard, H., Jarnegren, K., Kirkendall, L. R., Maren, I. E., Nilsen, E. B., Rueness, E. K., Nielsen, A., & Velle, G. (2020). *Assessment of the risk to Norwegian biodiversity and aquaculture from pink salmon* (*Oncorhynchus gorbuscha*). Scientific opinion on alien organisms and trade in endangered species (CITES) of the Norwegian Scientific Committee for Food and Environment. https://brage.nina.no/nina-xmlui/handle/11250/2729831

Holbrook, C., Hayden, T., Pye, J., & Nunes, A. (2018). *Glatos: A package for the Great Lakes acoustic telemetry observation system*. R package version 0.2.7.9000. https://gitlab.oceantrack.org/GreatLakes/glatos

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*(4), 955–964. https://doi.org/10.1006/jmsc.2000.0700

Holm, M., Holst, J. C., Hansen, L. P., Jacobsen, J. A., O'Maoileidigh, N., & Moore, A. (2003). Migration and distribution of Atlantic salmon post-smolts in the North Sea and north-East Atlantic. In D. Mills (Ed.), *Salmon at the edge* (pp. 7–23). Blackwell Science.

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 Document CM 2006/ Q:12, 16 pp. https://imr.brage.unit.no/imr-xmlui/bitstream/handle/11250/100901/Q1206.pdf?sequence=1&isAllowed=y

Holst, J. C (2012). Advancing understanding of Atlantic Salmon at Sea: Merging Genetics and Ecology to Resolve Stock-specific Migration and Distribution patterns (SALSEA-Merge project) Final Report. Norway: Institute of Marine Research.).

Holst, J. C., Shelton, R., Holm, M., & Hansen, L. P. (2000). Distribution and possible migration routes of post-smolt Atlantic salmon in the north-East Atlantic. In W. G. Pearcy (Ed.), *The ocean life of Atlantic salmon: Environmental and biological factors influencing survival* (pp. 65–77). Fishing News Books.

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*(1), 159–162. https://doi.org/10.1111/jfb.13650

Howarth, M. J. (2005). Hydrography of the Irish SEA: SEA6 technical report, POL internal document 174, 30. https://assets.publishing.service.gov.uk/government/uploads/system/uploads/attachment_data/file/197294/SEA6_Hydrography_POL.pdf

Hume, T. M., Snelder, T., Weatherhead, M., & Liefting, R. (2007). A controlling factor approach to estuary classification. *Ocean & Coastal Management*, *50*, 905–929. https://doi.org/10.1016/j.ocecoaman.2007.05.009

Hvidsten, N. A., Jensen, A. J., Rikardsen, A. H., Finstad, B., Aure, J., Stefansson, S., Fiske, P., & Johnsen, B. O. (2009). Influence of sea temperature and initial marine feeding on survival of Atlantic salmon *Salmo salar* post-smolts from the Rivers Orkla and Hals, Norway. *Journal of Fish Biology*, *74*(7), 1532–1548. https://doi.org/10.1111/j.1095-8649.2009.02219.x

ICES. (2019). *Celtic Seas ecoregion – Fisheries overview, including mixed-fisheries considerations*. https://doi.org/10.17895/ices.advice.5708

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

ICES. (2023). Working group on North Atlantic Salmon (WGNAS). *ICES Scientific Reports*, *5*(41), 1–478. https://doi.org/10.17895/ices.pub.22743713

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*(2), 273–279. https://doi.org/10.1111/j.1095-8649.1997.tb01358.x

Kahle, D., & Wickham, H. (2013). Ggmap: Spatial visualization with ggplot2. *The R Journal*, *5*(1), 144–161.

Kasai, A., Rippeth, T. P., & Simpson, J. H. (1999). Density and flow structure in the Clyde Sea front. *Continental Shelf Research*, *19*(14), 1833–1848. https://doi.org/10.1016/S0278-4343(99)00042-4

Kennedy, R. J., Barry, J., Roche, W., Rosell, R., & Allen, M. (2022). In-river behaviour and freshwater return rates of sea trout, *Salmo trutta* L., from two coastal river populations. *Journal of FishBiology*, *101*(4), 1008–1020. https://doi.org/10.1111/jfb.15162

Kennedy, R. J., & Crozier, W. W. (2010). Evidence of changing migratory patterns of wild Atlantic salmon *Salmo salar* smolts in the river bush, Northern Ireland, and possible associations with climate change. *Journal of Fish Biology*, *76*(7), 1786–1805. https://doi.org/10.1111/j.1095-8649.2010.02617.x

Kessel, S. T., Hussey, N. E., Crawford, R. E., Yurkowski, D. J., O'Neill, C. V., & Fisk, A. T. (2016). Distinct patterns of Arctic cod (*Boreogadus saida*) presence and absence in a shallow high Arctic embayment, revealed across open-water and ice-covered periods through acoustic telemetry. *Polar Biology*, *39*(6), 1057–1068. https://doi.org/10.1007/s00300-015-1723-y

Kiely, O., Ligard, D., McKibben, M., Connolly, N., & Baines, M. (2000). Grey seals: Status and monitoring in the Irish and Celtic seas. Maritime Ireland/Wales INTERREG Report no.3, Marine INstitute 2000, 76. https://oar.marine.ie/handle/10793/561

Lacroix, G. L., & McCurdy, P. (1996). Migratory behaviour of post-smolt Atlantic salmon during initial stages of seaward migration. *Journal of Fish Biology*, *49*(6), 1086–1101. https://doi.org/10.1111/j.1095-8649.1996.tb01780.x

Lacroix, G. L., McCurdy, P., & Knox, D. (2004). Migration of Atlantic salmon postsmolts in relation to habitat use in a coastal system. *Transactions of the American Fisheries Society*, *133*(6), 1455–1471. https://doi.org/10.1577/T03-032.1

Lefèvre, M. A., Stokesbury, M. J. W., Whoriskey, F. G., & Dadswell, M. J. (2012). Atlantic salmon post-smolt migration routes in the Gulf of St. Lawrence. *ICES Journal of Marine Science*, *69*(6), 981–990. https://doi.org/10.1093/icesjms/fss092

Lennox, R. J., Pulg, U., Malley, B., Gabrielsen, S.-E., Hanssen, E. M., Cooke, S. J., Birnie-Gauvin, K., Barlaup, B. T., & Vollset, K. W. (2021). The various ways that anadromous salmonids use lake habitats to complete their life history. *Canadian Journal of Fisheries and Aquatic Sciences*, *78*(1), 90–100. https://doi.org/10.1139/cjfas-2020-0225

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

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*, *1-19*, 2045–2063. https://doi.org/10.1007/s10641-021-01172-x

Limburg, K. E., & Waldman, J. R. (2009). Dramatic declines in North Atlantic diadromous fishes. *Bioscience*, *59*(11), 955–965. https://doi.org/10.1525/bio.2009.59.11.7

Lohmann, K. J., Goforth, K. M., Mackiewicz, A. G., Lim, D. S., & Lohmann, C. M. F. (2022). Magnetic maps in animal navigation. *Journal of Comparative Physiology A*, *208*(1), 41–67. https://doi.org/10.1007/s00359-021-01529-8

Lothian, A. J., Newton, M., Barry, J., Walters, M., Miller, R. C., & Adams, C. E. (2018). Migration pathways, speed and mortality of Atlantic salmon (*Salmo salar*) smolts in a Scottish river and the near-shore coastal marine environment. *Ecology of Fresh Water Fish*, *27*(2), 549–558. https://doi.org/10.1111/eff.12369

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

Luschi, P. (2013). Long-distance animal migrations in the oceanic environment: Orientation and navigation correlates. *ISRN Zoology*, *2013* (631839), 1–23. https://doi.org/10.1155/2013/63189

Mackey, M., Giménez, P. I., & Ó Cadhla, O. (2004). SEA678 data report for offshore cetacean populations. *Coastal and Marine Resources Centre, Cork*, *47*. https://assets.publishing.service.gov.uk/government/uploads/system/uploads/attachment_data/file/197025/SEA678_Cetaceans.pdf

Main, R. A. K. (2021). Migration of Atlantic salmon (Salmo salar) smolts and post-smolts from a Scottish east coast river. https://theses.gla.ac.uk/82089/13/2021MainMScr.pdf

Milner, N. J., Elliott, J. M., Armstrong, J. D., Gardiner, R., Welton, J. S., & Ladle, M. (2003). The natural control of salmon and trout populations in streams. *Fisheries Research*, *62*(2), 111–125. https://doi.org/10.1016/S0165-7836(02)00157-1

Minkoff, D., Putman, N. F., Atema, J., & Ardren, W. R. (2020). Nonanadromous and anadromous Atlantic salmon differ in orientation responses to magnetic displacements. *Canadian Journal of Fisheries and Aquatic Sciences*, *77*(11), 1846–1852. https://doi.org/10.1139/cjfas-2020-0094

Mork, K. A., Gilbey, J., Hansen, L. P., Jensen, A. J., Jacobsen, J. A., Holm, M., Holst, J. C., Maoiléidigh, N. Ó., Vikebø, F., McGinnity, P., Melle, W., Thomas, K., Verspoor, E., & Wennevik, V. (2012). Modelling the migration of post-smolt Atlantic salmon (*Salmo salar*) in the North-east Atlantic. *ICES Journal of Marine Science*, *69*(9), 1616–1624. https://academic.oup.com/icesjms/article/69/9/1616/639600#:~:text=https%3A//doi.org/10.1093/icesjms/fss108

Mueller, T., & Fagan, W. F. (2008). Search and navigation in dynamic environments – from individual behaviors to population distributions. *Oikos*, *117*(5), 654–664. https://doi.org/10.1111/j.0030-1299.2008.16291.x

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*(11), 2038–2052. https://doi.org/10.1139/cjfas-2017-0361

Nagy, H., Lyons, K., Nolan, G., Cure, M., & Dabrowski, T. (2020). A regional operational model for the north East Atlantic: Model configuration and validation. *Journal of Marine Science and Engineering*, *8*(9), 673. https://doi.org/10.3390/jmse8090673

Nash, A. J., Vollset, K. W., Hanssen, E. M., Berhe, S., Salvanes, A. G., Isaksen, T. E., Barlaup, B. T., & Lennox, R. J. (2022). A tale of two fishes: Depth preference of migrating Atlantic salmon smolt and predatory brown trout in a Norwegian lake. *Canadian Journal of Fisheries and Aquatic Sciences.*, *79*, 2216–2224. https://doi.org/10.1139/cjfas-2022-0016

Nathan, R., Getz, W. M., Revilla, E., Holyoak, M., Kadmon, R., Saltz, D., & Smouse, P. E. (2008). A movement ecology paradigm for unifying organismal movement research. *Proceedings of the National Academy of Sciences*, *105*(49), 19052–19059. https://doi.org/10.1073/pnas.0800375105

Newton, M., Barry, J., Lothian, A., Main, R., Honkanen, H., Mckelvey, S., Thompson, P., Davies, I., Brockie, N., Stephen, A., O'Hara Murray, R., Gardiner, R., Campbell, L., Stainer, P., & Adams, C. (2021). Counterintuitive active directional swimming behaviour by Atlantic salmon during seaward migration in the coastal zone. *ICES Journal of Marine Science*, *78*(5), 1730–1743. https://doi.org/10.1093/icesjms/fsab024

Olbert, A. I., Dabrowski, T., Nash, S., & Hartnett, M. (2012). Regional modelling of the 21st century climate changes in the Irish Sea. *Continental Shelf Research*, *41*(1), 48–60. https://doi.org/10.1016/j.csr.2012.04.003

Olbert, A. I., & Hartnett, M. (2010). Storms and surges in Irish coastal waters. *Ocean Modelling*, *34*(1–2), 50–62. https://doi.org/10.1016/j.ocemod.2010.04.004

Ounsley, J. P., Gallego, A., Morris, D. J., & Armstrong, J. D. (2020). 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*(1), 315–325. https://doi.org/10.1093/icesjms/fsz160

Pincock, D. G. (2012). *False detections: What they are and how to remove them from detection data, VEMCO whitepaper document DOC-004691*. Amirix Systems Inc.

R Core Team. (2021). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria http://www.R-project.org/

Righton, D., Metcalfe, J., & Connolly, P. (2001). Different behaviour of north and Irish Sea cod. *Nature*, *411*(156), 156. https://doi.org/10.1038/35075667

SALSEA_Merge. (2012). Advancing understanding of Atlantic salmon at sea: Merging genetics and ecology to resolve stock-specific migration and distribution patterns. 79. https://salmonatsea.com/wp-content/uploads/2020/09/Completed-Final-Report-SALSEA-Merge.pdf

Schwartz, M. L. (1982). Geographic terminology. In C. W. Finkl (Ed.), *Beaches and coastal geology: Encyclopaedia of earth sciences series* (pp. 442–445). Springer. https://doi.org/10.1007/0-387-30843-1_205

Shchepetkin, A. F., & McWilliams, J. C. (2005). The regional oceanic modeling system (ROMS): a split-explicit, free-surface, topography-following-coordinate oceanic model. *Ocean Modelling*, *9*(4), 347–404. https://doi.org/10.1016/j.ocemod.2004.08.002

Shelton, R. G. J., Turrell, W. R., Macdonald, A., McLaren, I. S., & Nicoll, N. T. (1997). Records of post-smolt Atlantic salmon, *Salmo salar* L., in the Faroe-Shetland Channel in June 1996. *Fisheries Research*, *31*(1–2), 159–162.

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*(1), 368–376. https://doi.org/10.1093/icesjms/fsaa079

Tamario, C., Sunde, J., Petersson, E., Tibblin, P., & Forsman, A. (2019). Ecological and evolutionary consequences of environmental change and management actions for migrating fish. *Frontiers in Ecology and Evolution*, *7*, 1–24. https://doi.org/10.3389/fevo.2019.00271

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

Thorstad, E. B., Bliss, D., Breau, C., Damon-Randall, K., Sundt-Hansen, L. E., Hatfield, E. M. C., Horsburgh, G., Hansen, H., Maoiléidigh, N. Ó., Sheehan, T., & Sutton, S. G. (2021). Atlantic salmon in a rapidly changing environment—Facing the challenges of reduced marine survival and climate change. *Aquatic Conservation: Marine and Fresh Water Ecosystems*, *31*(9), 2654–2665. https://doi.org/10.1002/aqc.3624

Thorstad, E. B., Uglem, I., Arechavala-Lopez, P., Økland, F., & Finstad, B. (2011). Low survival of hatchery-released Atlantic salmon smolts during initial river and fjord migration. *Boreal Environment Research*, *16*, 115–120.

Thorstad, E. B., Uglem, I., Finstad, B., Chittenden, C. M., Nilsen, R., Økland, F., & Bjørn, P. A. (2012a). Stocking location and predation by marine fishes affect survival of hatchery-reared Atlantic salmon smolts. *Fisheries Management and Ecology*, *19*(5), 400–409. https://doi.org/10.1111/j.1365-2400.2012.00854.x

Thorstad, E. B., Whoriskey, F., Uglem, I., Moore, A., Rikardsen, A. H., & Finstad, B. (2012b). 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*(2), 500–542. https://doi.org/10.1111/j.1095-8649.2012.03370.x

Utne, K. R., Pauli, B. D., Haugland, M., Jacobsen, J. A., Maoileidigh, N., Melle, W., Broms, C. T., Nøttestad, L., Holm, M., Thomas, K., & Wennevik, V. (2021a). Poor feeding opportunities and reduced condition factor for salmon post-smolts in the Northeast Atlantic Ocean. *ICES Journal of Marine Science*, *78*(8), 2844–2857. https://doi.org/10.1093/icesjms/fsab163

Utne, K. R., Thomas, K., Jacobsen, J. A., Fall, J., Maoiléidigh, N. Ó., Broms, C. T., & Melle, W. (2021b). Feeding interactions between Atlantic salmon (*Salmo salar*) postsmolts and other planktivorous fish in the Northeast Atlantic. *Canadian Journal of Fisheries and Aquatic Sciences*, *78*(3), 255–268. https://doi.org/10.1139/cjfas-2020-0037

Wickham, H. (2016). *ggplot2: Elegant graphics for data analysis*. Springer-Verlag https://ggplot2.tidyverse.org

Wilson, B., Thompson, P. M., & Hammond, P. S. (1997). Habitat use by bottlenose dolphins: Seasonal distribution and stratified movement patterns in the Moray firth, Scotland. *Journal of Applied Ecology*, *34*(6), 1365–1374. https://doi.org/10.2307/2405254

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*(4), 353–366. https://doi.org/10.1046/j.1365-2419.2001.00180.x

Zeileis, A., & Horthorn., T. (2002). Diagnostic checking in regression relationships. *R News*, *2*(3), 7–10. https://CRAN.R-project.org/doc/Rnews/

Zydlewski, G. B., Stich, D. S., & McCormick, S. D. (2014). Photoperiod control of downstream movements of Atlantic salmon *Salmo salar* smolts: Photoperiod and smolt downstream movement. *Journal of Fish Biology*, *85*(4), 1023–1041. https://doi.org/10.1111/jfb.12509

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. H., Rodger, J. R., del Villar, D., Boylan, P., Green, A., Pereiro, D., Wilkie, L., Kennedy, R., Barkley, A., Rosell, R., Maoiléidigh, N. Ó., O'Neill, R., Waters, C., Cotter, D., Bailey, D., Roche, W., McGill, R., Barry, J., … Adams, C. E. (2024). Migration patterns and navigation cues of Atlantic salmon post-smolts migrating from 12 rivers through the coastal zones around the Irish Sea. *Journal of Fish Biology*, *104*(1), 265–283. https://doi.org/10.1111/jfb.15591