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The behaviour of Atlantic salmon (*Salmo salar*) on first migration to sea.

by

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Abstract

The Atlantic salmon, *Salmo salar* Linnaeus 1758, is a charismatic species due to its cultural and economic importance across the North Atlantic. In addition, Atlantic salmon is one of the most well researched finfish species. However, there are still considerable knowledge gaps concerning their life history, particularly for salmon smolts migrating from rivers in the British Isles. To date management and research efforts have been largely focussed on improving and understanding salmonid migration through fresh water habitats. Despite these management efforts, Atlantic salmon populations continue to decline. This has led researchers to speculate that the decline may be related to factors encountered at sea, particularly within the early marine environment. This thesis has filled in knowledge gaps concerning the migratory behaviour of Atlantic salmon smolts migrating from rivers draining into the West Coast of Scotland and Ireland using acoustic telemetry.

Despite the fresh water environment being the main focus of Atlantic salmon research, very little is known about how Atlantic salmon navigate through fresh water standing bodies of water. This is concerning, as previous studies have suggested that smolts experience high rates of mortality in these regions and display non-directional movements. Through combining acoustic telemetry data with a correlated random walk model, I sought to determine what factors may increase the likelihood of smolts completing a successful migration through Scotland's largest lake. This study demonstrated that consistent with previous literature smolts experienced high overall loss (43%), slow migrations, and non-directional movements. Furthermore, there were no behavioural or morphological factors that differentiated a successful versus unsuccessful migrant, with most individuals travelling upwards of 50 km within the lake. In addition, migratory pathways of smolts closely resembled random walk models, suggesting that successful migration of smolts through lakes is due to chance. However, once smolts came near the lake outlet they tended to make a direct exit. Within the main body of most lakes, surface currents are largely driven by the wind. However, near the lake outlet currents are often directed towards the lake outflow. Future studies are required to

determine whether currents are the main environmental cue used by smolts to navigate through fresh water standing bodies of water.

Once Atlantic salmon smolts transit through their fresh water environment, many populations must first navigate through estuaries prior to reaching the early marine environment. Estuaries are thought to be a region of high mortality for Atlantic salmon post-smolts as they are exposed to a variety of novel natural and anthropogenic stressors such as predators and aquaculture sites. Scotland is one of the worlds largest producers of farmed salmon, with most aquaculture sites being present along the north-western coast within sea lochs and estuaries. However, despite the rapid expansion of aquaculture sites in the UK, there is limited knowledge concerning the behaviour of wild Atlantic salmon in estuaries and whether they could experience spatial overlap with these sites. The Clyde estuary located in west central Scotland is a region that currently contains 16 operational aquaculture sites with plans to develop more in the future. Using acoustic telemetry coupled with a mark-recapture model, this study predicted the migratory pathways and estimated loss rates of Atlantic salmon post-smolts from two distinctly different river systems (Endrick Water & River Gryffe). In comparison to most literature assessing smolt post-survival through estuaries, loss rates were low <1 $\%km^{-1}$. This is despite 37% of post-smolts making ~ 2 reversal movements near the riverine outlet upon entering the estuary, which is thought to be related to a need to adapt to the increase in salinity. In addition, post-smolts were found to make rapid migrations through this region and appeared to exit the estuary with the outgoing tide. Due to their rapid migrations through this region, and high rates of survival, it does not appear that aquaculture sites in the main body of the Clyde estuary have a significant effect on Atlantic salmon post-smolts from the Endrick Water and River Gryffe. This information is currently being used by the Scottish Environment Protection Agency (SEPA) to develop models assessing the impact of sea lice on wild Atlantic salmon.

Research directed surface trawls conducted along the continental shelf of Scotland have indicated that once post-smolts leave rivers located along the western coast of UK and Ireland they migrate north towards the slope current, using this current to reach their feeding grounds in the Norwegian Sea. However, to date very little is known about the migratory pathways taken and environmental cues used by post-smolts to reach the slope current. Particle tracking studies conducted along the western coast of Scotland have indicated that for post-smolts to reach the slope current during the period when they are captured by trawling studies, they would have to deviate from local current patterns early on in their migration. This thesis was the first to ground truth particle tracking studies in the Irish Sea region through collecting acoustic telemetry data from 582 Atlantic salmon post-smolts from 13 rivers in England (*n* = 1) and Scotland (*n* = 12) detected on a large acoustic telemetry array deployed at the Irish Sea exit (*n* = 108 receivers). Furthermore, using circular statistics detection data was combined with two hydrodynamic models (current/temperature data) to determine potential drivers of early marine migration. Post-smolts from all river systems were found to undergo relatively rapid migrations through the Irish Sea (> 10 km.day^{-1}) and loss rates were low. However, when loss rates were multiplied by the total distance travelled there was still substantial overall loss for post-smolts migrating from English and Scottish rivers. Post-smolts exit from the Irish Sea appeared to be initiated by water temperature with most post-smolts exiting when temperatures ranged from 9 - 11°C. These temperatures are similar to those reported when post-smolts are captured in the slope current. In addition, most post-smolts exited this region when currents were directed westwards towards the slope current located off the continental shelf. Thus, results from this study suggest that temperature and current direction may serve as environmental cues used by post-smolts during their early marine migration to determine when and where to migrate.

Similar to their migration through the Irish Sea, prior to this thesis there was limited information concerning the migratory pathways post-smolts may use to migrate along the west coast of Scotland towards the Norwegian Sea. Further research was needed, as the highest density of anthropogenic stressors (e.g. aquaculture sites, renewable energy developments) in Scotland are located to the east of the Outer Hebrides. Through collaborating with a colleague at the Atlantic Salmon Trust and combining data from seven acoustic telemetry projects taking place in England, Scotland, and Ireland during 2021, we were able to document the migration pathways of post-smolts through this region. This study incorporated data from 23 rivers (*n* = 1806 post-smolts), 398 acoustic receivers and one submersible glider. In total 34.7% of tagged post-smolts (*n* = 416) that left their natal river (*n* = 1200) were detected in the coastal marine environment. Furthermore, consistent with the results from my previous chapter, most post-smolts travelling from rivers south of the Outer Hebrides were found migrate in a north-westerly direction towards the slope current located off the continental shelf of Scotland. However, post-smolts migrating from rivers to the east of the Outer Hebrides travelled directly through the Minch.

The four chapters presented in this thesis have utilized acoustic telemetry data to model the behaviour and survival of Atlantic salmon smolts from multiple populations in lakes, estuaries, and the early marine environment. The results obtained from this thesis will be used by researchers and managers to help develop future studies aimed at identifying and mitigating the effects of potential stressors unique to each Atlantic salmon population mentioned in this project.

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Author's Declaration

I hereby declare that, except where explicit reference is made to the contribution of others, the material presented in this thesis is the result of original research conducted from January 2020 until December 2022 under the supervision of Professors Colin Adams and David Bailey. This included deploying acoustic receivers in the Loch Lomond catchment, River Gryffe and Clyde estuary as well as acoustically tagging Atlantic salmon smolts from the rivers Endrick and Gryffe. I also wrote this thesis and conducted all analyses that are not listed below. No part of this thesis has been submitted for another degree. In Chapter 2 the random walk analysis was conducted by Joseph M. McCallum. The acoustic telemetry data used in Chapter 4 was compiled by projects COMPASS and SeaMonitor oceanographic data used in Chapter 4 was extracted from hydrodynamic models by Dr. Diego Pereiro. Lastly, the acoustic telemetry data used in Chapter 5 was compiled from the West Coast Tracking Project, SeaMonitor, MEFS MPA, SAMOSAS Project, Torridon smolt Tracking Project, Nith smolt Tracking Project, Derwent Tracking Project and COMPASS. In addition, in Chapter 5 Dr. Hannele H Honkanen wrote the introduction and Dr. Jessica R Rodger produced the maps.

Jessie Marie Lilly
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Chapter 1. General Introduction

The common ancestor of the family Salmonidae is estimated to have originated during the upper Cretaceous Period (~100 MYA; (Jonsson & Jonsson, 2011)). Salmonidae is composed of the genera Salmon, Coregonus and Thymallus (Nelson, 2006). The sub family Salmoniae consists of approximately 30 species comprised of Salmon and Trout, within this sub family the Atlantic salmon (*Salmo salar*) is amongst the most heavily researched due to its cultural and economic importance throughout Europe and North America (Klemetsen et al., 2003; Thorstad et al., 2012b). Populations of anadromous and non-anadromous Atlantic salmon reside within river systems draining into the North Atlantic Ocean (Thorstad et al., 2011b). Due to their diverse occupation of habitat Atlantic salmon face several threats throughout their range including impediments to migration due to man-made structures (i.e. weirs, dams), pollution to natal rivers, and bycatch in commercial and recreational fisheries (ICES, 2019b). Many populations are currently listed as threatened and endangered under national and international regulations (ICES, 2019b; Thorstad et al., 2011b).

1.1 Range and Distribution

In North America Atlantic salmon's distribution ranges along the northeast coast of the United States to the northeast coast of Canada, and in Europe their range extends from northern Portugal to Norway, Iceland and Greenland, respectively (Fig. 1.1; Thorstad et al., 2011b). Atlantic salmon occupy more than 2000 rivers in the North Atlantic, and approximately 1500 of these drain into the North East Atlantic (Chaput, 2012; ICES, 2019b). This includes 218 rivers in Scotland that support salmon fisheries (ICES, 2019c). To aid in management decisions, Atlantic salmon populations have been subdivided into three separate groups according to their genetic diversity. These are the West Atlantic, East Atlantic and Baltic groups which utilise natal rivers draining off the coast of North America, Western Europe and the Baltic Sea, respectively (Jonsson & Jonsson, 2011). The number of extirpated populations is higher within Canada than in Europe, however, Atlantic salmon in both regions are currently undergoing substantial population declines (Limburg & Waldman, 2009; Ó Maoiléidigh et al., 2018).

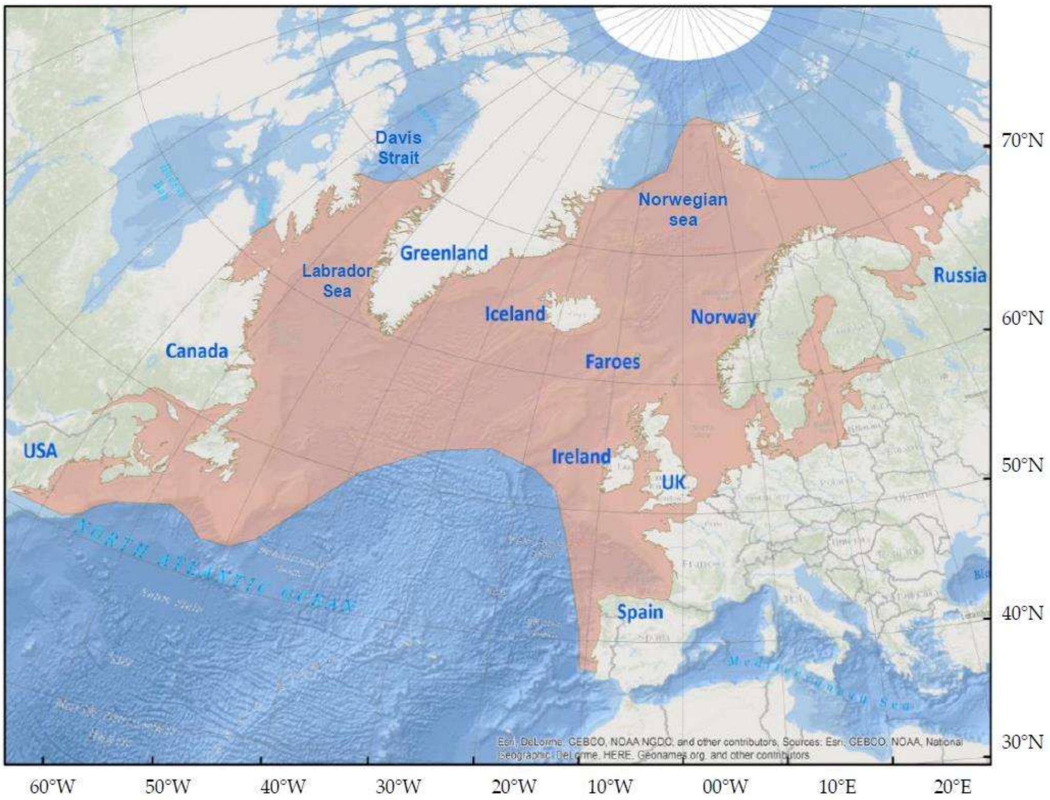


Figure 1.1 Distribution of Atlantic salmon throughout the North Atlantic (reproduced from Ó Maoiléidigh et al., 2018).

1.2 Stock Status

1.2.1 Global

Over the last three decades Atlantic salmon numbers have continued to decline. The total estimated number of pre-fishery abundance (i.e. the number of Atlantic salmon available before fishing takes place) of maturing 1SW (potential 1SW returns) and non-maturing 1SW Atlantic salmon (potential MSW returns) in the North East Atlantic (N-EAC) has declined by 51 and 13%, respectively (Ó Maoiléidigh et al., 2004; ICES, 2021; Figure 1.2). This decline is still occurring despite strict national and international regulations on fisheries and protection of habitat (Boisclair, 2004); including tighter regulations being placed on the international fishery off West Greenland, and the closure of the Faroes fishery during the early 1990s (ICES, 2019c). A combination of both anthropogenic and natural factors have been thought to contribute to the decline including fresh water habitat degradation (dams, pollution), national and international fisheries, bycatch in pelagic fisheries, predation, fish farms and an increase in both fresh water and Sea Surface Temperature's (SST; Forseth et al., 2017; Gilson et al., 2022).

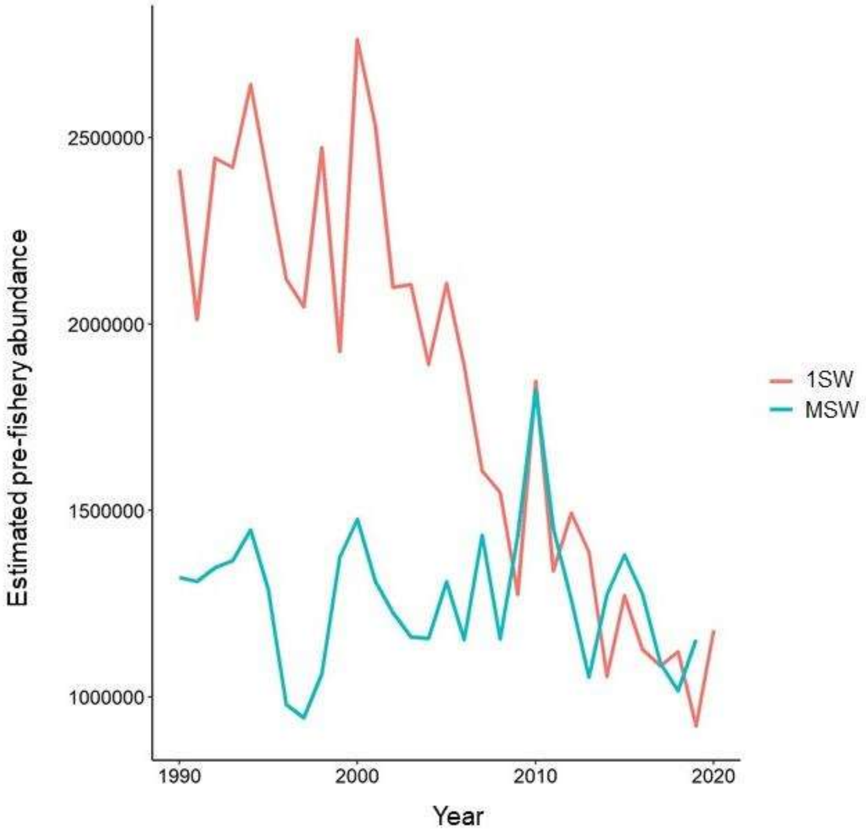


Figure 1.2 Estimated pre-fishery abundance of maturing 1SW salmon (potential 1SW returns; pink line) and estimated pre-fishery abundance of non-maturing 1SW salmon (potential MSW returns; blue line) in the North East Atlantic over the last three decades (1990-2020; ICES, 2021).

1.2.2 United Kingdom

Marine Scotland has been monitoring the total number of landed and catch and release of Atlantic salmon in Scotland since 1952 (Marine Scotland, 2021). During 2021, approximately 50,000 Atlantic salmon were retained or released from the fishery, which is 75% lower than the previous 5-year average (Marine Scotland, 2021; Figure 1.3). In 1994 approximately 8% of Atlantic salmon were caught and released, during 2021 this number increased to 95% (Marine Scotland, 2021). In the Foyle and Carlingford regions of Northern Ireland the total landed catches of Atlantic salmon have been monitored since 1952. It was noted that there was a peak in the total number of landed catches in 1996 at approximately 15,000 individuals (McCauley & Deehan, 2019). This number fluctuated during 1996 to 2015, but now appears to be declining (McCauley & Deehan, 2019). In 2018 the number of reported landed catches of Atlantic salmon in the Foyle and Carlingford regions was 1598 (McCauley & Deehan, 2019; Figure 1.4).

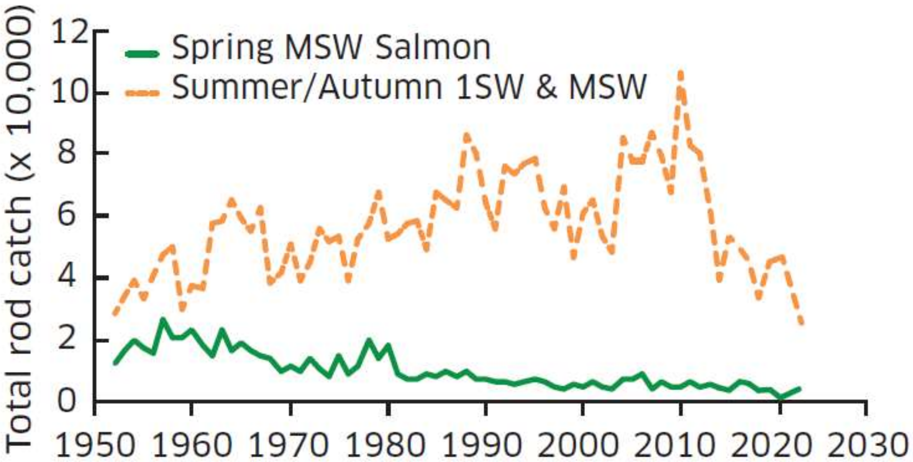


Figure 1.3 Total annual rod catches of Atlantic salmon in Scotland during 1952 to 2021 (Marine Scotland, 2021).

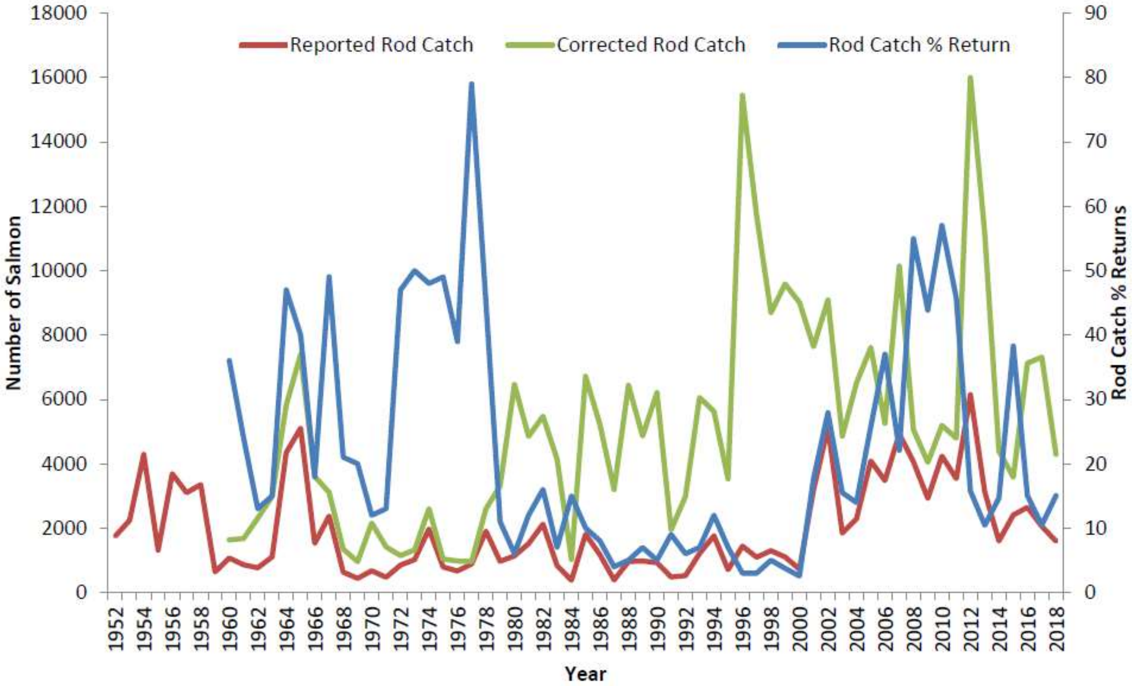


Figure 1.4 Total annual rod catches of Atlantic salmon and the total % of returns made during 1952 to 2018. Reported by the Loughs Agency for the Foyle and Carlingford regions and in Northern Ireland (McCauley & Deehan, 2019).

1.3 Conservation and Management

1.3.1 Global

The North Atlantic salmon Conservation Organization (NASCO) was established in 1984 to conserve and manage Atlantic salmon fisheries in the North Atlantic, specifically the international fisheries off of West Greenland and the Faroe Islands (ICES, 2019c). The objective of NASCO (NASCO CNL31.210) is "to contribute through consultation and cooperation to the conservation, restoration, enhancement, and rational management of salmon stocks, considering the best scientific advice" (Crozier et al., 2004, p.1345). NASCO has taken a precautionary approach and provides advice to countries on how to manage their Atlantic salmon fisheries according to conservation limits (CL; Crozier et al., 2004; ICES, 2019c; NASCO, 1998). If the status of an Atlantic salmon population falls below the CL then management restrictions are often implemented by countries to increase population abundance. CLs are often calculated as the spawning stock biomass (SSB) required for a population to achieve Maximum Sustainable Yield (MSY $B_{escapement}$, biomass left to spawn)), where the MSY is calculated from an adult-to-adult stock recruitment model (Crozier et al., 2004; ICES, 2012, 2019b). The problem with the MSY approach is that it assumes that other factors that could be influencing recruitment remain constant (ICES, 2018).

The International Council for the Exploration of the Sea is an intergovernmental marine science organization that provides advice to countries on how to meet conservation and management targets (ICES, 2022). To ensure the maintenance of fisheries, in general ICES advises that management jurisdictions take a precautionary approach and set target reference points (safe biological limits (B_{lim}) that are lower than the CL (Crozier et al., 2004). Calculation of B_{lim} extends beyond the biological considerations and incorporates other external factors that may be influencing Atlantic salmon stocks on a regional level, including environmental effects (i.e barriers, pollution), predation, population density and fishing pressures (Crozier et al., 2004). For populations that are short lived, such as Atlantic salmon, if the SSB falls below the B_{lim} ($\geq 5\%$) then the advice of ICES is fishery closure (ICES, 2018).

1.3.2 United Kingdom

In 1994 the UK produced a national Biological Diversity action plan, after the establishment of the Convention on Biological Diversity (JNCC, 2012). The Convention on Biological Diversity was established to provide an international legal framework for biodiversity conservation (JNCC, 2012). The UK Biodiversity Framework works in conjunction with the EU biodiversity strategy which was established in 2011 with the goal to "halt the loss of biodiversity and the degradation of ecosystem services in the EU by 2020" (JNCC, 2012). One of the main strategic goals of the UK Biodiversity Action Plan (UKBAP) is to "reduce the direct pressures on biodiversity and promote sustainable use" (JNCC 2012). England, Scotland, Wales and Northern Ireland have separate strategies for maintaining the biodiversity of their ecosystems, however, each management plan seeks to work under the key strategic goal outlined by the UK biodiversity framework (JNCC, 2012). The Species and Habitat review was established as part of the UK biodiversity framework to identify species of concern and critical habitat in the UK. Species are selected based upon four criteria: international threat to the species, international responsibility and moderate decline in UK, marked decline in the UK, and other important factors (JNCC, 2007). Atlantic salmon has met all four criteria and is listed as at risk under the UK list of Priority Species and Habitats. This list also contains three action plans developed by experts on the species to promote their recovery. The top action plan for Atlantic salmon in the UK is to continue to survey known sites (JNCC, 2007).

Additionally, Atlantic salmon (fresh water) is listed as an Annex II and of the European Union's Habitats Directive which protects the habitats of listed species from damage, destruction, and over-exploitation (Hendry & Cragg-Hine, 2003; McLeod et al., 2005). The Habitats Directive establishes a network of sites that will aid in the conservation of threatened or at-risk species throughout Europe (McLeod et al., 2005). Prior to the UK leaving the EU in 2020, for a site to be designated, a member state of the EU had to propose a list of sites to the European Commission (EC) that were designated as sites of community importance (SCIs; McLeod et al., 2005). Once approved it was up to the member state to designate a site as a Special Area of Conservation (SAC; McLeod et al., 2005). However, now that the UK has left the EU, after considering advice provided by local conservation organizations the selection and designation of SACs is conducted by UK government ministers. Once designated by ministers SAC's are then added to the Register of European sites (Scottish Government, 2020; UK Government, 2021). For example, in Scotland, ministers are advised by NatureScot and the Joint Nature Conservation Committee (JNCC; Scottish Government, 2020). Three study sites in my thesis are SAC's, the Endrick Water, Scotland, as well as the River Roe and River Faughan in Northern Ireland (JNCC, 2019).

1.4 Ecology

The Atlantic salmon is an anadromous species with a life span extending up to 10 years (Hendry & Cragg-Hine, 2003). Atlantic salmon occupy a variety of habitats throughout their life cycle, including fresh water, estuarine and marine environments and the extent to which each habitat is utilized varies between populations (Klemetsen et al., 2003). Atlantic salmon are iteroparous, which means they are capable of spawning multiple times throughout their lifetime. However, it has been reported that on average only 11% spawn more than once and the proportion of repeat spawners increases with decreasing latitude (Bordeleau et al., 2020; Fleming, 1998).

1.4.1 Fresh water

Atlantic salmon females return to their natal rivers during summer and spawn several months later in either autumn or winter (Fleming & Einum, 2011; Frechette et al., 2018; Jonsson & Jonsson, 2003). Spawning females dig nests called "redds", and disperse eggs in a low depth, high velocity environment over gravel and cobbled substrate (Bardonnet & Bagliniere, 2000; Fleming & Einum, 2011; Hendry & Cragg-Hine, 2003). Males actively compete for access to females expending a considerable amount of energy engaging in fighting. After the eggs are fertilized, they develop within gravel for multiple months (Bardonnet & Bagliniere, 2000; Fleming & Einum, 2011). Post spawning females then move directly back downstream where they reside for a few months in their natal river before exiting back to sea (Bardonnet & Bagliniere, 2000).

The eggs incubate for approximately 385-545 degree days, before hatching during the spring (Crisp, 1988; Jonsson & Jonsson, 2011). Hatching time is negatively correlated with temperature and can occur prematurely if eggs are exposed to environmental stressors (Klemetsen et al., 2003). After hatching, Atlantic salmon are referred to as alevins, and remain hidden in the benthic substrate, relying on a yolk sac for sustenance for a few weeks before emerging from their covered habitat (Crisp, 1988; Jonsson & Jonsson, 2011). Once the yolk sac is fully absorbed the Atlantic salmon are referred to as "fry". Fry passively drift downstream and remain in close proximity to the redd, feeding primarily on benthic invertebrates (Bardonnet & Bagliniere, 2000; Johansen et al., 2011b). Fry then develop into parr which are characterized by dark vertical bands on their sides (Jonsson & Jonsson, 2011). When access to habitat is limited and/or competition is high, some fry and parr lack access to resources and density dependent mortality occurs (Bujold et al., 2004; Hedger et al., 2013).

The age at which Atlantic salmon parr transform into smolts (smoltification) is dependent on their rate of growth, which is a function of riverine temperature and degree days (Metcalfe & Thorpe, 1990). Furthermore, there is a latitudinal gradient in age of smoltification and occurs later in northern river systems (McCormick et al., 1998; Metcalfe & Thorpe, 1990). After approximately one to eight years in fresh water, parr undergo morphological and physiological changes (smolting) that allow them to be adapt for survival in saltwater and begin a more directed downstream migration (Milner et al., 2003; Thorstad et al., 2012b; Zydlewski et al., 2014). This change in morphology has been hypothesized to occur when parr have accumulated sufficient lipid resources (Thorpe, 1986). In Scottish rivers parr transition to smolts most frequently at approximately two years of age and at that time are usually > 9 cm (Buck & Hay, 1984; Huntingford et al., 1992). A smolt can be defined as "a fresh water salmonid that has undergone metamorphic and physiological changes preparatory for seawater entry" (McCormick et al., 1985). During smolting parr marks disappear, the fins darken, the body of salmon begins to turn silver and changes in plasma ion concentrations allow smolts to survive in saltwater (McCormick, 2013a; McCormick et al., 1985; Stefansson et al., 2007; Zydlewski et al., 2014).

Smolt downstream migration has been categorized into initiation, downstream, estuarine and ocean migrations, which can take approximately 3-6 weeks (McCormick, 2013a; Zydlewski et al., 2014). The initiation of downstream migration is thought to be influenced by photoperiod, temperature, and stream discharge (McCormick, 2013a; Zydlewski et al., 2005). Smolt migrations tend to occur earlier in southern populations, than northern populations (Thorstad et al., 2012b). Migration mostly occurs during low levels of lunar brightness and the peak of the smolt run is reliant on elevated water temperature and high river discharge. Lothian et al. (2018) reported that in the River Deveron, Scotland, the highest proportion of downstream migrating smolts occurred when the water temperature reached ~8°C. Additionally, smolt downstream migration often co-occurs with stream discharge rates which are higher than the seasonal mean rate (Youngson et al., 1983). Smolts move downriver relatively quickly at a rate of approximately 2 body lengths.s^{-1} (L/s) (Lacroix & McCurdy, 1996). Smolts tend to initially engage in solitary migrations, and then exit their natal river in shoals which is thought to reduce the chance of predation (Olsén et al., 1998; Riley, 2007).

In addition to migrating through their natal rivers, many Atlantic salmon population must first migrate through lakes prior to reaching the estuarine environment (Hanssen et al., 2021; Honkanen et al., 2018,2021; Lennox et al., 2021). Little is known about how Atlantic salmon migrate through lakes and most research is limited to the smolt stage of their life cycle which have reported substantial overall loss in these systems (Hanssen et al., 2021; Honkanen et al., 2018,2021; Kennedy et al., 2018). In comparison to the riverine environment smolts spend more time transiting lakes, frequently engaging in pathways that deviate from the lake outlet (Hanssen et al., 2021; Honkanen et al., 2018, 2021; Thorpe et al., 1981). This behaviour has been predicted to be related to the lack of directed currents within lacustrine habitats (Lennox et al., 2021). Future studies are required to determine the mechanisms smolts and adults may use to navigate through lakes.

1.4.2 Estuary

Once in the estuary, smolts from both Canada and Europe have been reported to leave rapidly (~ 0.4 – 1.2 body lengths.s^{-1}) for the ocean during ebb tide and at night, usually travelling at rates faster than their riverine emigration (Hedger et al., 2008; Martin et al., 2009; Moore et al., 1998; Thorstad et al., 2012b). After Atlantic salmon leave their natal river they are referred to as post-smolts. Post-smolts that have a longer distance of migration have been reported to undergo more rapid migrations during their estuarine migration and have higher overall survival (Plantalech manel-la et al., 2011). Therefore, increased migratory speeds may decrease the likelihood of encountering predators (Plantalech manel-la et al., 2011). During their early marine migration, post-smolts have been reported to engage in active swimming, while also relying on surface currents and salinity to reach feeding grounds (Hedger et al., 2011; Mork et al., 2012; Okland et al., 2006). There have been few studies assessing the diet of post-smolts during their early marine phase, however, in Norwegian fjords they have been reported to feed primarily on invertebrates, whereas post-smolts reliance on sand-eel (*Ammodytes* spp.), cod (*Gadus morhua*) and herring (*Clupea harengus*) larvae increases the further they migrate to sea (Rikardsen et al., 2004). Atlantic salmon spend approximately 1-4 years at sea before migrating back to their natal rivers to spawn during autumn and winter (Chaput, 2012; Lacroix, 2013). One sea-winter (SW) salmon are referred to as grilse and those that spend more than 1SW at sea are referred to as Multi Sea Winter (MSW) Atlantic salmon.

1.4.3 Oceanic migration

The migratory patterns of Atlantic salmon at sea are dependent upon their continent of origin (Dadswell et al., 2010). Northern European stocks, as defined by ICES, consist of Atlantic salmon from Finland, Norway, Russia, the west coast of Sweden and northeast Iceland, and southern European stocks include Atlantic salmon from France, Ireland, and the UK (England, Wales, Northern Ireland, Scotland) and southwest Iceland (ICES, 2011). There are two main hypotheses for how Atlantic salmon post-smolts reach their feeding grounds, the first suggests that Atlantic salmon from rivers in North America, and Northern and Southern Europe make relatively direct migrations to their feeding grounds (Lacroix, 2013; Strøm et al., 2017, 2018). Atlantic salmon migrating from North America tend to remain within the Western North Atlantic, migrating as far as West Greenland (Dadswell et al., 2010; Maoiléidigh et al., 2018; Ritter, 1989). Whereas salmon from Northern and Southern Europe tend to mainly occupy waters off of the Faroe Islands and then migrate to the Norwegian sea or West Greenland, respectively (Dadswell et al., 2010; Maoiléidigh et al., 2018). The second hypothesis states that Atlantic salmon enter the North-Atlantic Sub-Polar gyre, with Atlantic salmon from Canadian rivers following the south flowing Labrador current to enter the Labrador Sea, entering the Gulf Stream which transports them to the West Coast of Greenland (Dadswell et al., 2010). Secondly, Southern European populations are hypothesized to utilize the North Atlantic Current and the Greenland current to reach feeding grounds off the west coast of Greenland, whilst Northern European populations utilize the East Greenland Current which converges with the Irminger Sea current to reach the Norwegian Sea (Dadswell et al., 2010; Strøm et al., 2017). However, tracking studies have not provided support for the second hypothesis and have indicated that Atlantic salmon make relatively direct migrations to their feeding grounds and their migratory patterns do not overlap strongly with oceanic gyres (Lacroix, 2013; Strøm et al., 2017, 2018).

It has been proposed that post-smolts from European rivers migrate to the Norwegian Sea travelling up to 7-30 km.day^{-1}, utilizing currents and salinity as directional cues (Barry et al., 2020; Mork et al., 2012; Ounsley et al., 2020; Thorstad et al., 2012b). Atlantic salmon may utilize the Norwegian Coastal Current (NCC), running along the coast of Norway to reach the Norwegian Sea. Hedger et al. (2008) reported that post-smolts are attracted to high salinity gradients. The inner NCC tracks towards the Barents Sea, whilst the outer NCC tracks towards the Norwegian sea. The outer NCC is characterized by higher salinity gradients, supporting the theory that this is a primary method of orientation for post-smolts (Hedger et al., 2011).

Particle tracking studies assessing the marine migration of post-smolts from the western coast of the northern UK have indicated that they migrate along the south-west coast of Scotland towards the Norwegian Sea travelling with the continental shelf current (Ounsley et al., 2020). For smolts travelling along the eastern coast of the UK, it has been hypothesized that they must actively swim to reach the Norwegian Sea since currents in this region flow in a south-easterly direction (Ounsley et al., 2020). Particle tracking studies have indicated that salmon migrating from the west coast of Ireland would travel clockwise around the Faroes, through the Faro-Shetland Channel and towards the Norwegian sea (Mork et al., 2012).

Once European Atlantic salmon reach the Norwegian sea they either remain for a year prior to migrating back to their natal rivers to spawn (1 Sea Winter Atlantic salmon; 1 SW) or spend multiple years at sea migrating to additional feeding grounds (Multi Sea Winter Atlantic Salmon; MSW) (Jacobsen, 2001; Rikardsen et al., 2008). The diet of Atlantic salmon in the Norwegian sea during the autumn includes hyperiid amphipods, euphausiids, and mesopelagic shrimp. In the winter the diet shifts to lantern fish (e.g. *Benthosema glaciale*), pearlsides (e.g. *Maurolicus muelleri*) and barracudinas (e.g. *Paralepis coregonoides*) (Jacobsen, 2001). Additionally, fish that return after 1 SW tend to prey more on amphipods compared to MSW salmon which fed more on fishes (Jacobsen, 2001). MSW spawners from northern European populations tend to remain within the Norwegian sea or migrate farther north to the Barents Sea and Svalbard archipelago (Jacobsen, 2001; Rikardsen et al., 2008; Strøm et al., 2018). Whereas MSW spawners from southern European (United Kingdom/Ireland) populations tend to migrate from the Norwegian Sea to West Greenland (ICES, 2015; Renkawitz et al., 2015; Sheehan et al., 2017). Most MSW fish migrating to the west coast of Greenland from European countries have been reported to be 2SW Atlantic salmon (73%) (Sheehan et al., 2017).

Tagging studies conducted within the Faroes marine fisheries for salmon during the late 1970's and 90's indicated that most fish were of Scottish, Norwegian, and Irish origin, with Norwegian fish making up the largest proportion (~40%; Hansen, 2003). The Faroe Islands serve as a transitory point for Atlantic salmon from southern and northern European populations immigrating or emigrating from important feeding grounds off West Greenland and the Norwegian sea, respectively (Jacobsen, 2001). The highest abundance of Atlantic salmon within this region occurs during late winter (Jacobsen et al., 2012). Atlantic salmon from southern Europe tend to use waters along the southern tip of the Faroe Islands, whereas Atlantic salmon migrating from northern populations utilize more northern reaches of the Faroe Islands (Jacobsen et al., 2012).

1.5 Current Pressures

1.5.1 Natural Pressures

1.5.1.1 Predation

The highest rates of mortality for Atlantic salmon are thought to occur within the marine environment, specifically during the smolt phase (Thorstad et al., 2012b). In Scottish waters, Grey seals, (*Halichoerus gyprus*) and Harbour seals, (*Phoca vitulina*) are highly abundant (Carter et al., 2001). It has been reported that > 90% of the UK population of Grey seals resides in Scotland (Carter et al., 2001). Carter et al. (2001) assessed consumption of adult Atlantic salmon by seals in two Scottish estuaries through observing feeding behaviour and analyzing seal scat (River Dee, River Don). Both Harbour and Grey seals tend to utilize estuaries during winter and spring and migrate to breeding sites during summer months, experiencing temporal overlap with the salmon smolt migrations (Carter et al., 2001). The number of adult Atlantic salmon consumed by Grey and Harbour seals was reported to be less in the River Dee and Don than the nominal catches of Adult Atlantic salmon by anglers during the study period (Carter et al., 2001). However, the diet of harbour seals has been reported to vary between rivers. In St. Andrews, Scotland it was noted that Atlantic salmon made up approximately 1% of the diet of Harbour seals diet (Sharples et al., 2009). In the Firth of Tay, Scotland during the spring Atlantic salmon made up most of the Harbour seal diet, comprising approximately 78% (Sharples et al., 2009). Studies conducted in Pugat Sound, Washington, USA used acoustic tagging technology to assess the interaction between Steelhead trout (*Oncorhynchus mykiss* (Walbaum, 1792)) smolts and Harbour seals (Berejikian et al., 2016). Small acoustic telemetry receivers (VMTs) were mounted to the seals, to record direct interactions with acoustically tagged Steelhead trout smolts. Results from this study indicated that Harbour seals were feeding on Steelhead smolts and may be a significant cause of mortality (Berejikian et al., 2016). Studies assessing seal diets in the UK have been observational and are limited to prey consumed on the surface. Future studies need to assess the underwater feeding behaviour of seals to clarify whether they are predating heavily on Atlantic salmon smolts.

Additionally, some birds and fish species have been proposed to contribute to the mortality experienced by smolts (Dieperink et al., 2002; Thorstad et al., 2011b). Avian predators of post-smolts during their marine migration include: Herring Gulls (*Larus argentatus*) Cormorants (*Phalacrocorax carbo sinensis*), Goosanders (*Mergus merganser*) and Mergansers (*Mergus serrator*) (Dieperink et al., 2002; Feltham & MacLean, 1996). These species of bird are commonly found within estuaries and rivers throughout Scotland, with their greatest concentration being within the Northern Isles and south of the Isle of Skye along the west coast of Scotland (Feltham & MacLean, 1996; Pollock et al., 2000). Dieperink et al. (2002) reported that the highest rates of predation occurred as soon as Atlantic salmon smolts entered the estuary of their natal river. It has been hypothesized that smolts adapting to salt water in their estuaries may utilize the upper portion of the water column where salinity is lower, making them easier targets for bird predation (Dieperink et al., 2002). In addition, Atlantic cod (*Gadus morhua*) are present throughout the North Atlantic and have been reported to predate on Atlantic salmon (Hedger et al., 2011; Wright et al., 2006). In a study assessing the early marine mortality of Atlantic salmon smolts in Norway by predation from cod or Saithe (*Pollachius virens*), it was noted that approximately 53% of acoustically tagged smolts were predated upon (Thorstad et al., 2011b). In Norwegian fjords, Atlantic cod have been shown to exhibit similar migratory patterns to Atlantic salmon smolts during the smolt run, occupying the upper water column primarily during night (Hedger et al., 2011b). This behaviour is unusual as cod are a demersal species, providing evidence that they may be engaging in predation tactics on smolts (Hedger et al. 2011). However, in Scotland populations of gadoids have declined to critical levels and are unlikely to have a significant effect on Atlantic salmon populations in this region (Fox, 2022). An additional predator of Atlantic salmon smolts in UK coastal waters are European Sea Bass (*Dicentrachus labrax*; Riley et al., 2011). Sea Bass populations in the UK have increased since the 1990's due to the establishment of juvenile nursery areas in estuaries and the warming of coastal waters (Pawson et al., 2007). Future research is required to determine whether Atlantic salmon smolts compose a large proportion Sea Bass diet during their estuarine migration.

1.5.1.2 Sea Surface Temperature (SST)

Increases in greenhouse gas emissions over the last few centuries have been correlated with increasing ocean temperatures (Beaugrand, 2002). Since 1990, SST in the eastern North Atlantic has been predicted to have risen by approximately 1.5°C per decade (Todd et al., 2008). Increasing SST have been positively correlated with marine survival of Atlantic salmon post-smolts, however this trend has been reported to vary amongst populations (Friedland et al., 2003). Warmer temperatures are correlated with faster growth, which is thought to aid in the avoidance of predators (Friedland, 2000; Friedland et al., 2003; Pepin, 1991). Friedland et al. (2000) reported that Atlantic salmon smolts migrating from the River Figgjo in Northern Norway and the North Esk in Scotland had higher rates of survival when SST during their first month in the ocean was between 8-10°C versus 5-7°C. Additionally, upon sea water entry post-smolts prey upon larvae of fishes (Lazzari, 2001). The survival of prey fish larvae that Atlantic salmon prey upon has been positively correlated with an increase in SST during spring and may increase the nearshore prey available to migrating post-smolts (Friedland et al., 2003; Lazzari, 2001). This may cause post-smolts to remain closer to their natal rivers instead of undergoing further offshore migrations (Kallio-Nyberg et al., 2004, 2020).

Changes in SST in the North Atlantic has been associated with a decline in the abundance of MSW Atlantic salmon returning to their natal rivers (Friedland et al., 2003; Scarnecchia, 1984; Thorstad et al., 2021). Temperature has been thought to be linked to the Atlantic salmon sea age at maturity (Martin & Mitchill 1985; Saunders et al., 1983; Scarnecchia, 1983). Globally there has been a decline in the number of MSW and an increase in the proportion of 1 SW Atlantic salmon (Chaput, 2012). Chaput (2012) reported that between 1971 and 2009, MSW salmon abundances declined by 54%, 81%, and 88% in N-NEAC (Northern North East Atlantic Commission), S-NEAC (Southern North East Atlantic Commission) and NAC (North American Commision) areas designated by NASCO, respectively (Chaput, 2012). The main reason for the proposed decline in MSW Atlantic salmon is thought to be partially attributed to the shift in prey available to MSW fish at their distant water feeding grounds off the West Coast of Greenland and within the Norwegian sea (Todd et al., 2008). Changes in climate affect the distribution and production of zooplankton in the North Atlantic which can initiate a downstream trophic cascade effect (Vollset et al., 2022). During the 1990's, approximately 20°W of the North Atlantic Ocean and European seas, there was a shift of warm water zooplankton species towards the poles, and a decline in the number of cold-water species in northern waters (Beaugrand, 2002). Capelin (*Mallotus villosus* (O.F. Müller, 1776)) are the main food source for Atlantic salmon off the western coast of Greenland and within the Norwegian sea (Dixon et al., 2019; Renkawitz et al., 2015). Starting in the early 1990's there was a northern shift in the distribution of Capelin within the Northwest Atlantic, and a decline in their abundance (Buren et al., 2014). Warming ocean temperatures have been linked to the melting of sea ice which initiates the phytoplankton bloom in the North Atlantic, in previous years the capelin migration coincided with the peak bloom during spring months (Buren et al. 2014). However, during the last decade the bloom is occurring earlier in the season limiting the prey available to capelin (Buren et al., 2014). The decline in capelin abundance could lead to a decline in Atlantic salmon abundance (Mills et al., 2013). Longer northerly migrations and lower prey abundance could also lead to declines in the deposition rate of lipids of Atlantic salmon and could adversely affect their condition and maturation schedule (Dixon et al., 2019; Olmos et al., 2019; Utne et al., 2022). This is evident by studies conducted in Scotland, Norway and France that have reported reduced weight and length of Atlantic salmon returning to their natal rivers (Bal et al., 2017; Olmos et al., 2019; Todd et al., 2012; Tréhin et al., 2021). The length reached by Atlantic salmon during their first summer at sea is thought to be predictive of whether they spend one or multiple years at sea prior to returning to their natal river (Tréhin et al., 2021). The ecological regime shift that is occurring in the North East Atlantic and reduction in prey available to post-smolts is likely to lead to an increase in Atlantic salmon maturing after one year at sea (Olmos et al., 2018; Utne et al., 2022).

1.5.2 Anthropogenic Pressures

1.5.2.1 Fish Farms

The salmon aquaculture industry has been increasing in Europe (Clarke & Bostock, 2017). It was reported that in 2014 salmon aquaculture accounted for 58% of all fishes raised in aquaculture facilities, and the industry experienced considerable growth (2010 £4.65 billion - 2015 £6.2 billion) (Clarke & Bostock, 2017). Scotland is the third largest producer of aquaculture salmon, with Atlantic salmon net pens spread throughout the western coast of Scotland, the Hebrides and the northern islands (McIntosh et al., 2022; Tett et al., 2018).

Two species of sea lice, *Lepeophtherius salmonis* and *Caligus elongatus* have been reported to be a common problem in the aquaculture industry within Europe, because they can spread to wild Atlantic salmon populations (Todd et al., 2006). Sea lice live for approximately 2 months, and feed on the mucous, tissue and blood of fishes (Costello, 2006). In salmon aquaculture, the abundance of sea lice has been positively correlated with the stock biomass and they are more abundant in high salinity regions (Kristoffersen et al., 2018). In rivers in northern Scotland, 1 Sea Winter (1 SW) and Multi Sea Winter (MSW) Atlantic salmon have been reported to have a 100% prevalence of sea lice, with MSW Atlantic salmon having the highest abundance (Susdorf et al., 2018; Todd et al., 2006). The density of sea lice is a predictor of the condition factor of salmonids (Moore et al., 2018; Susdorf et al., 2018). Susdorf et al. (2018) noted that sea lice infections on adult Atlantic salmon were predicted to reduce body mass by 3.7%. The effect of sea lice on Atlantic salmon post- smolts is not as well studied (Susdorf et al., 2018). This is concerning as Atlantic salmon post-smolts are most likely the most vulnerable, due to their small size and increased physiological stress due to seawater adaptation, and the highest sea lice prevalence in Scottish waters corresponds with smolt runs during early spring (Susdorf et al., 2018; Wells et al., 2006). Atlantic salmon post-smolts with a high prevalence of sea lice have been reported to have an increase in cortisol levels which increases the osmotic stress experienced by post-smolts (increase in plasma chloride levels) and ultimately levels of mortality (Finstad et al., 2000). In general, laboratory studies have indicated that an adult sea lice load of greater than 11 individuals often lead to mortality (Hoist et al., 2003). This is further supported by studies conducted in Norway on wild post-smolts, which indicate that post-smolts with a sea lice load greater than 10 are in poor condition, exhibiting little to no growth since sea entry and very low haemoglobin levels (Hoist et al., 2003).

In 2017, the Norwegian Government implemented a system for managing the expansion of the aquaculture industry in Norway in 13 designated management areas, and this system is now beginning to be adopted by other countries (Johnsen et al., 2021; SEPA, 2021). The system was defined as the “Traffic Light System” and is based on the estimated percentage of salmonid sea lice induced mortality in a management area. Furthermore, the traffic light system consists of three different designations, 1) if a management area is designated as “green” (<10% mortality) industry in that region can expand, 2) if a management area is “yellow” (10-30% mortality) industry can remain at its current production levels, and lastly, 3) if an area is designated as “red” (>30% of mortality) industry must decrease the production of farmed salmon (Johnsen et al., 2021). In 2021, the Scottish Government appointed the Scottish Environment Protection Agency (SEPA) in charge of developing a framework to mange the risk of sea lice from aquaculture farms on wild salmonids (SEPA, 2021). The two main goals of the framework are to 1) develop wild salmon protection zones along the coast of Scotland based upon the known migratory pathways of Atlantic salmon, and 2) utilize sea lice exposure thresholds similar to the Norwegian “Traffic Light System” to regulate the total number of farmed salmon at aquaculture sites (SEPA,2021).

1.5.2.2 Renewable Energy

Tidal energy devices are currently being tested throughout Europe, and Scotland serves as one of the most prominent areas for tidal energy pilot projects due to its rugged coastline and numerous channels (Neill et al., 2017). The Crown Estate has approved plans for the development of 30 UK tidal stream sites, with 17 in Scotland (Neil et al., 2017). The turbines being deployed can produce between 30 MW to 400 MW (Neil et al., 2017). The European Marine Energy Center (EMEC) was established in 2003 to test hydrokinetic devices tidal turbines off the coast of the Orkney Islands, Scotland at the Fall of Warness tidal site (Neil et al., 2017). Current speeds in this region can exceed 3.5 m s^{-1} (Fraser et al., 2018). The largest project thus far, has been headed by the company MyGen which has deployed four 1.5 MW devices (Neil et al., 2017). However, Fraser et al. (2018) used multibeam echosounders to assess the movement of fishes around hydrokinetic devices deployed at the EMEC tidal test site. It was reported that the number of fish schools increased during low flows, with fish aggregating in the wake flow. However, fishes exhibited avoidance behaviour of the turbine at high current speeds. It is currently unknown whether specific species of fish, such as Atlantic salmon smolts may contact turbine blades and future environmental impact assessments are required (Fraser et al. 2018).

Additionally, offshore wind energy farms have been expanding considerably throughout Europe, with approximately 33% of wind energy potential residing within the UK (O'Keeffe & Haggett, 2012). During 2018, it was reported that the UK produced over 8,500 MW of electricity through offshore wind farms which is enough to power the equivalent of approximately 16 million homes (renewableUK, 2019). Currently 37 operational offshore wind turbine projects exist along the coast of the UK which includes 2,016 wind turbines (renewableUK, 2019). Some of the main concerns of these sites are noise caused by pile driving during turbine deployment and operation, and increased risk of predation due to structures providing refuges for predatory fishes (Degraer et al., 2020). It has been reported by Bailey et al (2010) that noise caused by wind turbine installation exceeds ambient noise up to 70 km away from the deployment site. This has the potential to alter the migration of fishes and marine mammals (Bailey et al., 2010).

Additionally, at windspeeds up to 13 m/s it has been reported that Atlantic salmon can detect the sound from offshore wind turbines up to 25 km away, however, the noise is not enough to cause hearing loss in salmonids (Wahlberg & Westerberg, 2005). The pillars and bases of offshore wind turbines increase the amount of hard substrate available in a region, providing additional habitat for benthic fauna; this ultimately attracts species of various trophic levels (Andersson & Öhman, 2010). Griffen et al. (2016) used Baited Remote Underwater Video (BRUV) systems to assess the local fauna surrounding the Walney offshore windfarm site located in the Irish Sea off the coast of Walney Island. It was reported that both floral and faunal abundance increased near the turbine. The fish assemblages included both benthic and pelagic species, with a high proportion of observed fishes being classified as predators (Griffin et al., 2016). The increase in marine predators around wind turbines could pose a threat to Atlantic salmon smolts migrating through these regions. Future studies need to assess whether Atlantic salmon are deterred by wind developments due to ambient nose or attracted to them due to the increase in prey abundance and available habitat and the extent to which predators may concentrate around wind turbine structures and their potential impact on salmon smolts.

1.5.2.3 Pelagic Fisheries

Research directed trawling conducted in the Norwegian sea has indicated that Atlantic salmon are captured as bycatch in trawl fisheries targeting Atlantic mackerel (*Scomber scombrus*) (ICES, 2004). An attempt was made to estimate the potential bycatch of post-smolts in the commercial mackerel fishery in the North Sea, and along the west coast of Scotland and Great Britain (ICES, 2004). Atlantic salmon post-smolts utilize the upper 10m of the water column during their marine migration, and this is the depth at which the mackerel fisheries deploy trawling nets (ICES, 2004). Both mackerel and Atlantic salmon have been hypothesized to utilize the slope current off the west coast of the British Isles to reach feeding and spawning grounds in the Norwegian Sea, respectively, and experience overlap in their distributions west and north of the Vøring Plateau (Holm et al., 2000; ICES, 2004; Lothian et al., 2018). However, reports of Atlantic salmon adults and smolts in the Russian mackerel fishery (June – August) in the international waters in the Norwegian Sea have been low (ICES, 2004). With the ratio of Mackerel to Atlantic salmon during one fishing season (2002-2003) being 0.0015 (ICES, 2004). However, these numbers may not accurately represent the bycatch of Atlantic salmon in these fisheries as it is difficult to distinguish between Atlantic salmon and mackerel in pelagic trawl haul outs. A second spawning ground and fishery for mackerel exists of the west coast off the UK and Ireland (ICES, 2004). The highest abundance of mackerel catches in the UK occur off the west coast of Scotland and the Hebrides, and the distribution of the fisheries overlaps with the northern migration of post-smolts (ICES, 2004). The impact of that fishery on the post-smolt migration has yet to be quantified. An assessment of the amount of bycatch of post-smolts that occurs in the UK mackerel fisheries are required to determine if pelagic fisheries could pose a threat to Atlantic salmon (ICES, 2004).

1.6 Monitoring the Movement of Fishes

Recent advances in telemetry have provided researchers the means to continuously monitor the behaviour and distribution of salmon at sea (Thorstad et al., 2012b). The two main types of telemetry used in the marine environment are acoustic and satellite (Hussey et al. 2015). Prior to the development of telemetry, mark-recapture studies were used to analyze the distribution of species and were biased by the recapture locations (Hussey et al., 2015; Robinson et al., 2010). Acoustic telemetry involves the use of tags that emit an acoustic signal underwater. These tags can be attached externally or inserted internally to mark target animal and continuously transmit a signal at varying intervals to receivers placed throughout the species' range (Hussey et al., 2015). Tracking can occur either passively or actively (Crossin et al., 2017). During active tracking a hydrophone can be used to actively locate the specimen (Crossin et al., 2017). During passive tracking acoustic receivers with data logging capability are placed at fixed locations along the species' range and can decode the unique ID of each tagged individual (Hussey et al., 2015). Satellite telemetry tags are externally attached to the animal and transmit positional information using radio signals to satellites (Hussey et al., 2015; Matley et al., 2022). The most common type of satellite tag are pop-off tags, which are released from the animal after a pre-assigned time these can then be tracked and recovered by the researcher (Hussey et al., 2015).

For small species such as Atlantic salmon, acoustic telemetry is the most common method of tracking (Thorstad et al., 2011b). The smallest acoustic tag is 12mm in length and weighs 0.65g, which may be used to tag a variety of life stages and species, including Atlantic salmon smolts (Cooke et al., 2013; Honkanen et al., 2018; Smircich & Kelly, 2014). Additionally, depending on the tag size and battery, specimens can be tracked for periods ranging from a few months up to 10 years. Acoustic tags can also be programmed to record temperature, depth, acceleration, and predation events (Hussey et al., 2015). The tags can be programmed to turn on and off at varying intervals to preserve battery life (Lacroix et al., 2004a).

One of the limitations of acoustic telemetry are that the tag signals are adversely affected by strong current speeds and water turbulence and acoustic transmitters are limited in transmission range (Sanderson et al., 2017). Sanderson et al. (2017) noted that the probability of detecting an acoustic signal declines substantially when current speeds exceed 2 meters/second (m/s). Additionally, acoustic telemetry studies are often limited to small scale projects due to the high cost of equiptment. However, organizations such as the Ocean Tracking Network (OTN) are providing researchers the means to compile data from other ongoing projects to answer more broadscale questions about their target species (Cooke et al., 2013).

1.6.1 Effects on tagged fish

For telemetry to aid in making population level assumptions, the effects of tagging must not influence the fish's behaviour (Moore et al., 1990). Studies have indicated that in juvenile salmonids there are limited behavioural deficits (i.e. reduction in swimming speed) associated with tagging as long as the length and weight of the tag is less than 16% and 8% of the fish's length and weight, respectively (Lacroix et al., 2004a). However, if deficits occur, they normally last for only one week (Adams et al., 1998; Lacroix et al., 2004a). This includes a slight reduction in swim speed, which could be attributed to the additional weight of the tag. Tags are either attached externally or implanted into the intraperitoneal cavity of the fish (Jepsen et al., 2015; Moore et al., 1990). If the size of an internally implanted tag is too large for the fish it can put pressure on the wall of the body cavity, and either be expelled or cause inflammation and possible damage to internal organs (Lacroix et al., 2004a; Smircich & Kelly, 2014). However, expulsion of tags can occur in fishes of sufficient size (Lacroix et al. 2004a). It has been noted that tag expulsion normally occurs after five months of tagging, providing researchers time to assess the movement of their target species (Lacroix et al., 2004a).

The likelihood of tag retention is influenced by the experience of the surgeon, the type of suture material used, and water temperature (Deters et al., 2010; Wagner & Cooke, 2005). The most used suture materials for acoustic telemetry research are vicryl, silk and monocryl (Deters et al., 2010). Monocryl has been reported to result in the greatest tag retention, reduction in healing time, and reduced inflammation (Deters et al., 2010; Wagner & Cooke, 2005). Deters et al. (2010) assessed the likelihood of tag retention in juvenile Chinook Salmon (*Oncorhynchus tshawytscha* (Walbaum, 1758) and it was reported that after a period of two weeks, fish held at 12°C had 86% tag retention, however, at 17°C it declined to 64 %. Additionally, ulceration was more common if fish were held at higher temperatures (Deters et al., 2010).

External tag attachment is less common than internal implantations in fishes (Jepsen et al., 2015). Some of the advantages of external tagging is that there is a reduction in tagging time, recovery time of the fish, and the amount of training required by the researcher (Jepsen et al., 2015). The downside to using external tags is that they can impinge on features of a fish's environment (Jepsen et al., 2015). Additionally, external tags are often attached around the dorsal musculature of fishes and can result in fouling of the attachment as well as tissue damage (Jepsen et al., 2015; Thorstad et al., 2001). Jepsen et al. (2015) reported that external tags can increase the drag experienced by a fish through modification of their streamlined body shape (Jepsen et al., 2015). Its important to note that these effects differ between species, and their life history characteristics need to be taken into consideration before choosing a tagging procedure (Thorstad et al., 2000).

1.7 Outline of thesis

It is believed that the declining numbers of Atlantic salmon may be attributed to mortality at sea (Klemetsen et al., 2003). Understanding not only the fresh water portion of their lifecycle, but the early marine migration of Atlantic salmon smolts is needed to determine if their migratory patterns overlap with possible anthropogenic and natural stressors. This thesis comprises four separate studies which provide novel information concerning the fresh water, estuarine, early marine and coastal marine migration of Atlantic salmon smolts migrating from rivers in Ireland and the UK. These studies are:

Chapter 2: There is currently limited knowledge around the strategies smolts may use to navigate through fresh water standing bodies of water. Using acoustic telemetry combined with a mechanistic model, this study examined potential morphological and behavioural factors that differentiate successful from unsuccessful lake migrants.

Chapter 3: It is thought that survival during early marine migration is particularly poor for Atlantic salmon post-smolts immediately after entry into sea and particularly in the estuarine environment. This study used acoustic tagging technology to estimate loss rates and compare the behaviour of Atlantic salmon post-smolts migrating from two distinctly different river systems draining into the Clyde estuary, in Scotland. In addition, this study assessed potential environmental drivers of estuarine migration including time of day and point in the tidal cycle.

Chapter 4: Upon exiting the estuarine environment, Atlantic salmon post-smolts from rivers in Ireland and the United Kingdom are thought to migrate towards the slope current located off the continental shelf of Scotland. However, there is limited information on survival rates through their early marine environment and the environmental cues smolts may use to aid in migration towards the slope current. This study is the first to ground truth the existing particle tracking studies by undertaking a large-scale acoustic telemetry study utilizing data from 12 rivers and their tributaries (n = 2) draining into the Irish Sea region to address these questions.

Chapter 5: The early phase of the marine migration of Atlantic salmon (*Salmo salar*) post-smolts remains poorly documented for many populations. Previous trawling studies have shown southern European salmon post-smolts migrate towards the slope current over the Vøring plateau near Norway, however, the migration pathways that post-smolts take to reach this area are unknown. Therefore, this collaborative study investigated the migration pathways of post-smolts during the early phase of their marine migration, by drawing together acoustic telemetry data collected from seven projects.

Lastly, Chapter 6 provides a summary of the previous chapters and highlights the knowledge gaps filled by this thesis. In addition, it provides a summary of current stressors faced by Atlantic salmon and suggestions for future research.

Chapter 2: Combining acoustic telemetry with a mechanistic model to investigate characteristics unique to successful Atlantic salmon smolt migrants through a standing body of water

**Note this chapter is published in Environmental Biology of Fishes*

Abstract

The Atlantic salmon, *Salmo salar*, is a charismatic, anadromous species that has faced dramatic declines throughout its range. There is currently a lack of information on the effect of fresh water free-standing bodies of water on a key life event, sea migration, for the species. This study extends our understanding in this area by combining acoustic telemetry with a correlated random walk model to try to examine potential morphological and behavioral factors that differentiate successful from unsuccessful migrants through Loch Lomond, Scotland's largest lake. Consistent with other studies, we found that smolts experienced a high rate of mortality in the lake (~ 43%), with approximately 14% potentially predated upon by birds and 4% by Northern pike (*Esox lucius*). Migration speed in the lake was slow (the mean minimum movement speed between centres of activity was 0.13 m/s), and pathways frequently deviated away from the lake exit. There was no evidence of a morphological or behavioural trait or migratory pathway that distinguished successful from unsuccessful smolts. This suggests that migration movement direction in the main body of Loch Lomond appeared to be random. This was further supported by the output of a correlated random walk model which closely resembled the pathway and migration speed and distance patterns displayed by successful migrants. However, once successful smolts came within ~2 km of the lake exit, a high proportion remained in this region prior to entering the River Leven. We suggest that this "goldilocks zone" is where directional cues become apparent to migrating fish. Future studies should combine random walk models with environmental variables to determine if external factors are driving the apparently random movement patterns exhibited by smolts in lakes.

2.1 Introduction

Migration is the process of animals transitioning amongst different environments, interspersed with periods of residency and can often vary based on life stage (Mueller & Fagan, 2008; Avgar et al., 2014). Migration differs across temporal and spatial scales and across species and is often initiated by the need to avoid predation, mate or find food (Avgar et al., 2014; Mueller & Fagan, 2008; Tamario et al., 2019). Long distance migration is relatively common in avian and marine animals, which often traverse large expanses of ocean to reach their feeding or mating grounds (Alerstam et al., 2003; Horton et al., 2020; Vogel et al., 2021).

One group of animals that undergo long distance migrations through multiple habitat types are diadromous fishes (Limburg & Waldman, 2009). A number of diadromous fish species have experienced dramatic declines throughout their range due to disruption of habitat connectivity due to anthropogenic barriers such as weirs, dams and hydropower facilities (Birnie-Gauvin et al., 2018; Dadswell & Rulifson, 1994; Puijenbroek et al., 2019). Many fresh water systems have anthropogenic barriers impeding fish movement, as well as lakes that diadromous fishes must navigate through to reach the marine environment (Honkanen et al., 2018, 2021; Limburg & Waldman, 2009; Nunn & Cowx, 2012). How diadromous fishes navigate through standing waters is poorly understood (Honkanen et al., 2018, 2021; Lennox et al., 2021).

The Atlantic salmon, *Salmo salar*, is an anadromous species commonly studied because of its cultural and economic importance throughout Europe and North America and is a prime candidate to study migration behaviour through fresh water standing bodies of water (Honkanen et al., 2018; Klemetsen et al., 2003; Thorstad et al., 2012b). Atlantic salmon populations are distributed throughout river systems draining into the North Atlantic, and many of these populations are currently listed as threatened or endangered (Thorstad et al., 2011b). The focus of this paper is on the smolt stage of the Atlantic salmon life cycle. A smolt can be defined as a young fresh water salmonid that has undergone physiological and morphological changes that allow them to adapt to the marine environment (McCormick et al., 1985; Thorstad et al., 2012b; Zydlewski et al., 2014). Loss rates during this life stage are high and have been reported to vary between 0.3 and 7.0 %.km^{-1} migration distance in river systems (Jepsen et al., 1998; Thorstad et al., 2012b).

A large proportion of river catchments that support Atlantic salmon populations flow through large fresh water free-standing bodies of water through which smolts must navigate before entering the marine environment (Honkanen et al., 2018). For example, in Norway approximately 1/3 of river systems drain through lakes (Hanssen, 2021), and in Scotland, there are approximately 30,000 lakes many of which are components of Atlantic salmon rivers (Smith & Lyle, 1979). Smolt riverine migration has been well studied and it has been reported that smolts utilize currents to rapidly migrate downstream towards the marine environment (Davidsen et al., 2009; Lacroix et al., 2004a, b; Svendsen et al., 2007). However, in fresh water standing bodies of water with a lack of directional flow, we do not know what cues smolts use, or behaviours they adopt, to successfully migrate through this environment (Hanssen, 2021; Honkanen et al., 2018; Lennox et al., 2021). This is particularly important in interpreting how newly created standing waters (impoundments) may influence smolt migration success.

One technique that can help to further our understanding of smolt behaviour through fresh water standing bodies of water is passive acoustic telemetry (Honkanen et al., 2018, 2021; Hanssen, 2021). This is a technique commonly used to assess the behaviour and survival of fishes (Hussey et al., 2015). The few studies utilizing acoustic telemetry to assess smolt migration through lakes have indicated that smolts experience disorientation and migration speed is slow (Aarestrup et al., 1999; Honkanen et al. 2018; Thorstad et al., 2011b). Honkanen et al. (2018) assessed the movement of Atlantic salmon smolts (n = 10) through Loch Lomond, Scotland, using a small array of acoustic receivers (n = 10). The estimated loss rate of smolts through Loch Lomond was high (60%). Additionally, smolts were reported to make frequent movements away from the exit point from the lake, travelling at a slow estimated rate of ~0.05 m/s.

The high rates of mortality of smolts in lakes may be attributed, at least in part, to the lack of directional migration and energy expended in movements frequently away from the lake exit, thus, ultimately increasing their risk of predation (Hanssen, 2021; Honkanen et al., 2018, 2021; Jepsen et al., 1998). In riverine systems there has been conflicting information concerning which factors influence migration success of Atlantic salmon. Most have noted that larger individuals with a high condition factor are more likely to be successful due to their increased ability to endure long distance migrations and evade predators (Kennedy et al., 2007; Tucker et al., 2016). To date no studies have assessed whether this is also a trend found in fresh water free-standing bodies of water.

This current study built on that of Honkanen et al. (2018) by increasing the effective resolution at which we were able to address several important questions regarding smolts behaviour in Loch Lomond. We did this by increasing the area in the lake of which we were able to track fish. In addition, we improved the precision with which we were able to identify position in the lake. We used empirical data from this to compare some aspects of actual migration behaviour with that of a correlated random walk model (Hanssen, 2021). There were three main hypothesis of this study: (1) consistent with Honkanen et al. (2018), the loss rate of Atlantic salmon smolts through Loch Lomond would be high (~ 60%), specifically amongst small smolts with a low condition factor; (2) due to a potential lack of directional current in the main body of Loch Lomond, both successful and unsuccessful migrants would exhibit indirect migration pathways; (3) once near the lake outlet where the direction of the current flowing into the river may be detected, Atlantic salmon smolts would orientate towards the outflowing river and make a direct exit.

2.2 Materials and Methods

2.2.1 Study area

The Loch Lomond catchment in west/central Scotland has a total catchment area of 696 km^2; approximately one-tenth of the catchment is contained in Loch Lomond lake (Murray & Pullar, 1910, Fig. 2.1). Loch Lomond is the largest fresh water body in Britain, covering 71 km^2 and has a maximum depth of 190 m (Maitland et al., 2000). The northern and southern portions of Loch Lomond are separated by the Highland Boundary Fault (Maitland et al., 2000). The northern lake is relatively narrow and deep, whereas the southern basin is shallow with many interspersed islands (Murray & Pullar, 1910; Maitland et al., 2000). Monthly mean temperatures in the lake range between 4 and 15 °C (Maitland et al., 2000). The River Endrick drains into Loch Lomond and is 49 km long (Maitland et al., 2000; Fig. 2.1). Loch Lomond drains into the River Leven (~ 13 km long) which then discharges into the Firth of Clyde (Adams, 1994; Fig. 2.1). The Firth of Clyde covers an area of approximately 100 km^2 (Thurstan & Roberts, 2010).

2.2.2 Acoustic telemetry

2.2.2.1 Fish capture and tagging

Between April 15 and 20, 2020, 125 Atlantic salmon smolts were captured in a 1.2-m rotary screw trap placed in the River Endrick (lat. 56.0492°, long.−4.43991°, Fig. 1). The trap was located 12.7 km upstream from the mouth of the River Endrick as it discharges into Loch Lomond. The trap was checked and emptied every 24 hours. For this study, Innovasea V7-2L tags were used; these have a weight and length of 1.5 g and 19.5 mm, respectively. The tags emitted a coded sound signal at a frequency of 69 kHz every 18–38 s. The tags have a power out- put of 137 dB and an estimated tag life of 75 days. Tags were assumed to stop transmitting in the period June 29–July 4. After smolts were captured, they were anaesthetized in 0.1 g/L of tricaine methane- sulfonate (MS222) buffered with 0.1 g/L of sodium bicarbonate. It took approximately 5 min for smolts to enter stage three anaesthesia (loss of equilibrium), which is a requirement for tagging. Smolts were then measured for weight (± 0.1 g) and length (fork length, mm) and a photograph taken for morpho- metric analysis. Surgical equipment was disinfected and rinsed with distilled water (Honkanen et al., 2018).

An approximately 10 mm incision was made in the ventral abdominal wall, anterior to the pelvic girdle, and an Innovasea V7-2L 69 kHz (Innovasea Ltd., Nova Scotia, Canada) coded transmitter was inserted into the abdominal cavity. Tagging was conducted under UK Home Office licence number PP0483054. Only Atlantic salmon smolts >130 mm fork length and > 20 g weight were tagged. During surgery water containing a low dose of MS222 and river water was poured into a wash bottle and inserted into the fish's mouth via a nozzle. The solution was flushed over the gills of the fish by slowly squeezing the bottle to ensure they remained sedated. Incisions were closed by applying two interrupted surgeon knots with 4/0 Ethilon nylon sutures. Upon completion of tagging, smolts were placed into a recovery tank, and once they began to exhibit normal swimming behaviour, they were placed into an in-river containment cage that had throughflow of fresh water. Fish remained in the cage for approximately 30 min to ensure full recovery before release.

2.2.2.2 Acoustic receiver deployment

Sixty-nine kilohertz receivers deployed in this study consisted of three main types, VR2W, VR2Tx and VR2AR (Innovasea Ltd., Nova Scotia, Canada). VR2ARs have an acoustic release that can be initiated upon receiving a signal at 69 kHz emitted from a VR100 control device (Reubens et al. 2019). This decreases the effort required to retrieve receivers in deep water environments (Goossens et al., 2020). Acoustic receivers deployed in the River Endrick and the River Leven consisted of VR2W (Endrick, $n = 3$) and VR2Tx (Endrick, $n = 4$; Leven, $n = 3$), while acoustic receivers deployed in Loch Lomond consisted of VR2AR ($n = 38$) and VR2W ($n = 1$) acoustic receivers (Fig. 2.1). Acoustic receivers were deployed in the River Endrick and River Leven from April 7 to August 23 and April 11 to August 22, respectively. Acoustic receivers in Loch Lomond were deployed in a grid-like system from April 14 to October 13 (Fig. 2.1). Receivers in the River Endrick and River Leven were attached to a mooring comprising vertical steel pin on a 20 kg weight; the mooring was attached to chain which was anchored onto the shore. VR2AR receivers deployed in Loch Lomond were bolted onto an acoustic release canister (ARC; RS Aqua, UK) attached to a 35 kg weight and an anchor line holding the receiver approximately 1.5 m above the lakebed. The ARC lid was attached to three trawl floats which ensured the retrieval of the receivers and mooring upon initiation of the acoustic release (De Clippele & Risch, 2021). The range of acoustic receivers used in this study is unknown as range testing was not conducted, therefore, any estimates of mortality are minimum estimates as Atlantic salmon smolt detections may have been missed (Hanssen et al., 2021).

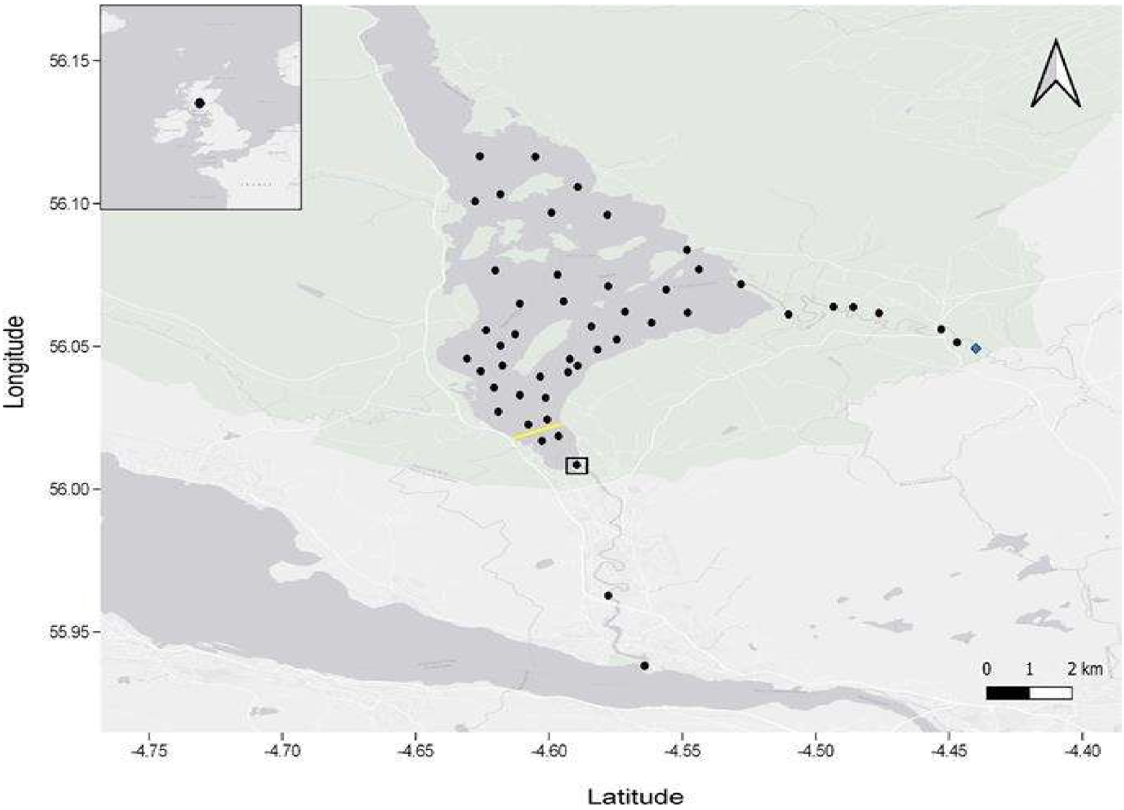


Figure 2.1 Map of the Loch Lomond catchment including locations of acoustic receiver deployments during the period April 7–August 23, 2020, in the River Endrick (*n* = 7), from April 14 to October 13 in Loch Lomond (*n* = 39) and from April 11– August 22 in the River Leven (*n* = 3). The smolt trap in the River Endrick is represented by the blue diamond (lat. 56.0492°, long. −4.43991°). The first acoustic receiver on the River Leven is represented by the black box (lat. 56.00812°, long. −4.5886°), and the Goldilocks zone is represented by the area below the yellow line (see the “Results” section). The outer boundary of the Goldilocks

zone was defined as the mean distance (mean ± SD; 1.75 ± 0.8 km) that successful smolts (*n* = 28) engaged in their final movement into the River Leven.

2.2.3 Data Analysis

2.2.3.1 False detections

All analysis was conducted in R (R Development Core Team 2020). Detection data retrieved from receivers was filtered for false detections using the package GLATOS (Holbrook et al., 2018) using the short-term interval criterion. The short-term interval used in this study was calculated based upon the minimum delay of tags used using the methods outlined in Pincock (2012). Single detections at a receiver without a repeat within 14 min were removed from the analysis (Hayden et al., 2016; Pincock, 2012).

2.2.3.2 Smolt migration success

A successful smolt, that is one that successfully migrated through Loch Lomond, was defined as one detected having entered the loch from the River Endrick and later the first receiver in the outflowing River Leven (Fig. 1, lat. 56.00812°, long. −4.5886°) without having subsequent detections in Loch Lomond. Unsuccessful migrants were likely resident in the lake for longer than successful individuals. The three main potential predators of Atlantic salmon smolts in Loch Lomond are the avian piscivores *Mergus merganser* (the goosander), Phalacrocorax carbo (the Great cormorant) and the fish *Esox Lucius* (Northern pike). Potential avian predation was identified and defined as when tag detections skipped two intermediate receivers or where consecutive tag detections occurred within a time resulting in a speed of travel that was greater than the maximum swimming speed reported for an Atlantic salmon smolt (5.7 body lengths.s^{-1}; Jepsen et al., 1998; Pedersen et al., 2008). Northern pike are common in Loch Lomond and are a primary aquatic predator of Atlantic salmon smolts in lakes throughout Europe (Adams,1991; Jepsen et al., 1998; Kennedy et al., 2018). They are known to occupy small core home ranges (Guzzo et al., 2016); therefore, potential predation by a pike was defined as repeated consecutive detections between an adjacent group of receivers over at least one day, followed by repeated detections at one receiver until the end of the detection stream, indicating that the tag was likely passed by the predator (Weinz et al., 2020). There are additional species of predatory fish in Loch Lomond including *Perca fluviatilis* (perch) and piscivorous brown trout (Ferox trout), *Salmo trutta*; however, predation of smolts by these species were assumed to be inconsequential in this study since perch in Scottish lakes have been reported to feed almost completely on benthic and planktonic invertebrates, and the abundance of Ferox trout in Scottish lakes is extremely low (Thorpe, 1977; Thorne et al., 2016). To avoid biasing a comparison of successful and unsuccessful migrant behaviour, fish that were potentially preyed upon were removed from the dataset, and the time of analysis was reduced for unsuccessful migrants. We thus filtered the data from unsuccessful migrants to include only detections from the time period up to 95% CI of the duration that successful smolts occupied Loch Lomond. The period of time that successful smolts spent in Loch Lomond was calculated based upon their last detection on the final receiver in the River Endrick (Fig. 2.1) and their first detection on the upstream receiver in the River Leven (Fig. 2.1). This filtered dataset was used for all analysis of behaviour and space use of Atlantic salmon smolts in Loch Lomond. Nine unsuccessful migrants were included in the analyses comparing the behaviour and space use of Atlantic salmon smolts in Loch Lomond, since the time they spent in the lake was within the 95% CI duration in which successful smolts were detected (6.02 days).

2.2.3.3 Smolt morphology

Four metrics were used to determine if smolt loss rate was related to the morphology of Atlantic salmon smolts that entered Loch Lomond; this included fork length (fl; mm), weight (g), condition factor (k) and tag burden. The condition factor of a smolt was calculated using the methods outlined in Barnham and Baxter (1998), and tag burden was calculated by dividing the weight of the tag (1.5 g) by the weight of the Atlantic salmon smolt (g) (Brown et al. 2013).

2.2.3.4 Smolt behaviour

Centres of activity (COA) were calculated for successful and filtered unsuccessful migrant data to determine the location of smolts in Loch Lomond. COA positions are a measure of the mean position (latitude and longitude) of a fish obtained by weighting the detections of a fish between adjacent acoustic receivers with non-overlapping ranges during a specified duration of time (Simpfendorfer et al., 2002; Espinoza et al., 2015). The duration utilized for COA positions was 15 min and was determined using the methods outlined in Villegas-Rios et al. (2015) using data from smolts that completed successful migrations into the River Leven (n = 28). COA positions were calculated using the COA function in the Animal Tracking Toolbox (ATT) for R (Udyawer et al., 2018, R Development Core Team, 2020). COA position data was used to calculate Atlantic salmon smolts non-resident events, behavioural metrics and space use in Loch Lomond. Estimates of position using COA while not providing as precise a location as alternatives such as VEMCO Positioning System (VPS) or YAPS (Yet Another Positioning Solver) (Baktoft et al., 2017; Guzzo et al., 2018) were used in this study because the receiver density required for these more precise positioning methods could not be accommodated without loss of geographic coverage in this relatively large lake (71 km^2). As the risk of losing fish from the study area (i.e. into the area of the lake not instrumented by receivers) in this study was high, thus fish location estimation precision was exchanged for an extended detection zone and thus greater study area.

Several behavioural metrics were defined from multiple measures of COA positions. A non-residence event was defined as the movement of an Atlantic salmon smolt between two COA positions and is referred to as a “movement” for the remainder of the manuscript. Movements were identified using the *RunResidenceExtraction* function in the VTrack package in R (Campbell, 2012).

The timing of smolt movement into, and out of, Loch Lomond was determined by their time of emigration from the River Endrick and last detection on the first River Leven receiver, respectively (Fig. 2.1). The hour of entry into Loch Lomond comprised the frequency of all

Atlantic salmon smolts that successfully migrated out of the River Endrick and into Loch Lomond for that hour of the day across the whole migration period, while movement patterns within and out of Loch Lomond only comprised data from successful migrants. Sunset and sunset times over the duration of the study were extracted from the *getSunlightTimes* function in the package suncalc (Thieurmel & Elmarhraoui, 2019). Days were split into three periods as defined by Hanssen (2021) and included dim periods (interval of 2 h after sunrise and before sunset), daytime hours (between the dim periods) and night-time hours (between sunset and sunrise).

Additional behavioural metrics assessed in this study included the *maximum distance detected away from the River Leven;* this was measured as the furthest COA position an Atlantic salmon smolt was detected in Loch Lomond as measured from the River Leven exit. The estimated *minimum total distance travelled* is the summation of distances between all measures of COA positions, while the smolt was in the study area of Loch Lomond. If smolts were taking the most direct route to exit Loch Lomond they would be expected to travel a minimum total distance of approximately 9 km (distance between the outlet of the River Endrick to the entrance of the River Leven). As fish position was not estimated constantly but only when the fish was within detection range of a receiver and that a straight-line movement between two COA positions was unlikely; this estimate of distance travelled is realistically only an estimate of the minimum distance travelled and likely lower than the actual distance travelled, *Relative turning angle* is the change in direction (°) of a smolt relative to its previous movement. The relative turning angle was converted to a circular object using the circular function in the circular package in R (Agostinelli & Lund, 2017), and the *mean turning angle* was calculated for each smolt. *Estimated minimum total number of turns* made by each smolt over their entire migration route was the number of movements that resulted in a *relative turning angle* greater than 0° (i.e. a straight line). These metrics were calculated using the *as.ltraj* function in the adehabitatLT package in R (Calenge, 2006). Again, because of the study design, the fact that position was not constantly estimated and that fish were unlikely to always take a direct route from one COA position to another, the estimated minimum total number of turns is very likely less than the actual number of turns made by each fish. Although less clear, it is possible that the relative turning angle measured is unlikely to include all turns taken for each fish; however, it is unlikely that this estimate is directionally biased.

Lastly, the *estimated average minimum speed* at which successful Atlantic salmon smolts swam through Loch Lomond was estimated by dividing the total distance travelled between successive COA positions by the duration of the lake migration from the River Endrick to the River Leven. As with other metrics above and based upon minimum estimates of distance travelled but a relatively exact measure of time elapsed, the average speed is thus a minimum estimated speed of travel.

2.2.3.5 Smolt space use

To assess Atlantic salmon smolt space use in Loch Lomond, we calculated their core (50%) and extended (90%) home ranges (kernel utilization distribution (KUDs)) using the adehabitathr package (Calenge, 2006). A land barrier polygon was used to remove any portions of the KUDs that would overlap with land (Duffing Romero et al., 2021). In addition, trajectories of smolts were overlaid on a map of Loch Lomond using the *plot.ltraj* function (Calenge, 2006).

Lastly, the final migratory trajectory of successful smolts was extracted based on a direct trajectory from Loch Lomond into the River Leven (Fig. 2.1). The mean distance from which successful smolts initiated a direct trajectory into the River Leven from Loch Lomond was determined by using the *ComputeDistance* function in the R package VTrack (Campbell, 2013), and this marked the outer edge of the “goldilocks zone” (a reference to the fact that the cues enabling the fish to find the lake exit (i.e. the entrance to the River Leven) were at this point presumed to be “just right”).

2.2.4 Statistical Analysis

2.2.4.1 Morphological predictors of migration success

A binomial GLM model was used to determine whether morphological factors (fork length, weight, condition factor (k), tag burden) influenced the potential mortality of smolts in the lake (Lothian et al., 2018). Collinearity amongst variables was assessed using Spearman's rank correlation tests. Fork length was highly correlated with weight ($r = 0.89$) and tag burden ($r = -0.81$). Therefore, only fork length and condition factor were included in the GLM. The top candidate models were obtained using the "glmulti" (Calcagno, 2020) package and compared using bias-corrected second-order information criterion (AICc) (Burnett et al., 2013). Likelihood ratio tests were then used to determine the final model by comparing the models with and without explanatory variables (Burnett et al., 2013).

2.2.4.2 Timing of migration

A Rayleigh test of uniformity was performed using the *r.test* in the CircStats package (Lund & Agostinelli, 2018) to determine if the movement of smolts moved into, and out of, Loch Lomond was evenly distributed throughout all hours of the day. Hour of the day was converted to radians prior to performing the test using the *hms2rad* function in the package astroFns in R (Harris, 2012).

2.2.4.3 Behavioural predictors of migration success

A binomial GLM was used to determine whether behavioural factors (average relative turning angle (°), estimated minimum total number of turns, maximum distance away from the Leven (m) and estimated minimum total distance travelled (m) influenced the successful migration of smolts through Loch Lomond (Lothian et al., 2018). Model selection procedures were the same as the model previously discussed.

2.2.4.4 Comparison of space use

Comparisons between the size of core (50% KUD) and extended (95% KUD) home ranges of successful and unsuccessful migrants were calculated using a Wilcoxon rank sum test.To determine if the Goldilocks zone served as a unique region utilized by successful smolts, the proportion of unsuccessful migrants that entered this area was calculated. Additionally, once successful smolts entered the Goldilocks zone, the proportion of movements that occurred in this zone was compared to the number movements that resulted in movement northwards and thus away from the lake exit and out of this zone, using a paired Wilcoxon signed-rank test.

2.2.4.5 Random walk model

To test if Atlantic salmon smolts are migrating through random lake movements, a random walk model from the glatos package (Holbrook et al., 2018) in R was used to simulate correlated random walks (CRW) within the boundary of Loch Lomond. A CRW model was chosen as it reflects an animal's tendency to move, where the direction of each new step is correlated with the previous one. Simulated paths followed the assumption that the turning angle for sequential directional movements was drawn from a Gaussian distribution with mean (μ) and standard deviation (σ). For the walk to be correlated, μ was always set to 0, and five levels of σ were modelled separately in increments of 5° (5, 10, 15, 20, 25°). A range of σ was tested to (1) determine how varying turning angle in evenly spaced increments influenced migration success and (2) to find a value that resulted in a random walk that most closely resembled the estimated empirical data on minimum distance travelled and duration spent in Loch Lomond by successful Atlantic salmon smolt migrants in this study.

Step lengths were set to 0.05 km and assumed to be constant (Hanssen, 2021). The number of steps each model simulated was set to a maximum of 1500. This meant that the maximum distance simulations could travel would not exceed 75 km and would therefore allow an approximate comparison with the measured distance travelled by successful smolts in this study. The starting location for the simulations was set as the point where the River Endrick discharges into Loch Lomond with an initial bearing of 301° from north (the direction of inflowing water from the River Endrick to Loch Lomond). The end point for the simulation was set to encompass the detection area covered by the first receiver located on the outflowing River Leven (lat. 56.00812°, long. -4.5886°, Fig. 2.1). When a simulated track reached this region it was classed as a successful simulated migration; tracks that did not reach this point were deemed to be an unsuccessful simulated migration.

For each of the five σ values, 200 migration simulations were generated. The distance travelled for each simulated individual was calculated by multiplying the step length (0.05 km) by the total number of steps taken to reach the detection zone of first River Leven receiver (Fig. 2.1). There is a lack of information concerning the accurate swim speeds (body lengths.s^{-1}) of Atlantic salmon smolts through fresh water free-standing bodies of water. Therefore, the swim speed set for the simulated Atlantic salmon smolts in this study was derived from a study tracking hatchery post-smolts through a fjord system that showed a mean swimming speed of smolts was 1.2 body lengths.s^{-1} (Thorstad, 2004). The mean absolute swimming speed of simulated smolts was calculated using (Hanssen, 2021):

$$V = 1.2 \text{ body lengths.s}^{-1} * (L_m)$$

where L_m is the mean fork length of Atlantic salmon smolts that successfully migrated through Loch Lomond (n = 49, mean = 0.145 m) and V is equal to the swim speed in m.s^{-1}. Therefore, the estimated swim speed of simulated smolts was 0.17 m.s^{-1}. This assumes a constant swim speed over 24 h. Telemetry data of real Atlantic salmon smolts indicated that movement predominantly occurs at night (Kennedy et al., 2018); thus, in some simulations, migration speed was halved to account for possible inactivity during the day, (assuming 12 h of daylight). Essentially this simulated 12 h of movement followed by 12 h of inactivity (Hanssen, 2021).

2.3 Results

2.3.1 Mortality

Of all smolts tagged and released in the River Endrick (n = 125), 39% (n = 49) successfully migrated into Loch Lomond. Fifty-seven percent (n = 28) of lake migrants (n = 49) successfully migrated out of the lake. Of those fish that migrated in the lake (n = 49), 18% (n = 9) were likely preyed upon, with 14% (n = 7) which were likely predated upon by a bird and 4% (n = 2) by Northern pike. The remaining causes of loss of detection (n = 12) are unknown and may have due to missed detections, tag loss or tag failure.

The average fork length of Atlantic salmon smolts that successfully migrated (n = 49) into Loch Lomond was 145.47 ± 12.29 mm (mean ± SD; range: 130–206 mm). A binomial regression model assessing the effect of morphological factors included fork length and condition factor (weight and tag burden were highly correlated with included variables) and showed that migration success was not dependent on the condition factor (k; t = 0.94, p = 0.76) or the fork length of the smolt (FL; $t = -0.03$, $p = 0.22$).

2.3.2 Migration timing

On average, smolts were detected 10.09 ± 9.33 (range: 1–54) times on 1.49 ± 0.87 (range: 1–7) receivers for each case where a COA position could be measured. Successful smolt migration through Loch Lomond was slow; on average, successful smolts migrated at an estimated average minimum speed of 0.13 $m.s^{-1}$ ± 0.04 $m.s^{-1}$ over 5.23 ± 4.2 days (0.86–21.90; mean ± SD). The migration into Loch Lomond (n = 49) and the initiation of a movement once in the lake (n = 2879 observed movements) were dependent on the hour of the day (entrance: Rayleigh test, $r.bar = 0.59$, Fig. 2.2a, $p < 0.01$; In: $r.bar = 0.24$, $p < 0.01$; Fig. 2.2b). Movements into Loch Lomond occurred primarily during the day (Day, n = 40, 83.0%; Dim, n = 7, 14.30%; Night, n = 2, 4.08%; Fig. 2.2a), with a mean entrance time of 13:00 British Summer Time (BST, GMT + 1).

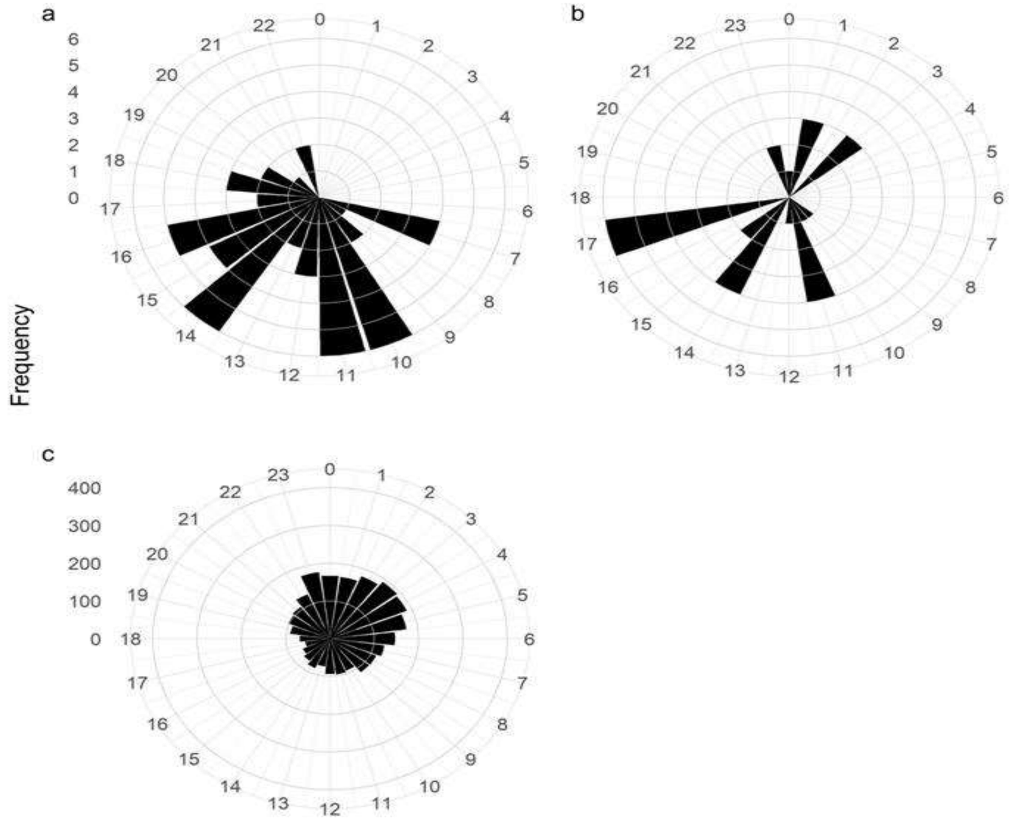


Figure 2.2 Circular plots depicting the hour (British Summer Time; BST) smolts were last detected on the final receiver in a) the River Endrick (*n* = 49), b) the initial receiver in the River Leven (*n* = 28), and c) the initiation of a movement by a successful migrant in Loch Lomond (*n* = 2879). The hour of entry into Loch Lomond comprised data on all Atlantic salmon smolts that successfully migrated out of the River Endrick and into Loch Lomond (*n* = 49). While movements within, and out of Loch Lomond only comprise data from successful migrants. The hour Atlantic salmon smolts initiated a movement in Loch Lomond was determined based upon the start of a non-residency event for smolts that were known to successfully migrate into the River Leven (*n* =28).

In contrast migration out (*n* = 28) of Loch Lomond was not dependent upon the time of the day (Rayleigh test: *r.bar* = 0.24, *p* = 0.20; Fig. 2.2b). Initiation of movement in Loch Lomond itself occurred primary during the night (day, *n* = 921, 32.0%; dim, *n* = 446, 7,15.5%; night, *n* = 1512, 52.5%), with the mean time of movement being 3:00 BST (Fig. 2.2c).

2.3.3. Behavioural predictors of migration success

The estimated minimum total distance smolts travelled and their estimated minimum frequency of turns were highly correlated (*r* = 0.86); therefore, only the estimated minimum total distance travelled was included in the model assessing behavioural factors influencing migration success. The logistic regression model included the mean relative turning angle, estimated minimum total distance travelled and the maximum distance a fish was detected at any point in time from the River Leven. The final model showed that migration success was not dependent on their relative turning angle ($t = -0.51$, $p = 0.16$), estimated minimum total distance travelled ($t = 1.3 \times 10-3$, $p = 0.90$) or maximum distance detected away from the Leven ($t = -0.41$, $p = 0.22$).

2.3.4 Home range

Successful (*n* = 28) and unsuccessful (*n* = 9) migrants did not differ in their space use of Loch Lomond, mainly utilizing the mid and lower reaches of the lake (Fig. 2.3). However, one successful (ID: 36568) and two unsuccessful migrants (ID: 36556, 36496) had core utilization distributions that occurred near the most northern receivers in our study (Fig. 2.3). There was no significant difference between the size of the core (successful, 5.66 ± 2.95 km^2, Fig. 2.3a; unsuccessful, 5.62 ± 3.03 km^2, Fig. 2.3b) and extended (successful, 16.72 ± 7.02 km^2, Fig. 2.3a; unsuccessful,15.74 ± 7.39 km^2, Fig. 2.3b) space use distributions of successful and unsuccessful migrants (Wilcoxon sum rank test; KUD 50, *n* = 37, *p* = 0.82; KUD 95, *n* = 37, *p* = 0.85; Fig. 2.3).

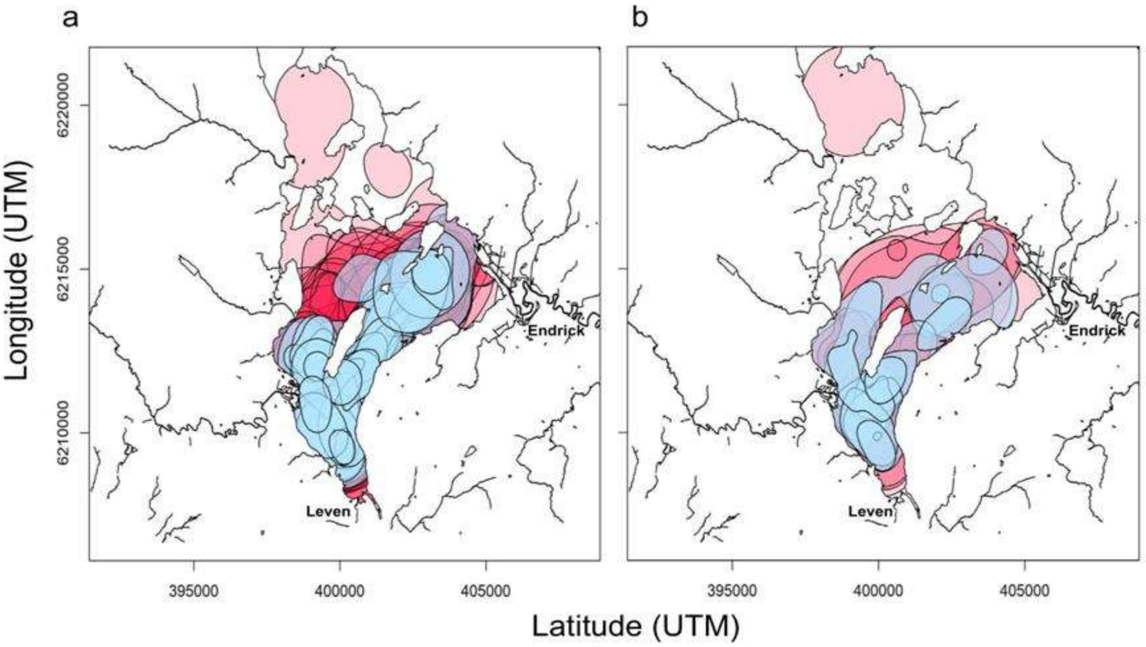


Figure 2.3 Map displaying the home ranges of a) successful (*n* = 28) and b) unsuccessful (*n* = 9) migrants in Loch Lomond (UTM Zone 30U). Blue regions represent 50% utilization distributions (KUD) of Atlantic Salmon smolts in Loch Lomond, whereas the red regions represent their 90% KUD. KUD calculations were based upon the Centre of Activity (COA) calculations for salmon smolts in 15-minute intervals. The dataset of unsuccessful migrants was filtered to include only detections within the 95% Confidence Interval (CI) of the time successful smolts occupied Loch Lomond. This was calculated based upon their last detection on the final receiver in the River Endrick and initial receiver on the River Leven.

2.3.5 Migration trajectories

On average, successful smolts (*n* = 28) travelled an estimated minimum total distance of 55.87 ± 49.52 km in the lake and were detected for 5.23 ± 4.20 days (mean ± SD). There was no one distinct migratory pathway that was unique to successful smolts (Fig. A1.1). Examples of migration route amongst successful smolts: one individual (ID: 36662) made a direct migration towards the River Leven travelling an estimated minimum distance of approximately 16.86 km over 0.86 days (Fig. 2.4a). Another successful individual (ID: 36553) travelled around the most southerly island before making an exit (Fig. 2.4b). This smolt travelled an estimated minimum distance of 35.42 km over 5.94 days. Lastly, one smolt (ID: 36568) migrated quite far north, travelling an estimated minimum total distance of 245.82 km over a duration of 21.90 days (Fig. 2.4c).

Unsuccessful migrants displayed similar variation in movement patterns as for successful smolts (Fig. A1.2). For example, after exiting the River Endrick, one smolt (ID: 36589) made a direct movement towards the River Leven prior to making repetitive back movements in the southern portion of the lake (Fig. 2.4d). A second smolt (ID: 36526) made a circular migration of an estimated minimum distance of 72.57 km over 6.04 days around the island of Inchmurrin (Fig. 2.4e). Lastly, like one successful smolt, an unsuccessful individual migrated to the northernmost portion of the receiver range (ID:36496) travelling an estimated minimum distance of 66.01 km over 6.06 days (Fig. 2.4f) but ultimately did not successfully migrate out of Loch Lomond.

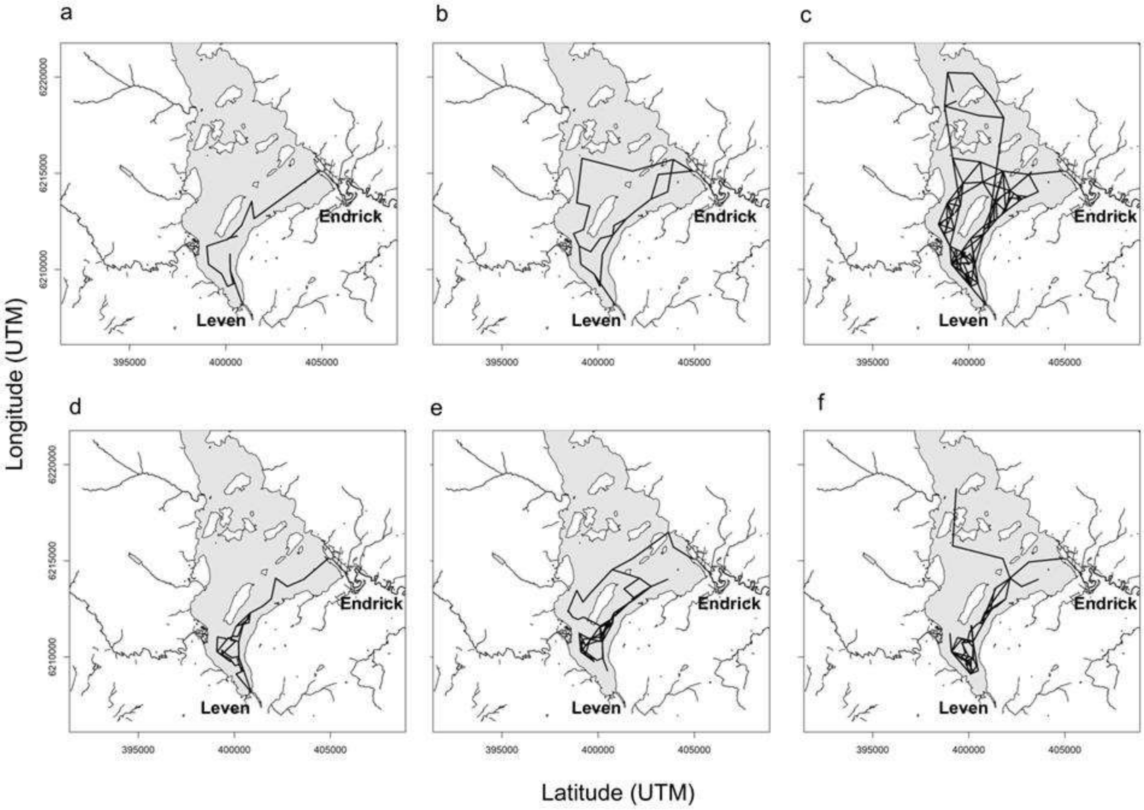


Figure 2.4 Examples of successful (a: 36662, b: 36553, c: 36568; *n* = 28) and unsuccessful migrants (d: 36589, e: 36526, f: 36496; *n* = 9) displaying different migratory patterns in Loch Lomond during 2020 (UTM Zone 30U). The dataset of unsuccessful migrants was filtered to include detections that extended to the 95% Confidence Interval (CI) of the duration successful smolts occupied Loch Lomond. The time successful smolts spent in Loch Lomond was calculated based upon their last detection on the final receiver in the River Endrick and initial receiver on the River Leven.

2.3.6 Goldilocks zone

Once Atlantic salmon smolts entered the River Leven, they were not detected returning to Loch Lomond. The point in the lake at which successful smolts (*n* = 28) made a direct movement into the River Leven occurred at an average estimated minimum distance of 1.75 ± 0.80 km (mean ± SD; range: 1.19–4.27) away from the lake exit. We define this point as representing the outer bounds of the Goldilocks zone (Fig. 2.1). These exit trajectories took a mean duration of 7.58 ± 12.89 h (mean ± SD; range: 0.75–60 h). Once fish entered the Goldilocks zone, 67% (n = 19) of smolts made movements that resulted in migrating northwards outside of the zone. The remaining 29% (n = 9) only engaged in movements in the Goldilocks zone prior to migrating into the Leven. Successful Atlantic salmon smolts had a significantly higher number of movements in the Goldilocks zone (n = 19, 6.58 ± 6.82 (range: 0–24)) than movements that resulted in migrating northwards and outside the Goldilocks zone (n = 19, 2.89 ± 0.53 (range: 1–7); paired Wilcoxon signed rank test, V = 111, p = 0.04). However, 56% (n = 5) of unsuccessful migrants entered this area, suggesting entry to the Goldilocks zone does not guarantee successful migration out of the zone.

2.3.7 Random walk model

The current study did not allow for accurate measures of the actual swim speed of smolts in Loch Lomond (only estimated minimum speed between two known points). Thus, swim speeds and step lengths utilized for the simulated smolts were derived from the literature (Hanssen, 2021). The simulated swim speed of a smolt in Loch Lomond (0.17 m.s^{-1}) was derived from the speed (bl.s^{-1}) of smolts in the standing water of a fjord system as described in Thorpe et al. (1981). Assuming a constant swimming speed of 0.17 m. s^{-1} and step length of 0.05 km through both day and night, random walk simulations beginning at the mouth of the inflowing River Endrick and terminating at the outflowing River Leven, revealed a negative correlation between the increasing turn angle (σ; 5, 10, 15, 20, 25) of a simulated smolt and the success rate. Furthermore, there was a positive correlation between the increasing turning angle of a simulated smolt and the duration and total distance travelled through Loch Lomond (Table 2.1; Fig. 2.5). For simulations accounting for diurnal migration, the mean travel time for all turning angle groups doubled (Table 2.1). When excluding nocturnal migration, simulations with a turning angle σ of 15 with 24 hour migration (58.54 km over 3.98 days; Table 2.1; Fig. 2.5) were found to result in a model that best fit empirical data of the minimum estimated mean distance travelled, and time taken resulting in 55.87 km over 5.23 days.

Table 2.1 Results from correlated random walk models of simulated Atlantic salmon smolts in Loch Lomond. This includes the success rate (%), mean distance travelled and mean duration of loch migration for each simulation group. Simulations were assigned a maximum number of 1500 steps with a length of 0.05 km. Simulated paths assumed a mean (μ) turning angle of 0, and the standard deviations of turning angles (σ) consisted of five groups (5, 10, 15, 20, 25). For each of the five groups, 200 simulations were generated. The estimated swim speed of simulated smolts was 0.17 $m.s^{-1}$, and to account for diurnal migration, the swim speed was halved (0.085 $m.s^{-1}$).

Turning angle (σ)	**Success % (No.)**	**Mean distance (km)**	**Mean duration at 0.17 $m.s^{-1}$ (days)**	**Mean duration at 0.085 $m.s^{-1}$ (days)**
5	14.5 (29)	46.33	3.15	6.31
10	5.5 (11)	42.80	2.91	5.83
15	4 (8)	58.54	3.98	7.96
20	1.5 (3)	60.22	4.1	8.2
25	0	NA	NA	NA

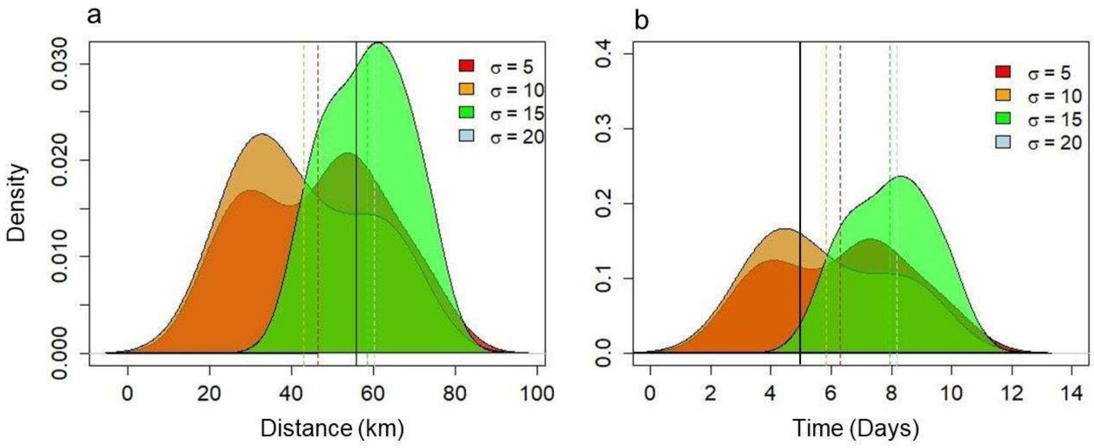


Figure 2.5. Graphs displaying results from correlated random walk models of simulated Atlantic salmon smolts in Loch Lomond including the density of a) the distance travelled (km) and b) the duration (days) of simulated smolt tracks. Simulations were assigned a maximum number of 1500 steps with a length of 0.05 km. Simulated paths assumed a mean (μ) turning angle of 0 but drawn from a normal distribution of turning angles of with standard deviations (σ) from five groups (5, 10, 15, 20, 25). The 25° group was not included in the figure as no simulated smolts in this group completed a successful migration into the River Leven. For each of the five groups, 200 simulations were generated. The estimated swim speed of simulated smolts was 0.17 $m.s^{-1}$. The dotted lines reflect the estimated average minimum distance (a) and duration (b) of each of the five simulated groups within Loch Lomond. The black line in both plots is the estimated average minimum distance (a) and duration of successful smolts in Loch Lomond.

2.3.7.1 Simulated tracks

Consistent with the tracks displayed by actual successful smolts in this study, simulated smolts with a σ of 15 displayed varying migratory pathways to reach the lake outlet. We present four examples here; one simulated smolt (Fig. 2.6a) travelled 51.5 km over 3.51 days, following a similar trajectory to ID:36662 (Fig. 2.4a) albeit at a slower pace, whereas another (Fig. 2.6b), travelled 69.5 km, spending a large portion of time around the most southerly island in the lake before exiting the River Leven after 4.73 days. Another simulated smolt (Fig. 2.6c) travelled 44.15 over 3 days and travelled in a fairly linear path at the start of their migration but spent a considerable amount of time in the southern portion of the lake before exiting. The last simulated smolt (Fig. 2.6d) travelled 72.35 km over 4.93 days and displayed the most erratic path of the four simulated smolts, heading northwards upon exiting the River Endrick and spending time around the most southerly island before heading in the direction of the outflowing river.

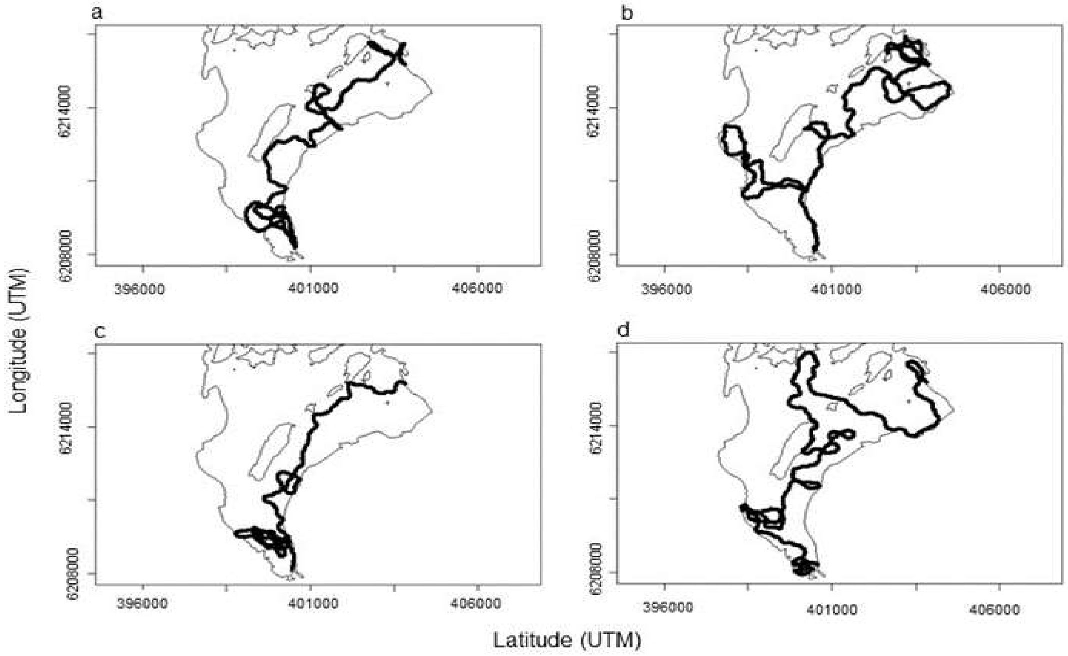


Figure 2.6. Simulated tracks for four successful smolts (a, b, c, d) with a turning angle σ of 15 and step length of 0.05 km, moving at 0.17 m/s. Successful smolts were defined as those which were detected in the region covered by the first acoustic receiver on the River Leven (lat. 56.00812°, long. -4.5886°).

2.4 Discussion

Loss rates of acoustically tagged salmonid smolts in fresh water free-standing bodies of water have been reported to be as high as 88% (Jepsen et al., 1998). Consistent with other studies, here we provide further evidence that the loss rate of Atlantic salmon smolts through large fresh water free-standing bodies of water is substantial (Aarestrup et al., 1999; Berry., 1933; Thorpe et al., 1981; Bourgeois & O'Connell, 1988; Honkanen et al., 2021). The likelihood of Atlantic salmon smolts released from the River Endrick (*n* = 125) and completing a successful migration through the Loch Lomond was very low, with only 57% (*n* = 28) being detected in the River Leven. The highest loss rate occurred within the Endrick, with only 39% (*n* = 49) successfully migrating into Loch Lomond. This is consistent with Honkanen et al. (2018) who reported a smolt loss rate of 40% in the River Endrick. It is unlikely that the high mortality rates in this region were related to environmental parameters such as water level as the variation in flow rate in the River Endrick is low across years and very low within the period of this study (SEPA, 2021b). Additionally, the average water level during the dates when successful lake migrants exited the River Endrick (0.41 m, April 17–May 19) was similar to the average water level that would have been experienced by smolts during this study (0.55 m, April 15–August 23), indicating that the water level during the study period was sufficient for smolts to exit the River Endrick.

A recent study has shown that smolt mortality during migration in the River Endrick is mainly the result of high rates of avian and piscine predation (Chavarie et al., 2022). The high loss rates of salmon smolts in Loch Lomond may in part also be related to both avian and piscine predation. Goosanders, cormorants and Northern pike are relatively common in Loch Lomond (Adams, 1994). Goosanders and cormorants have been reported to predate on Atlantic salmon smolts during their spring migration, and a disruption to their foraging activity increases the likelihood of salmon smolt survival (Hawkes et al., 2013; Kennedy & Greer, 1988). Fourteen percent of the 49 smolts that entered Loch Lomond were categorized as being subject to avian predation and a further 4% to piscine predation (most likely pike predation). This compares with 42 and 14%, respectively, for smolts migrating down the River Endrick (Chavarie et al., 2022), thus suggesting that salmon smolts are vulnerable to predation throughout the Loch Lomond catchment.

Kennedy et al. (2018) analysed the movement of Atlantic salmon smolts through the Lough Erne catchment in the Fermanagh District, Northern Ireland. They noted that the highest rates of mortality attributed to pike predation in the river to lake confluence part of the migration route. Northern pike spawn in shallow regions with dense vegetation, habitats which are often found in river mouths (Kekäläinen et al., 2008). Northern pike may have increased in numbers in recent years due to the introduction of the invasive *Gymnocephalus cernuus* (ruffe) (Adams, 1991). We are less certain about the fate of the remaining 57% (n = 12) of unsuccessful migrants. These smolts exhibited normal smolt behaviour up until a string of repeat detections occurred at a single receiver. The cessation of detections of these tags may be attributed to a movement out of the detection zone, tag loss, tag failure, predation by another aquatic predator, or stress induced by the capture and acoustic tagging procedure (Cooke et al., 2011; Klinard & Matley, 2020).

No significant morphological (fork length, condition factor) factors predicted the successful migration of a smolt within and through the lake. If unsuccessful migrants experienced mortality due to predation, the relationship observed in this study does not support the central food web theory which states that a larger body size is positively correlated with body condition and predator avoidance. Both unsuccessful (n = 21, k = 0.96 ± 0.13) and successful migrants (n = 28; k = 0.99 ± 0.11) analysed in this study had condition factors (k) which are considered normal for Atlantic salmon smolts (McCormick & Björnsson, 1994). This may have been due to the slight bias in the analysis introduced due to being only able to acoustically tag smolts greater than 130 mm and 20 g for tagging. Therefore, to adequately detect a size effect on predation, future studies may need to include enough small and large Atlantic salmon smolts to get a better representation of varying cohorts.

Atlantic salmon smolts in Loch Lomond appeared to migrate primarily during the night, which is thought to decrease the likelihood of being spotted by predators and is consistent with the pattern observed by smolts migrating through a Norwegian lake (Hanssen et al., 2021; Haraldstad et al., 2017; Kennedy et al., 2018). However, the benefit of this tactic was likely mitigated by their slow migration speed and apparently random migration pathways which delayed lake exit (Jepsen et al., 1998). The maximum sustained swimming speed of an

Atlantic salmon smolt has been reported to be 0.50 $m.s^{-1}$ and is well above the estimated average minimum swimming speed observed in our study (Virtanen & Forsman, 1987). Successful smolts in this study migrated at an estimated average minimum speed of 0.13 $m.s^{-1}$ over 5.23 days (range: 0.86 – 21.90; Hanssen, 2021; Honkanen et al., 2018, 2021). This is consistent with a study conducted by Honkanen et al. (2021) that reported that Atlantic salmon estimated average minimum migration speed through three lakes in Scotland varied between 0.09 and 0.15 $m.s^{-1}$, presumably because they are not going in a straight line between receivers.

In support of our hypothesis, there was no discernible difference in the space use and migratory trajectories between successful and unsuccessful individuals. The pathways of both those fish that did migrate successfully and those that did not apparently do not differ from random movements. Unlike riverine migration, where subsequent movements occur in the direction of the river outlet, smolts in our study frequently chose pathways that deviated from progressing towards the outflowing River Leven (Thorstad et al., 2012b; Urke et al., 2013; Flávio et al., 2021). For example, some smolts circled the most southern island prior to travelling towards the River Leven, while others were found to engage in long distance migrations towards the northern portion of Loch Lomond before successfully exiting the lake.

Here we used a correlated random walk model to directly test whether the migrations of Atlantic salmon smolts through Loch Lomond can be described as random. The simulated tracks of Atlantic salmon smolts fitted using a random walk model displayed varying migratory trajectories that closely resembled the trajectories of successful smolts in Loch Lomond. Simulated smolts with a σ of 15° spent up to 3.98 days in the lake travelling up to 58.54 km, in comparison to real successful smolts which on average travelled 55.87 km over 5.23 days. Hanssen (2021) found that a nocturnal correlated random walk model more accurately represented the movement of Atlantic salmon smolts through Lake Evangervatnet, Norway. These results may be attributed to the fact that smolts in their study were mostly inactive during daylight hours with 91% of smolts engaging in nocturnal migration. Nocturnal migrations in Loch Lomond only accounted for 68% of movements, indicating that movement patterns of smolts in Loch Lomond are not wholly nocturnal. Therefore, the model assuming a realistic swim speed and turn rate migrating during the day and night may most accurately represent the movement activity of smolts in this lake.

While the random walk model was found to closely resemble successful salmon smolt movement through Loch Lomond, the behavioural metrics used could, and should, be refined in future studies. Although there were data to draw from to characterize swim speed and step lengths of Atlantic salmon smolts, this information is not yet available for smolts migrating in standing water. To better parameterise future random walk modelling of wild smolt movement through lakes, future empirical studies should deploy a grid of receivers with overlapping detection ranges to enable more precise positional estimates using VEMCO Positioning System (VPS) or Yet Another Positioning Solver (YAPS; Baktoft et al., 2017; Guzzo et al., 2018).

While the migratory behaviour of successful smolts through Loch Lomond appears to be random, there was a distinctive difference in the behaviour of successful smolts once they came within approximately 2 km of the mouth of the River Leven (the outlet to Loch Lomond), the "Goldilocks zone". Contrary to our hypothesis, the Goldilocks zone was not only used by successful migrants as 56% of unsuccessful migrants (n = 5) entered this region. However, the Goldilocks zone was effectively defined as an important area in the lake, as once the fish entered the area, they had a high chance of migrating out of Loch Lomond, and successful migrants had a significantly higher number of movements in that area compared with outside of the zone. We may hypothesise this is because the cues available to them allow for much more directed migration into the River Leven. In rivers and estuaries, Atlantic salmon smolts have been reported to use the outflowing current to aid in migration towards the marine environment (Hedger et al., 2008; Lothian et al., 2018; Mcilvenny et al., 2021; Thorstad et al., 2012b).

2.4.1 Conclusion

Thus, we conclude that, at least in this study, the survival of Atlantic salmon smolts through a fresh water standing body of water does not appear to be dependent on unique morphological or behavioural characteristics. Additionally, movement through standing waters appears to be through a series of random movements that continue until the smolts are near the lake out-flow at which point the migration returns to directed movements informed by possible lake cues. While it has been reported that there is a lack of distinctive currents in large fresh water free-standing bodies of water, surface currents generated by wind may in part explain the movement patterns exhibited by smolts as smolts are known to primarily migrate within the top few metres of the water column (Svendsen et al., 2007, Mcilvenny et al., 2021). For example, Thorpe et al. (1981) noted that smolt movement in Loch Voil, Scotland, were found to swim parallel to the direction of eddies generated by wind driven surface currents. Future studies should assess whether the success of Atlantic salmon smolts in lakes is dependent upon wind-driven surface currents and currents generated at the lake outlet. This could be done through combining the known current patterns in the lake with a correlated random walk model. The River Endrick, including Loch Lomond, has been classified as a Special Area of Conservation, and Atlantic salmon is a feature of interest there being listed under Annex II in the EU habitats directive (JNCC, 2019); however, numbers have been declining (Adams et al., submitted). Determining what cues are driving successful migration during a period of the life cycle typified by high mortality (this study) could help predict the response of Atlantic salmon populations to varying environmental conditions and aid in the conservation and habitat protection of smolts migrating through the River Endrick and Loch Lomond.

Chapter 3: Investigating the behaviour of Atlantic salmon (*Salmo salar* L.) post-smolts during their early marine migration through the Clyde Marine Region.

**Note this chapter is published in the Journal of Fish Biology*

Abstract

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

3.1 Introduction

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

The Atlantic salmon (*Salmo salar*) is a charismatic anadromous salmonid that in Northern Europe undergoes long-distance migrations during its first year at sea from its natal river to feeding grounds in the North-East Atlantic (Holm et al., 2000; Jacobsen et al., 2012; Mork et al., 2012; Ounsley et al., 2020). Currently, the Atlantic salmon is of high conservation interest due to diminishing numbers throughout their range (Gilbey et al., 2021; ICES, 2021). This decline has ultimately led to the categorization of Atlantic salmon as an Annex II species under the EU Habitats and Species Directive while in their fresh water habitat (Crozier et al., 2004; McLeod et al., 2005). This directive establishes a network of locations for conservation of threatened or at-risk species throughout Europe (McLeod et al., 2005). Despite considerable research aimed at understanding the fresh water phase of Atlantic salmon, the global decrease in Atlantic salmon is thought to be attributed to losses during marine migration (Parrish et al., 1998; Thorstad et al., 2012b).

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

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

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

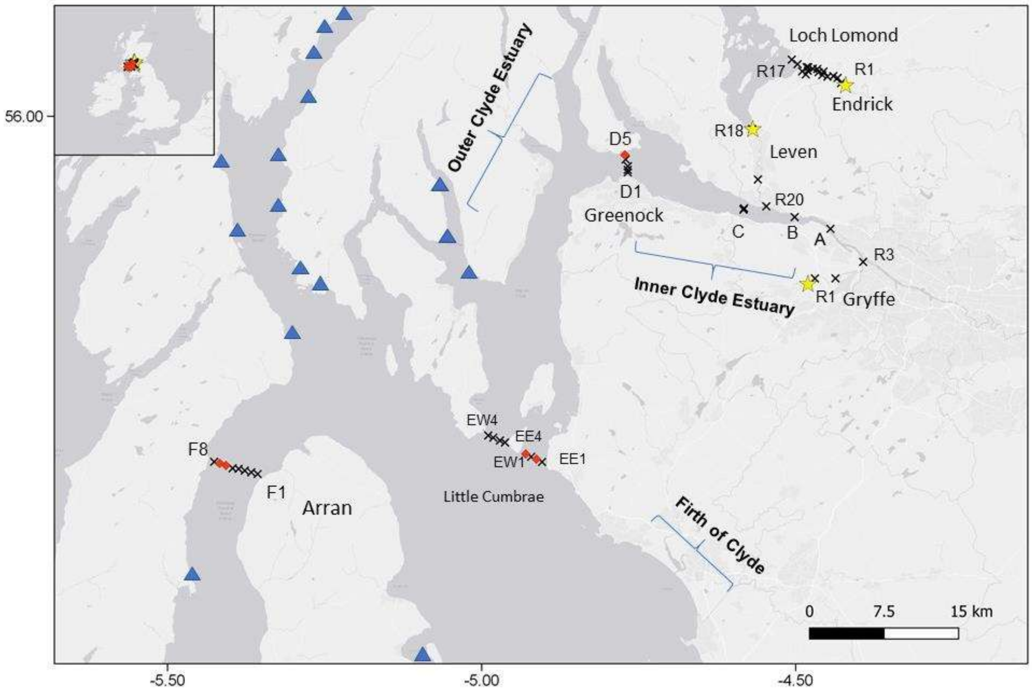


Figure 3.1 Map of acoustic receivers deployed (black crosses) within the Clyde Marine Region (Inner Clyde Estuary, Outer Clyde Estuary, Firth of Clyde), and rivers draining into Loch Lomond (River Endrick) as well as the Clyde Estuary (River Leven, River Gryffe). The red diamonds represent receivers that were not retrieved, and the yellow stars represent locations where Atlantic salmon smolts were released in this study (River Endrick: *n* = 98, lat. 56.0492°, long. -4.43991°; River Leven: *n* = 47, lat. 56.0076°, long. -4.58749°; River Gryffe: *n* = 102; 55.8693°, long. -4.49366°). The blue triangles depict the locations of operational fish farms (n = 16) in the Clyde Marine Region (Marine Scotland, 2022).

Research investigating the specific components of their migration pathway where post-smolts are most vulnerable is essential to determine the potential mechanisms of population decline, and thus aid management decisions for the species (ICES, 2020). In this study the authors used acoustic tracking technology to monitor the movement of Atlantic salmon post-smolts from two distinctly different river systems draining into the Inner Clyde Estuary: the River Endrick and the River Gryffe in west-central Scotland. The Inner Clyde Estuary is part of the Clyde Marine Region, which also consists of the Outer Clyde Estuary and the Firth of Clyde (Marine Scotland, 2015; Fig. 3.1; see Methods).

The River Endrick is of particular interest as it has been classified as a special area of conservation (SAC) due to important populations of brook lamprey (*Lampetra planeri*) river lamprey (*Lampetra fluviatillis*) and Atlantic salmon (JNCC, 2019). Prior to reaching the Inner Clyde Estuary, smolts migrating out of the River Endrick must travel a minimum total distance of c. 30 km through the Loch Lomond catchment (Honkanen et al., 2018), navigating through the largest fresh water body in Britain (Loch Lomond) and the River Leven (Maitland et al., 2000). Acoustic telemetry studies conducted in the Loch Lomond catchment have reported that smolts undertake very indirect migration routes, and survival rates during migration through the loch are extremely low (50%–57%; Honkanen et al., 2018; Lilly et al., 2021). The low survival rates are thought to be attributed to the increased energy expended while navigating through this region, which may increase the risk of predation (Honkanen et al., 2018). Previous studies have indicated that transporting salmonid smolts around migratory barriers increases their likelihood of reaching the estuary (Rechisky et al., 2012). To test whether high loss rates in the River Endrick and Loch Lomond could be mitigated, in this study, a proportion of Atlantic salmon smolts captured and tagged from the River Endrick were transported and released in the upper River Leven, the river which connects Loch Lomond and the estuary (Fig. 3.1). Lastly, in comparison to the Loch Lomond catchment, the River Gryffe has limited obstructions to smolt migration. Due to the absence of a lake, it was hypothesized that the fresh water mortality rate of migrating River Gryffe smolts would be lower than for River Endrick smolts.

The main contemporary threats to Atlantic salmon migrating through the Clyde Marine Region include the development of fish farms and predation. Scotland is the second-largest producer of farmed salmon in Europe, with net pen production occurring along the western coast of Scotland (Tett et al., 2018; Whitmarsh & Wattage, 2006). Currently, in the Clyde Marine Region (Fig. 3.1) there are active fish farms sites (*n* = 16), located on the east and west coasts of Arran (*n* = 2) as well in two adjoining sea lochs (*n* = 14), with plans to develop more in the coming years (Marine Scotland, 2022; Fig. 3.1). One of the main concerns with fish farms is that the high density of farmed salmon contained in pens can enhance local populations of parasitic sea lice (*Lepeophtheirus salmonis*) (Todd et al., 2006), which are known to cause osmotic stress and mortality in post-smolts migrating in coastal zones (Finstad et al., 2000; Shephard & Gargan, 2021; Susdorf et al., 2018).

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

The overall purpose of this study was to elucidate the behaviour of Atlantic salmon post-smolts in the Inner and Outer Clyde Estuary (Fig. 3.1). This study had three main objectives; the first objective was to compare the fresh water and estuarine loss rates of Atlantic salmon smolts emigrating from the Rivers Endrick and Gryffe and to test whether individual characteristics of the fish influenced survival. We had two main hypotheses regarding estuarine loss: (a) estuarine loss rate would be higher than that of fresh water, and within the estuary the loss rate would be highest in the inner reaches, and (b) estuarine loss would be dependent on post-smolt size with larger post-smolts having a higher likelihood of completing a successful migration.

The second main objective of this study was to examine the environmental drivers of the movement of smolts through the Inner and Outer Clyde Estuary. Our two main pathway hypotheses were: (c) that, consistent with previous estuarine studies, post-smolts would engage in passive reversal movements with the tide in the Inner Clyde Estuary (Halfyard et al., 2017; Martin et al., 2009) and (d) as their migration progresses towards the Outer Clyde Estuary (Fig. 3.1) post-smolts would engage in faster more unidirectional migrations towards the estuarine outlet, travelling primarily during the night (Hedger et al., 2008). The last and third objective of this study was to determine the main migratory pathways of post-smolts in the Clyde Marine Region and compare the migratory patterns of smolts from two different river systems. This information will inform management of the potential overlap between Atlantic salmon post-smolts and anthropogenic stressors during their spring migration.

3.2 Materials and Methods

3.2.1 Description of study area

The Clyde Marine Region is located on the west coast of Scotland and is composed of the Clyde Estuary (Inner and Outer Clyde Estuary) and Firth of Clyde (Marine Scotland, 2015). The Firth of Clyde is the most southerly fjord in the North Atlantic, and it extends c. 100 km into the Scottish coast (Karunarathna, 2011; Thurstan & Roberts, 2010; Fig. 3.1). The Firth of Clyde system is heavily influenced by semidiurnal tides of up to 3 m (Bekic et al., 2006). Draining into the Firth of Clyde is the Clyde Estuary, where the inner estuary extends for c. 40 km between the town of Greenock and the tidal weir in Glasgow, whereas the outer estuary extends c. 30 km between Greenock and Cumbrae (Fig. 3.1). The Inner Clyde Estuary has been extensively modified through dredging over the past few centuries to allow for shipping and navigation: modifying it from a relatively shallow and narrow estuary in the 17th century to a more open fjordic embayment (Bekic et al., 2006; Karunarathna, 2011; Pye & Blott, 2014; Sabatino et al., 2017). Six rivers (Rivers Clyde, Kelvin, White Cart, Black Cart, Gryffe and

Leven) supply the main fresh water input to the Clyde Estuary, and the long-term average river inflow is c. 110 m^3 s^{-1} (Bekic et al., 2006; Karunarathna, 2011).

3.2.2 Fish capture and tagging

Between 15 April and 4 May 2021, 145 Atlantic salmon smolts were captured in a rotary screw trap and tagged with acoustic tags in the River Endrick. The rotary screw trap was located 12.7 km upstream of its confluence with Loch Lomond, and a minimum distance of *c*. 30 km from the Inner Clyde Estuary (lat. 56.0492°, long. – 4.43991°; Fig. 3.1; Honkanen et al., 2018). Similarly, between 12 and 19 April 2021, 102 Atlantic salmon smolts were captured in a rotary screw trap and tagged with acoustic tags in the River Gryffe. The Rotary screw trap deployed in the River Gryffe was located 8.4 km upstream of its confluence with the Inner Clyde Estuary (lat. 55.8693°, long. -4.49366°; Fig. 3.1). Only smolts greater than 130 mm fork length (FL) and 20 g mass were tagged with V7-2L acoustic tags (Innovasea). These tags have a length of 20 mm and weight of 1.6 g in air. Tags were programmed to emit a signal of 69 kHz at 137 dB every 18–38 s giving tags a lifespan of 75 days. Prior to tagging, smolts were anaesthetized in 0.1 g l^{-1} of tricaine methanesulfonate (MS222) buffered with 0.1 g l^{-1} of sodium bicarbonate. Once smolts entered stage three of anaesthesia (loss of equilibrium), they were measured for weight (g) and length (FL, mm). Using a scalpel, an incision of *c*. 10 mm was made in the ventral abdominal wall, anterior to the pelvic girdle and the V7-2L–coded transmitter inserted into the peritoneal cavity. During surgery the smolts' gills were washed with a low dose of MS222 and river water to ensure they were supplied with oxygen and remained sedated. Incisions were closed using two interrupted surgeon knots with 4/0 Ethilon nylon sutures. Smolts were then placed into a recovery tank until they retained equilibrium and exhibited normal swimming behaviour, and then transferred into a container in the river with free-flowing water for *c*. 45 min before being released.

Atlantic salmon smolts from the River Endrick were released at two locations: 99 were released 10 m below the River Endrick trap (dates: 15 April–4 May 2021; lat. 56.0492°, long.

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

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

3.2.3 Acoustic receiver deployment

For the purpose of analysing smolt movement through different habitats, the authors divided the study area into three separate ecological zones: the fresh water zone, estuarine zone and coastal marine zone (Kocik et al., 2009). The fresh water zone included all fresh water habitats; the estuarine zone (Clyde Estuary) was divided into two sub-zones: the inner (Inner Clyde Estuary) and outer estuary (Outer Clyde Estuary); and lastly, the coastal marine zone consisted of the Firth of Clyde (Fig. 3.1). Receivers deployed in the fresh water zone (*n* = 23) included those deployed in the Loch Lomond catchment (River Endrick (*n* = 17; VR2W, *n* = 4 and VR2Tx, *n* = 13; Fig. 3.1, R1–R17) and Leven (*n* = 3; VR2W, *n* = 2 and VR2Tx, *n* = 1; Fig. 3.1, R18–R20)) and River Gryffe (*n* = 3; VR2W, *n* = 2, VR2Tx, *n* = 1; Fig. 3.1, R1– R3), and comprised VR2W and VR2Tx receivers (Fig. 3.1; see Lilly et al. (2021) for a description of acoustic receiver types). Acoustic receivers used in this study have been reported to have a detection efficiency of *c*. 80%–90% at distances of up to 200 m in riverine and estuarine environments (Honkanen et al., 2020). Receivers deployed at the entrance and exit of each section of the fresh water zone spanned distances ranging from 52 m at the exit of the River Endrick to 153 m at the exit of the River Gryffe, suggesting that receiver range would cover the full width of the river. Acoustic receivers were deployed in the River Endrick, River Leven and River Gryffe during 1 April to 5 July, 16 March to 5 July and 16 March to 20 July, respectively.

In the estuarine and coastal marine zones receiver sites were labelled in alphabetical order based on decreasing longitude (Fig. 3.1). Receivers located adjacent to one another at the same site, providing full shore-to-shore coverage, were referred to as monitoring lines, whereas sites with a single receiver were referred to as monitoring points (Kocik et al., 2009). In the estuarine zone, 18 acoustic receivers (VR2W, *n* = 1; VR2Tx, *n* = 7 and VR2Ar, *n* = 10) were deployed in the inner and outer estuary, during 10 April to 30 July. This consisted of a monitoring line of five receivers deployed off the coast of Greenock, excluding D5 which could not be retrieved at the end of the study (Fig. 3.1, D1–D5), which allowed the authors to estimate the number of smolts transitioning from the inner to the outer estuary. Furthermore, to estimate the number of post-smolts transitioning from the estuarine zone (Outer Clyde Estuary) to the coastal marine zone (Firth of Clyde), four VR2Ars were deployed on the east and west coasts of Little Cumbrae (line E), forming monitoring lines EE (EE1–EE4) and EW (EW1–EW4), respectively (Fig. 3.1). The authors were unable to retrieve two VR2ARs on the east coast of Little Cumbrae (EE4, EE2). Lastly, in the coastal marine zone, eight VR2ARs were deployed during 10 April to 30 July 2021 in Kilbrannan Sound located off the west coast of Arran, forming monitoring line F (Fig. 3.1). They were unable to retrieve two VR2ARs in Kilbrannan Sound (F6, F7).

3.2.4 Statistical analysis

3.2.4.1 False detections

All analyses in this study were conducted using R version 3.5.3 (R Core Team, 2019). Prior to data analysis, false detections were removed. Detection data were filtered for false detections using the short-interval criterion in the R package GLATOS (Holbrook et al., 2018; Pincock, 2012). The short interval criterion was defined as a single detection that occurred at one receiver within a duration greater than 30 times the average signal delay (14 min) of the tag (Hayden et al., 2016; Kneebone et al., 2014; Lilly et al., 2021). In addition, consecutive detections that occurred during a duration less than the tag's minimum signal delay (18 s) were removed from the data set (Hanssen et al., 2022). In total, 0.16% (*n* = 2151) of detections (*n* = 1,332,256) were considered false. Therefore, 1,330,095 detections were used for analyses.

3.2.4.2 Loss estimates

To determine regions that may pose the most risk to migrating salmonids, the authors assessed the likelihood of smolts migrating through receiver regions in the fresh water zone and past monitoring lines/points in the estuarine zone. In this study a successful migrant was considered as a smolt that migrated through the fresh water and/or the estuarine zone. Receiver regions in the fresh water zone included the River Endrick, River Leven and the River Gryffe. Monitoring points and lines in the estuary included points and lines A, B and C, D, E (EW, EE combined; Fig. 3.1), respectively. Nonetheless, the detection efficiency of acoustic telemetry is not always 100%, and therefore it must be assessed when providing estimates of survival (Halfyard et al., 2013). Receiver efficiency in the fresh water zone was assessed for the final River Endrick receiver (Fig. 3.1, R17) as well as for the receivers deployed in the River Leven (Fig. 3.1, R18–R20) and Gryffe (Fig. 3.1, R1–R3) by calculating the proportion of smolts detected at a downstream receiver that were not detected at the prior upstream receiver (Chavarie et al., 2022). Receiver efficiency for the final River Leven and Gryffe receiver was estimated by calculating the proportion of smolts detected on monitoring line E as monitoring line E had the greatest shore-to-shore coverage within the estuarine zone. Lastly, receiver efficiency in the estuarine zone was calculated using a mark-recapture model as discussed next (Halfyard et al., 2013).

3.2.4.3 Mark-recapture model

Cormack Jolly Seber mark-recapture models (CJS) for live recaptures (Cormack, 1964; Jolly, 1965; Larocque et al., 2020; Seber, 1965) have been used in acoustic telemetry to estimate both migration success (*S*) of the target species and the detection efficiency of acoustic receivers (*p*) (Halfyard et al., 2013; Kocik et al., 2009; Larocque et al., 2020). Here CJS models (logit-link) were fitted, using maximum likelihood estimation, to determine the apparent success of River Endrick combined and River Gryffe post-smolts past monitoring lines in the estuarine zone using the RMark package (Laake, 2013) in R, which is based on the MARK programme (White & Burnham, 1999). Detection efficiency (*p*) is calculated as the percentage of post-smolts detected at a monitoring line that were missed on the previous. Sites used for this analysis included the last fresh water receiver (release site), as well as monitoring lines C, D and E (EW and EE combined) (Fig. 3.1). Unfortunately, *p* could not be estimated at monitoring line E (Fig. 3.1) as there were no monitoring lines beyond this point. CJS models were fitted separately for River Endrick combined and Gryffe post-smolts as River Gryffe post-smolts had a farther distance to travel to reach the first monitoring line (Fig. 3.1, D) in comparison to River Endrick combined post-smolts.

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

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

3.2.4.4 Estuarine movement

3.2.4.4.1 Space use

The number of Atlantic salmon post-smolts detected at each receiver in the estuarine zone was overlaid on a map to determine if they exhibited preferred migratory routes through this region. χ^2 tests were then used to (a) determine if the distribution of post-smolts detected at monitoring lines D and E (Fig. 3.1) differed between the River Endrick combined and River Gryffe post-smolts and (b) determine if there was a significant difference between the number of post-smolts from each river detected at each receiver on monitoring lines D and E (Fig. 3.1).

3.2.4.4.2 Non-residency events

To determine the number of movements of post-smolts between monitoring points and lines in the estuarine zone, non-residency events were calculated using the RunResidenceExtraction function in the VTrack package in R (Campbell, 2012). A non-residency event is the movement of a post-smolt from one monitoring point/line to the next. For the purposes of this analysis, monitoring locations in the estuarine zone included points A and B as well as lines C, D and E (Fig. 3.1). In addition, monitoring line F in the coastal marine zone was included to determine the amount of post-smolts migrating to the west of Arran (Fig. 3.1, F). Westward movements between monitoring points/lines were categorized as forward, and eastward as reversals. Reversal movements were minimum estimates and ranged in distance from 3.66 (Fig. 3.1, B to A) to 32.50 km (Fig. 3.1, A to D).

In addition, the swim speed of smolts migrating through the Inner (Fig. 3.1 riverine exit to D) and Outer Clyde Estuary (Fig. 3.1, D to E) was calculated by dividing the duration it took smolts to migrate through each section of the estuary divided by the total length of each section. A Linear Mixed Effect Model (LMM) was fit using the R package *nlme* (Bates et al., 2015) to test whether there was a difference in swim speed of Atlantic salmon smolts between the inner versus outer estuary. For this analysis only smolts that were detected in both sections (inner and outer estuary) of the estuary were included. In addition, individual transmitter identification (ID) number was included as a random effect to account for non-independence of detections from the same Atlantic salmon smolt.

3.2.4.4.3 Environmental factors influencing non-resident events

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

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

3.2.5 Ethical statement

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

3.3 Results

3.3.1 Fresh water zone loss

The final River Endrick receiver successfully detected all smolts detected on the initial River Leven receiver (Table A2.1, R17; 100% efficiency). However, the efficiency of the initial River Leven receiver (Fig. 3.1, R18) was low, only detecting 70% (n = 23) of River Endrick release smolts that were detected on the nearest downstream receiver. The final River Leven (Table A2.1, R20) and River Gryffe (Table A2.1, R3) receiver detected all smolts that were detected on monitoring line E (100% efficiency).

Of the 99 smolts tagged and released in the River Endrick, 78% (*n* = 77) were estimated to have failed to complete a successful migration through the fresh water zone. In addition, despite accounting for the reduced detection efficiency of the initial River Leven receiver (Table A2.1), smolts that were transported and released at the River Leven still had a higher overall estimated loss rate through the River Leven (*n* = 18; 3.32 $\%.\text{km}^{-1}$; Table 3.1) than those released from the River Endrick (*n* = 11; 2.83 $\%.\text{km}^{-1}$). Lastly, the overall loss rate of smolts in the River Gryffe (1.08 $\%.\text{km}^{-1}$) migrating through the fresh water environment was substantially lower than both River Endrick and River Leven release smolts (Table 3.1).

Table 3.1 The percentage of Atlantic salmon smolts captured and tagged in the River Endrick and River Gryffe that were detected at key regions (fresh water zone) and monitoring points/lines (estuarine zone) in this study (Fig. 3.1). For assessing fresh water zone loss rates, the Loch Lomond catchment was subdivided into three sections (River Endrick, Loch Lomond, River Leven). The fresh water zone loss of River Gryffe smolts was assessed based on whether they were detected on the final River Gryffe receiver. Early estuarine zone loss was based upon the number of post-smolts detected at monitoring points/lines in the Clyde Estuary (Fig. 3.1 A-E). Lastly, an overall minimum estimate of loss was given for the fresh water zone (Loch Lomond Catchment; River Endrick release only) and estuarine zone (Est; Clyde Estuary; see methods for zone descriptions).

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

3.3.2 Estuarine zone loss

In contrast to the fresh water zone, the difference in loss rate between River Endrick (0.67 %.km^{-1}) and River Leven smolts (0.45 %.km^{-1}) was small (0.22 %.km^{-1}), and slightly lower for

River Leven smolts (Table 3.1). After the data from both groups were combined, the total proportion of unsuccessful River Endrick combined migrants in the estuarine zone (28%) was lower than that in the fresh water zone (66%; Table 3.1) In addition, although the overall loss rate of River Endrick and Leven smolts in the fresh water zone was 2.27 and 3.32 %.km^{-1}, respectively, it did not exceed 1 %.km^{-1} in the estuarine zone (Table 3.1). Loss rate appeared to decline with the distance River Endrick combined post-smolts travelled in the estuarine zone (Table 3.1). Mortality estimates were initially high, at 8.70 %.km^{-1} during the first few kilometres of their estuarine migration but then drastically declined as their migration progressed reaching 0%.km^{-1} between monitoring lines D and E (Fig. 3.1; Table 3.1). The same pattern was exhibited by River Gryffe post-smolts, with the highest loss rates occurring between monitoring lines B and C (3.07 %.km^{-1}) and then declining to 0 %.km^{-1} between monitoring lines D and E (Fig. 3.1; Table 3.1).

3.3.3 Capture-mark-recapture model

For River Endrick combined and Gryffe post-smolts, migration success through the estuarine zone was not dependent on FL, tag burden, release site or receiver location. The best fitting model for both rivers suggested that there was no difference in survival between monitoring lines and that detection probability was similar among consecutive monitoring lines (Table 3.2). The model-averaged migration success of post-smolts from the River Endrick and Gryffe between monitoring lines in the estuarine zone was estimated to be 96% (CI: 88%–99%) and 98% (CI: 94%–99%), respectively; and the average detection probability of post-smolts from the River Endrick combined and River Gryffe at monitoring lines in the estuarine zone was estimated to be 82% (CI: 73%–89%) and 85% (CI: 80%–90%), respectively (Table 3.2).

Table 3.2 Pool of the top five tested Cormack-Jolly-Seber models for River Endrick combined and River Gryffe salmon post-smolt migration success (*S*) in the estuarine zone (Fig. 3.1, Clyde Estuary) and detection probability (*p*).

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

Notes. Covariates as predictors of *S* included release site (only for River Endrick combined post-smolts), monitoring line (Fig. 3.1, C,D,E) (EW and EE combined), fork length and tag to body mass ratio (TMR). Monitoring line was the only covariate tested against *p*. Models were ordered based on quasi- likelihood QAIC.

3.3.4 Migratory speed

On average it took River Endrick release smolts 15.99 ± 7.07 (± S.D) days to migrate through the entire fresh water zone (minimum distance: 34.22 km). Loch migration was substantially slower than riverine migration for River Endrick release smolts. Migratory speed was calculated by dividing the minimum distance a smolt could travel to migrate downstream, divided by the duration of migration. Therefore, successful Loch migrants (*n* = 23) travelled at an estimated speed 0.03 ± 0.02 m s^{-1} over 9.17 ± 7.52 days (distance: 9.75 km; Table 3.3) through Loch Lomond. There was no substantial difference between the estimated migration speed of River Endrick release and River Gryffe release smolts in the riverine environment.

On average Endrick release smolts travelled through the River Endrick (12.70 km; $n = 75$) and River Leven (11.78 km; $n = 22$) at c. 0.2 ms^{-1}, over 2.40 ± 3.29 and 3.92 ± 5.12 days, respectively (Table 3.3). In comparison, River Gryffe smolts (8.14 km, $n = 93$) migrated through the River Gryffe at c. 0.2 m s^{-1} over 5.06 ± 3.75 days (Table 3.3). The duration of the riverine migration of River Leven release smolts was *c*. 2–3 times longer compared to River Endrick and Gryffe smolts, taking *c*. 10 days to migrate c. 12 km, respectively (Table 3.3).

River Endrick combined and River Gryffe smolts were first detected entering the estuarine zone on 27 April 2021 and 15 April 2021, respectively, and were last detected in the estuarine zone on 31 May and 15 May (final detection monitoring point E; Fig. 3.1), respectively. Based on the approximate distance from the River Leven/Gryffe exit and monitoring line E (River Leven: 47.46 km; River Gryffe: 59.32 km) the estimated speed of post-smolts through the estuarine zone was c. 0.16 m s^{-1} for River Endrick combined (0.16 ± 0.09 m s^{-1}) and (0.16 ± 0.06 m s^{-1}) for River Gryffe post-smolts. For all Atlantic salmon post-smolts combined that were detected in both the inner and outer estuary, speeds through the outer estuary ($n = 95$; D-E (Fig. 3.1), 0.28 m s^{-1} ± 0.14 m s^{-1}) were found to be significantly faster than speeds through the inner estuary (riverine exit – D (Fig. 3.1), $n = 95$, 0.15 ± 0.12 m s^{-1}; coef: 0.14, SE = 0.02, $t = 7.59$, $p < 0.001$).

Table 3.3 Mean migration speed (m s^{-1}) of smolts released from the River Endrick (End), Leven (Lev) and Gryffe (Gry) as well as the Endrick and Leven combined (Combo) as they migrate through the fresh water zone (Loch Lomond catchment (End, Lev, Combo; Fig. 3.1, R1–R20), River Gryffe (Gry; Fig. 3.1, R1–R3)) and the estuarine zone (Combo/Gry; Fig. 3.1 A-E).

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

Note. The total number of smolts used in this estimate (No.) is based on the number of smolts detected at both the start and end points of each measurement (Fig. 3.1).

3.3.5 Migratory pathways

Upon entering the inner estuary, 37% (*n* = 44) of post-smolts that completed a successful migration into the Firth of Clyde (*n* = 118) were detected making a mean number of 1.75 ± 1.16 reversal movements (movements in the upstream direction) prior to exiting to the Firth of Clyde (Fig. 3.2). On average reversals were found to occur 1.55 ± 1.43 days (range: 0.04–

5.91) after exiting the fresh water zone. The mean number of reversals per individual was similar between both River Endrick combined and River Gryffe post-smolts (River Endrick combined, *n* = 7; 1.14 ± 0.38; River Gryffe, *n* = 37; 1.86 ± 1.23). The remaining 62% (*n* = 72) post-smolts that completed a successful migration through the estuary were not detected making reversal movements. The highest proportion of detected reversals in the inner estuary for both successful River Endrick combined and River Gryffe post-smolts were detected between the receivers located closest to the fresh water outlet (Fig. 3.2). For River Endrick combined post-smolts and River Gryffe post-smolts 78% (n = 7) and 72% (n = 63) of reversal movements were detected between monitoring line C and point B and points B to A, respectively (Fig. 3.1 and 3.2).

There was no significant difference between the proportion of detected River Endrick combined and River Gryffe post-smolts at each receiver at monitoring line D (Fig. 3.1 and 3.2; $\chi^2 = 3.32$, $p = 0.35$). In addition, the number of post-smolts from both groups detected at each receiver was found to not differ significantly from the expected distribution (River Endrick combined: $\chi^2 = 4.32$, $p = 0.23$; Fig. 3.2).

On monitoring line E (Fig. 3.1), a higher proportion of River Endrick combined and River Gryffe post-smolts were detected on the west side (EW) of Little Cumbrae (Fig. 3.1 and 3.2; River Endrick combined: *n* = 36, 25%; River Gryffe: *n* = 78, 75%); vs. the east side (EE) (River Endrick combined: *n* = 3, 2%; River Gryffe: *n* = 2, 2%). For River Endrick combined post-smolts, there was a significant difference ($\chi^2 = 14.61$, $p = 2.18$ x 10-3) between the proportion of post-smolts detected at each receiver to the east of Little Cumbae (Fig. 3.1 and Fig. 3.2b), but not for River Gryffe post-smolts ($\chi^2 = 1.67$, $p = 0.64$, Fig. 3.2d). The highest proportion of River Endrick combined post-smolts (*n* = 29, 81%) were detected at the EW2 receiver (Fig. 3.1 and 3.2b).

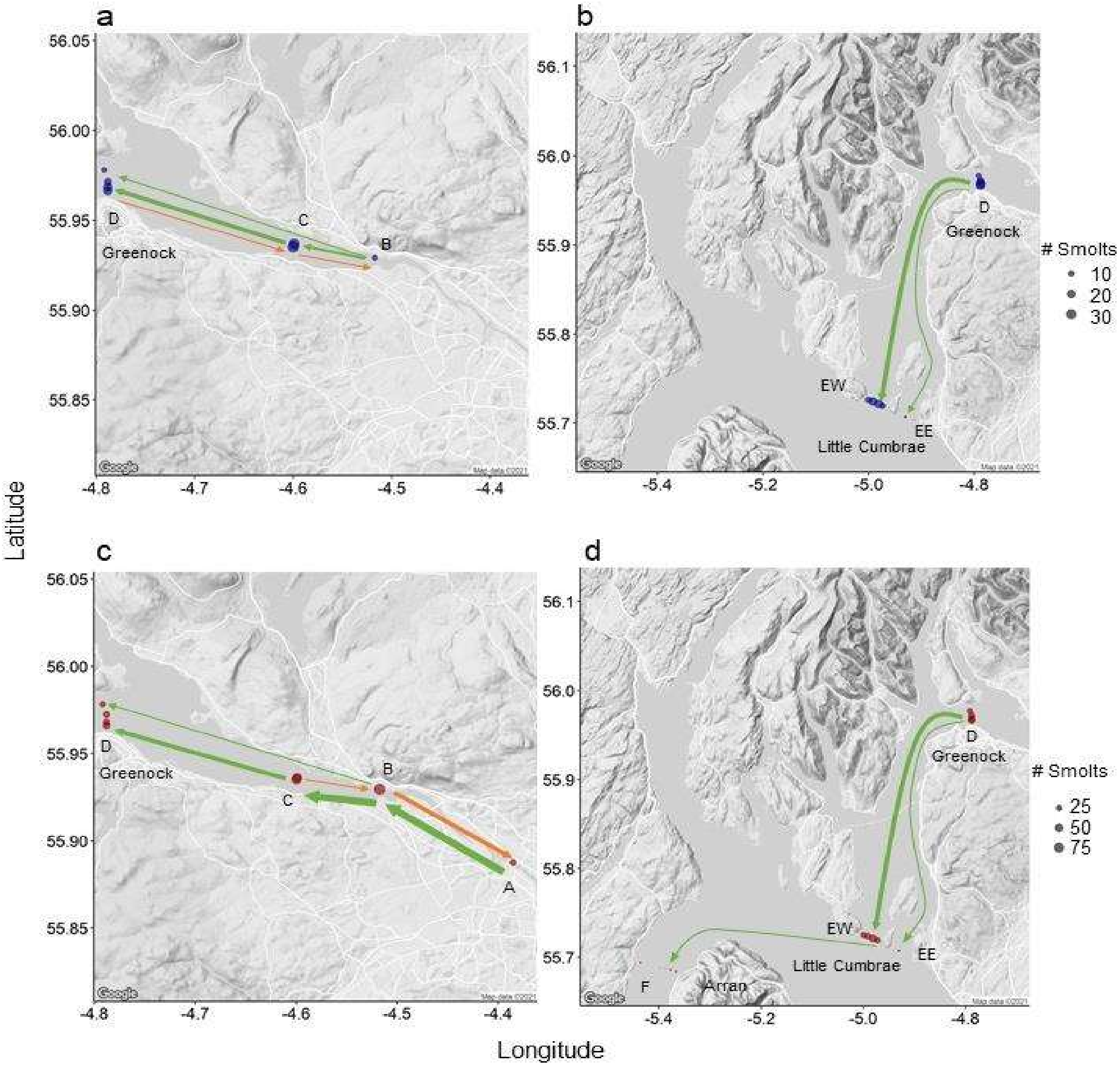


Figure 3.2 Maps representing the number of River Endrick combined (a,b) and River Gryffe (c,d) salmon post-smolts that were detected at monitoring points/lines in the estuarine and coastal marine zones (see methods; Fig. 3.1; A,B,C,D,E (EW,EE),F) and their movement pathways between monitoring points/ lines. The size of the circles in the maps reflects the number of post-smolts detected at a receiver. The total number of forward movements between monitoring points/lines is represented by the thickness of the green lines, and that of reversal movements is represented by the thickness of the orange lines.

3.3.6 Environmental predictors of movement and exit

The timing of forward and reversal movements in the estuarine zone (monitoring lines A–E) was found to be dependent on the tidal state (forward: $z = 0.36$, $p < 0.001$; reversal: $z = 0.83$, $p < 0.001$). The circular mean degree of forward movements occurred at $241.54 \pm 1.43^{\circ}$, indicating that post-smolts engaged in forward movements during ebb tide (Fig. 3.3a). The circular mean degree of reversal movements occurred at $24.04 \pm 0.61^{\circ}$, indicating that post-smolts engaged in reversal movements during the beginning of flood tide (Fig. 3.3b). The mean duration of half the tidal range for dates when successful post-smolts were detected in the estuarine zone ($n = 16$) was 6.22 ± 0.62 h; by converting the circular mean degree to hours this assumes that on average forward and reversal movements occurred at *c*. 2.13 h after high tide and 0.82 h after low tide, respectively.

The average range of sunrise and sunset times (hh:mm) when successful post-smolts ($n = 108$) engaged in forward movements ($n = 381$) in the estuarine zone (20 April 2021 to 28 May 2021) ranged from 04:47 to 05:43 and from 20:52 to 21:48, respectively (Fig. 3.3d). Furthermore, the average range of sunset times when successful post-smolts ($n = 40$) engaged in reversal movements ($n = 67$) in the estuarine zone (23 April 2021 to 27 May 2021) ranged from 04:48 to 05:54 and from 20:42 to 21:46, respectively (Fig. 3.3e). The timing of forward (Fig. 3.3d) movements was dependent on the time of day (forward: $z = 0.26$, $p = 0$). On average post-smolts engaged in forward movements during the night, the mean time (hh:mm) they initiated a forward movement occurred at 23:47 ± 01:38 (Fig. 3.3d). Contrary to forward movements, the timing of reversal movements was not dependent on the time of day (reversal: $z = 0.21$, $p = 0.06$; Fig. 3.3e).

The final detection of post-smolts in the outer estuary (Fig. 3.1; monitoring line E) was also found to be dependent on tide state with successful post-smolts migrating out of the outer estuary during ebb tide ($z = 0.35$, $p < 0.001$; Fig. 3.3c). The mean circular degree of post-smolts' final detection at monitoring line E (Fig. 3.1) was $290.07 \pm 1.44^{\circ}$ (Fig. 3.3c). Based on the mean duration of half the tidal cycle when post-smolts were present in the estuarine zone (indicated above), this assumes that they migrated out of the outer estuary at *c*. 3.8 h after high tide. However, final detections were found to be not dependent on time of day ($z = 0.06$, $p = 0.62$; Fig. 3f).

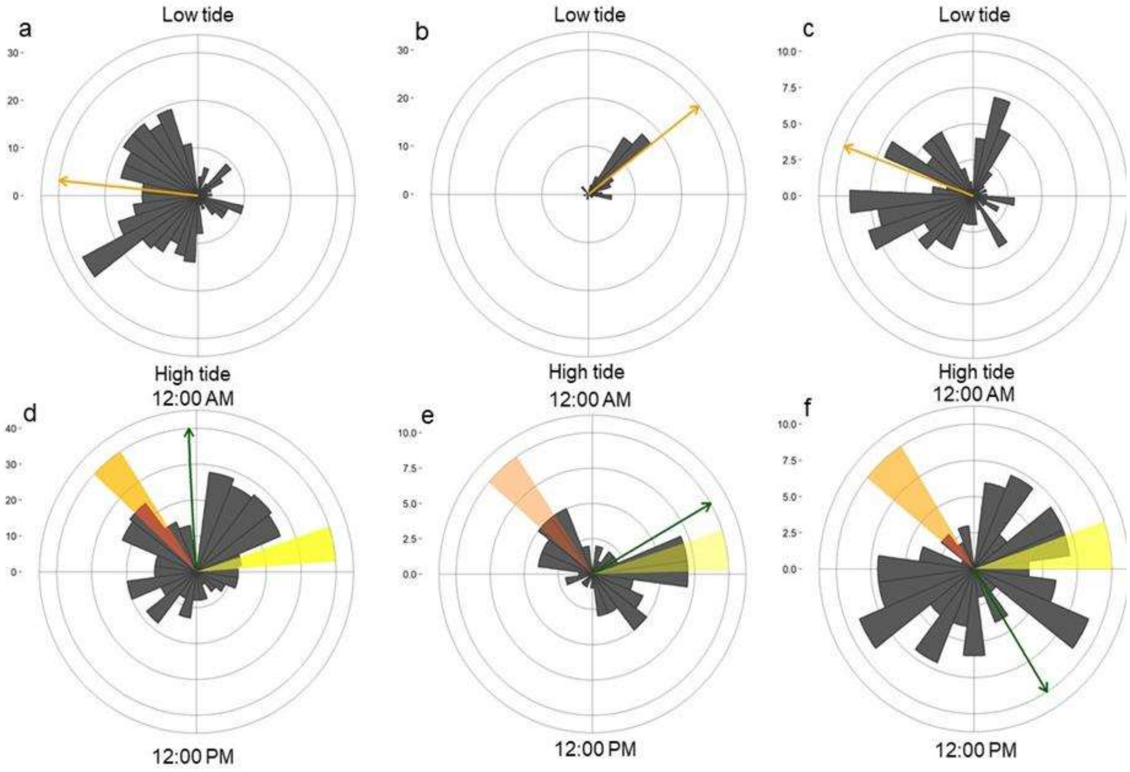


Figure 3.3. Rose diagram depicting the influence of tidal phase (a,b,c) and time of day (hours; d,e,f) when Atlantic salmon post-smolts engaged in forward (a,d) and reversal (b,e) movements and exited the estuarine zone (c,f), respectively. The orange and green arrows reflect the mean circular degree in the tidal phase (a,b,c), and mean time of day (d,e,f) when these movements occurred. In the time-of-day plots (d,e,f) the yellow and orange shaded bars reflect the variation in times when sunrise and sunset occurred throughout the time period when forward (20 April 2021 to 28 May 2021) and reversal movements (23 April 2021 to 27 April 2021) were initiated as well as exit movements (22 April 2021 to 31 May 2021).

3.4 Discussion

This study has provided new insights into the fresh water and estuarine migration of Atlantic salmon post-smolts moving through the Clyde Estuary. Consistent with the authors' hypothesis, the fresh water loss rates of post-smolts migrating from the River Gryffe (1.08 %. km^{-1}) were found to be approximately half than for fish released from the River Endrick (2.27 %.km^{-1}; Table 3.1). Previous studies have indicated that fresh water mortality is positively associated with the total length of a system, as well as the presence of anthropogenic barriers and lakes (Chaput et al., 2019; Lilly et al., 2021; Stitch et al., 2015). Lilly et al. (2021) assessed the movement of smolts through the Loch Lomond catchment and reported high travel times (*c.* 5 days) and high overall fresh water mortality in the loch (43%). Consistent with this study, here the authors report that smolts also experienced long travel times (*c.* 9 days) and, after accounting for the detection efficiency of receivers (Table A2.1), still experienced high overall mortality (56%) in Loch Lomond.

In comparison to smolts that had to navigate through the entire Loch Lomond catchment (nominally River Endrick release smolts in this study), transporting smolts around Loch Lomond (nominally River Leven release smolts) did appear to increase the overall likelihood and absolute number of smolts surviving to the Clyde Estuary. However, the rate of loss defined as the rate per distance travelled (%.km^{-1}) of smolt movement through the fresh water environment (all habitat types combined) was lower for River Endrick released smolts. This high rate of loss near the release site for River Leven release smolts may be related to the stress induced by transport. In hatchery reared salmonid smolts this effect has been reported to last up until 48 h after transport and increases the likelihood of mortality (Iversen et al., 1998, 1998; Rechisky et al., 2012; Schreck et al., 1989). Furthermore, transported smolts have been reported to have reduced overall marine survival, which is potentially related to impaired homing abilities (Keefer et al., 2008). Therefore, before transporting smolts is implemented by managers as a management technique, more research is needed to determine: (a) how transport-induced stress can be mitigated and (b) whether transporting smolts increases the overall adult return rate.

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

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

Furthermore, loss rates of post-smolts in estuaries are thought to be positively associated with the complexity of the system, as predators of Atlantic salmon are known to utilize the tide to predict when fishes will migrate past constriction points (Hastie et al., 2016; Zamon, 2001). This pattern was shown by Chaput et al. (2019) who assessed post-smolt movement through two estuaries on the east coast of Canada and reported that loss rates were lower for post-smolts migrating through a wide-open bay (5%–33% loss rate) in comparison to the semi-enclosed constricted estuary (18%–72%) (Chaput et al., 2019). However, this pattern was not consistent among other studies that have reported relatively low levels of loss for post-smolts migrating through complex fjord systems (Dempson et al., 2011; Halfyard et al., 2012). This suggests that loss rates of post-smolts in estuaries may be the result of a complex combination of local stressors as well as the physical and geographic nature of the system (Chaput et al., 2019). For example, the density of predators can vary widely amongst estuaries and is likely an important determinant of the rate of post-smolt survival through these systems (Lacroix, 2008; Gibson et al., 2013).

The unexpectedly low overall mortality rates of post-smolts in the Clyde Estuary may be a combination of the low complexity of the estuary and low abundance of predators. The highest loss rates of post-smolts in this study occurred as they migrated past monitoring line C (Fig. 3.1; Table 3.1). This region served as the main migratory constriction point in the estuarine zone for both River Endrick combined and Gryffe post-smolts. At this location, River Endrick combined post-smolts had just exited from the River Leven, whereas River Gryffe post-smolts would have migrated *c*. 9 km from their river outlet through a narrow channel that has a maximum width of 200 m at high tide (Bekic et al., 2006).

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

Unlike the inner estuary, once post-smolts from both river systems successfully migrated past monitoring line D (Fig. 3.1), there were no observed mortalities or reversal movements. Nonetheless, the reduction in observed reversal movements may be due to reduced receiver infrastructure in this region and thus poor detection of such movements. Forward movements out of the estuary were found to occur mainly during the night. The underlying reason for nocturnal movement of post-smolts in the Clyde Estuary is not known. However, some studies have hypothesized that post-smolts migrate during the night to decrease the chance of being spotted by predators and that they utilize daylight hours to feed during their estuarine migration (Andreassen et al., 2001; Fiske, 2020; Kadri, 1997).

Previous studies have reported that in estuaries with weak salinity gradients and tidally driven currents, smolts appear to actively migrate towards the estuarine outlet regardless of the direction of current (Økland et al., 2006; Thorstad et al., 2004). In contrast, the ground speed and number of net-seaward movements of smolts in estuaries with strong salinity gradients and tidally driven currents appear to be positively correlated with salinity and the outflowing tide (Martin et al., 2009). The salinity of the water near monitoring line C (Fig. 3.1) where most reversal movements were recorded ranges from c. 20 to 25 ppm during low to high water, respectively (Allen, 1966) and is heavily influenced by fresh water input mainly from the Rivers Clyde and Leven. In comparison, the salinity of the surface water near monitoring line D (Fig. 3.1) ranges from 24 to 32 ppm during low to high water, respectively (Allen, 1966). The higher salinity at monitoring line D (Fig. 3.1) is due to its proximity to the sea as well as the displacement of inflowing fresh water water into surrounding sea lochs during a flood tide (Allen, 1996). In addition, the geography of the plateau extending across from monitoring line D creates a strong seaward residual current in the surface layer (Allen, 1966).

In the study reported here, the authors were unable to measure salinity or current speed at monitoring points and lines in the Clyde Estuary, which prevented the authors from determining whether post-smolts were actively swimming with the current. Nonetheless, due to the higher survival rates and swim speeds of post-smolts in the outer compared with the inner estuary, we can hypothesize that post-smolts were using both salinity gradients and currents to efficiently navigate through the outer estuary. This hypothesis is further supported by the fact that most post-smolts were detected leaving the estuarine zone mainly on the west side of Little Cumbrae (Fig. 3.1) where the principle ebb tide flow is orientated (Davies & Mofor, 1990; Sabatino et al., 2017).

Based on the findings of this study it appears that the risk to post-smolt salmon migrating from the Rivers Endrick and Gryffe in the Clyde Estuary may currently be low. In the Clyde Marine Region there are currently active salmon farms within two adjoining sea lochs and along the coast of Arran (Marine Scotland, 2022; Fig. 3.1). Sea lice larvae are known to drift up to 30 km with local currents for *c*. 4 days prior to settling at new locations as adults (Adams et al., 2016; Rees et al., 2015). Therefore, lice from farms in the Outer Clyde Estuary could drift into the inner estuary (Adams et al., 2016; Krkošek et al., 2009; Rees et al., 2015). The likelihood of infestation has been positively correlated with the salinity in the region, and mortality is thought to occur when smolts spend greater than a few weeks near a site (Krkošek et al., 2009). Therefore, due to the large fresh water input into the Inner and Outer Clyde Estuary and short duration smolts spent in this region (c. 5 days) the risk of River Endrick and Gryffe post-smolts becoming exposed to sea lice is likely low. Nonetheless, once smolts enter the Firth of Clyde their risk of sea lice exposure may increase as salinities near the surface more closely resemble full strength sea water (*c*. 33 ppt; Slesser & Turrell, 2005). Because few smolts were detected on line F, it is assumed that they migrate along the east coast of Arran to reach the Irish Sea. Future studies are required to determine the duration spent in this region and potential risk of fish farm exposure.

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

3.4.1 Conclusion

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

Chapter 4: Migration patterns and navigation cues of Atlantic salmon post-smolts migrating from 14 rivers through the coastal zones around the Irish Sea

Abstract

The drivers of Atlantic salmon migration as fresh water fish have been well studied, however relatively less is known about migration and its drivers in the early marine environment, particularly for post-smolts. Upon entering the marine environment, post-smolts from United Kingdom (UK) waters are thought to migrate towards the Norwegian Sea. Most studies to date have relied on fisheries trawl data to predict the migratory patterns of post-smolts complemented with particle tracking studies to determine the main environmental drivers of movement. Furthermore, particle tracking studies have indicated that post-smolts likely rely on shelf currents to reach their feeding grounds. This study is the first to ground truth the existing particle tracking studies for Northeast Atlantic post-smolts in the Irish Sea region by undertaking a large-scale acoustic telemetry study. During 2021, 1008 wild and 60 ranched Atlantic salmon smolts were tagged with acoustic transmitters in 14 rivers in England, Scotland, Northern Ireland and Ireland. In addition, a large marine array, consisting of 108 acoustic receivers, was deployed between Malin Head, Ireland to Port Wemyss, Scotland. This array marks the transition of the Irish Sea into the North Atlantic. Consistent with previous studies, after leaving their natal rivers or estuaries post-smolts in this study underwent rapid migrations through the Irish Sea, travelling at mean rates ranging between 9.69 to 39.94 km/day. In comparison to other early marine migration studies, estimated loss rates through the Irish Sea appeared to be low (<1 %.km^{-1}). However, when multiplied by the total distance travelled, there was substantial early marine loss of Scottish post-smolts (~ 70%). Using a hydrodynamic model of the Scottish west coast, this study also investigated whether temperature, and current direction accurately predicted the temporal and spatial patterns of post-smolt distribution and movement through the Irish Sea. Consistent with temperatures reported during their offshore marine migration, post-smolts appeared to exit the Irish Sea during the end of May/beginning of June when water temperatures ranged between 9-11°C. In addition, post-smolts appeared to migrate with currents flowing in a northwest direction,

towards the slope current. Thus, results suggest that current direction may serve as the primary cue utilized by post-smolts of this region during early marine migration to determine when to navigate to northern feeding grounds.

4.1 Introduction

Migration is common across both aquatic and terrestrial organisms and involves population-level directed seasonal movements amongst habitats (Avgar et al., 2014; Dingle & Drake, 2007; Mueller & Fagan, 2008). These movements often occur over long distances and are initiated if the fitness benefits, such as increasing the likelihood of finding prey and/or mates, outweigh the costs of migration (Avgar et al., 2014; Mueller & Fagan, 2008; Tamario et al., 2019). The costs associated with long-distance migration 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). Developing an understanding of the navigational cue's organisms may use to guide the timing and paths of movement is required to understand the ecological processes that lie behind migration (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 sea. This is mainly due to the lack of visual landmarks in pelagic environments (Luschi, 2013), and it is thought that marine migrants may rely on earth's magnetic field, localized currents, and salinity and/or temperature gradients to aid in navigation (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 anadromy are that it is thought to reduce the likelihood of predation and intraspecific competition for food resources during the pre-adult stage in the fresh water habitat as individuals attain maturity in the marine habitat (Quinn & Myers, 2004). However, there are costs associated with this migratory strategy including increased energy expenditure and exposure to anthropogenic and natural stressors in both the fresh water and marine environment (Alerstam et al., 2003; Limburg & Waldman, 2009). Due to strong potential navigation cues available to salmon post-smolts, Atlantic salmon post-smolts are thought to initiate migration when water temperatures are within a narrow range and then to engage in active swimming with prevailing currents to reach their northern feeding grounds, increasing the likelihood of arriving in offshore marine regions during peaks in prey abundance (Dadswell et al., 2010; Harden Jones, 1968; Hvidsten et al., 2009; Mork et al., 2012). Results from riverine, estuarine and offshore marine studies suggest that currents may serve as the primary cue post-smolts use to determine where to migrate (Gilbey et al., 2021; Lacroix et al., 2004b; Thorstad et al., 2012b).

After spending 1-7 years in their natal river Atlantic salmon smoltify and begin to migrate downstream towards the estuarine environment (Milner et al., 2003; Thorstad et al., 2012b; Zydlewski et al., 2014). This downstream migration tends to occur during the night and is rapid with smolts displaying multimodality in their migration timing which is linked to periods of high river discharge (Bjerck et al., 2021; Lothian et al., 2018). Nocturnal migration is thought to be a predator avoidance tactic, as it decreases the likelihood of being spotted by visual predators (Lefèvre et al., 2012). In addition, larger smolts are thought to be better able to evade predators due to their faster swimming speeds (Flávio et al., 2021). After Atlantic salmon smolts from the British Isles enter the estuarine environment during late April and May, smolts 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 exit this habitat, and consistent with the fresh water environment, they mainly exit during the night at ebb tide (Lacroix et al., 2004b; Lothian et al., 2018). Studies assessing the relationship between ocean entry timing on the early marine survival of Atlantic salmon post-smolts have reported a positive relationship between smolt sea entry date and marine survival. Atlantic salmon post-smolts migrating later in the smolt run have a higher likelihood of experiencing spatial overlap with spring marine plankton blooms that ultimately increase coastal marine feeding opportunities (Friedland, 1998; Kennedy & Crozier, 2010).

Knowledge concerning the distribution of post-smolts in the offshore marine environment has largely been limited to genetic stock identification determined from post-smolt capture in research directed surface trawls (Gilbey et al., 2021; Holst et al., 2000; SALSEA-Merge, 2012). For post-smolts migrating from rivers in the British Isles, trawl data have shown that post-smolts from multiple river systems overlap temporally (in May and June) and spatially in the slope current which flows along the west coast 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 are captured during the month of August (Gilbey et al., 2021; Holm, 2000; Shelton et al., 1997). In addition, similar to the temperatures reported during the final stages of their riverine migration, post-smolts are present in the slope current and Vøring plateau when water temperatures range between 6-12°C (Gilbey et al., 2021; Hindar et al., 2020; Holm, 2000; Holm et al., 2003). Migrating through the early marine environment at these temperatures increases the likelihood of post-smolts overlapping with key prey items (Thorstad et al., 2012b; Utne et al., 2021a).

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 within 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 concerning the environmental cues that post-smolts may use in coastal marine regions are limited to inferences from the results of particle tracking studies. These studies suggest that the navigational cues salmonid post-smolts use to migrate in coastal areas are likely to be dependent on the geographic location of each river system (Furey et al., 2015; Mork et al., 2012; Ounsley et al., 2020). Post-smolts may adopt strategies that increase metabolic output and deviate from local current patterns if such tactics increases their chances of arriving at feeding grounds during periods of high prey abundance and/or decreases their exposure to predators (Ounsley et al., 2020). For example, Mork et al. (2012) predicted that simulated post-smolts emigrating from rivers along the western coast of Ireland would engage in active swimming in the same direction as the slope current early in their coastal marine migration. In contrast, Ounsley et al. (2020) simulated coastal marine post-smolt movements from rivers that drain to the west coast of Scotland and noted that for simulated post-smolt migration to coincide with the temporal patterns noted by trawling studies, movements would have to deviate from local current patterns early in their migration and the fish would actively swim in a northwest direction.

In this study we used acoustic telemetry to examine the migration of salmon from 14 rivers through the Irish Sea. Acoustic telemetry involves inserting a small transmitting tag into a study animal, the tag then emits a sound signal coded with a unique identification number that can be detected by acoustic receivers placed in the marine environment to identify the migratory pathway of the species (Crossin et al., 2017).

Knowing the migratory pathways and cues for salmon navigation through this region is important information to help to mitigate the potential effects of anthropogenic and natural stressors on populations (Furey et al., 2015; Gilbey et al., 2017). This study had three main objectives; the first was to compare the loss rate amongst post-smolts migrating through the Irish Sea from different river systems. We tested three hypotheses related to salmon post-smolt migration success: 1) that post-smolts travelling a greater distance through the Irish Sea would experience higher overall loss, 2) that loss would be dependent on post-smolt size, with large post-smolts having a higher likelihood of surviving transit of the Irish Sea, and lastly 3) loss would be higher for those with an earlier marine entry date.

We tested two hypotheses around the distribution of post-smolts migrating through the Irish Sea: 1) smolts entering the Irish Sea from similar coastal regions would show spatial and temporal overlap at their point of exit through this region and, 2) consistent with the predictions of Ounsley et al. (2020), post-smolts travel in a north-westerly direction (away from the Scottish coastline and towards the Irish coast).

We tested three hypotheses around the environmental cues for navigation of post-smolt transition into the North Atlantic; 1) similar to the riverine and offshore marine environment, post-smolts would exit the Irish Sea when water temperatures were in the range of 6-12°C (Gilbey et al., 2021; Holm, 2000; Milner et al., 2003), 2) this transition would primarily occur during the night and lastly, 3) post-smolts exit from the Irish Sea would not be dependent on current direction.

4.2 Materials and Methods

This study was made possible by an extensive collaboration of four different projects (SeaMonitor; West Coast Tracking Project; COMPASS, Derwent Tracking Project) comprising six different organizations (SeaMonitor: Marine Institute, Agri-Food and Biosciences Institute, Loughs Agency, University of Glasgow; West Coast Tracking Project: Atlantic Salmon Trust; Environment Agency) who shared tasks and data to enable us to address the regional scale questions we were interested in.

4.2.1 Study area

The Irish Sea (Lat. 51 – 56° N, Long. -2.5-7°W) is a semi-enclosed channel that extends approximately 300 km North-South and connects to the North Atlantic Ocean in the north via the North Channel and to the Celtic Sea in the south (Fig. 4.1; Dabrowski et al., 2010; Howarth, 2005). For the purpose of this paper the North Channel is defined as part of the Irish Sea. The main drivers of the current in the Irish Sea are the M2 and S2 tidal constituents with the dominant flow directed northwards (2.50 $km^3.day^{-1}$; (Olbert et al., 2012; Olbert & Hartnett, 2010).

4.2.2 Fish capture and tagging

In this study, 1008 wild and 60 ranched (River Burrishoole) Atlantic salmon smolts greater than 130 mm fork length and 20 g mass were captured during April and May in 14 Rivers. Wild smolts were captured using a 1.5 m diameter rotary screw trap and fyke nets. Ranched smolts from the River Burrishoole were captured in ponds adjacent to their natal rivers and released at the same location as wild smolts. Smolts were tagged in one river in England (River Derwent, *n* = 150), four rivers in Scotland (the Rivers Gryffe, *n* = 102; Endrick, *n* =

145; Nith, *n* = 130, Bladnoch, *n* = 130) plus one tributary of the River Nith (the River Crawick, *n* = 5), six rivers in Northern Ireland (rivers Glendun, *n* = 24; Carey, *n* = 9; Bush, *n* = 80, Bann, *n* = 59; Roe, *n* = 11; Faughan, *n* = 53) and one tributary of the River Bann (Agivey, *n* = 41) and one river in Ireland (River Burrishoole, *n* = 85; Fig. 4.1; Table 4.1). There were two release locations for River Endrick and River Derwent smolts (Fig. 4.1; Table 4.1). Additionally, data from the two tributaries was combined with those from the mainstem river (Table 4.1; River Nith (River Nith & Crawick); River Bann (Agivey River & River Bann); Fig. 4.1). Salmon smolts were tagged with five models of acoustic tags (V7-2x, V7-4x, V7-4L, V8-4x, V7D-2x; InnovaSea, Bedford, Nova Scotia, Canada). V7 model tags were generally of similar size, however, the V8 model was slightly larger, V7 tags were appropriate for smaller smolts, and the V8 tags for larger individuals. The minimum size and weight of smolts tagged with V7-2x, V7-4x and V7-4L tags was 130 mm and 20 g, respectively. Furthermore, the minimum size of smolts tagged with V8-4x and V7D-2x tags was 140 mm. Smolts in all rivers (excluding the River Bush and Burrishoole) were tagged with V7-2x tags that had a battery life extending up to 99 days (range: 75 – 120; Table 4.1), as well as a mass and length of 1.5 g (in air) and 19.5 mm, respectively. River Bush smolts were tagged with V7-4x tags which had a battery life of 522 days, as well as a mass and length of 1.8 g (in air) and 21.5 mm, respectively (Table 4.1). River Burrishoole smolts were tagged with V8-4x and V7D-2x tags which had a battery life of 173 and 100 days, respectively. These tags had a mass and length of 2 g (in air) and 20.5 mm and 1.7 g (in air) and 22 mm, respectively. All tagging was conducted using the methods outlined in Lilly et al. (2021) and tagging in Scotland, England and Northern Ireland was conducted under licences from their national authorities (UK Home Office licence PP0483054; UK Home Office licence PPL2869; HPRA Licence AE19121/P003 Case No. 7028960; Roger & Lilly et al., 2022).

In total, 582 Atlantic salmon smolts successfully exited their natal river and were included in this study. The means of fork length (mean cm ± SD, n = 527), mass (g, n = 489) and tag burden (fraction of tag mass to body mass, n = 489) of wild smolts in this study was 149.63 ± 12.73 mm, 34.97 ± 9.28 g and 0.05 ± 0.01, respectively. Additionally, the mean fork length, mass and tag burden of ranched smolts (n = 55) in this study from the River Burrishoole was 197.36 ± 11.76 mm, 87.30 ± 17.72 g and 0.02 ± 5 x 10^{-3}, respectively.

Table 4.1 The number of smolts tagged with acoustic tags in England (Derwent), Scotland (Bladnoch, Nith, Crawick, Endrick, Gryffe), Northern Ireland (Bann, Agivey, Bush, Carey, Glendun, Roe, Faughan) and the Republic of Ireland (Burrishoole) by five different projects (SeaMonitor (SM); West Coast Tracking Project (WCTP); Nith Smolt Tracking Project (NSTP); Derwent Salmon Tracking Project (DTP)) during this study that successfully exited their natal river or estuary (No.) out of the total number tagged (n), as well as their date tagged (dd – mm; all smolts were tagged during 2021), tag expiry date (dd-mm-yy), mean fork length (Mean FL; mm ± SD) and Mean Mass; g ± SD). The format of this table was based upon that of Chapter 5. All smolts were wild, excluding River Burrishoole smolts tagged with V8-4x and V7-2x tags.

Partner	**River**	**Release site (lat, long º)**	**Tag Type**	**Tag life (days)**	**No. (n)**	**Nom. Delay (sec)**	**Date Tagged**	**Tag expiry date**	**Mean FL (mm)**	**Mean Mass**	**Mean Tag Burden**
EA	Derwent	54.6105, -3.0616 54.6876, -3.2978	V7-2x	75	41 (150)	18-38	29-04 to 03-05	13-07 to 17-07-21	141.37 ± 7.33	30.04 ± 5.02	0.05 ± 0.01
WCTP	Bladnoch	54.8672, -4.4989	V7-2x	75	54 (130)	18-38	20-04 to 14-05	04-07 to 28-07-21	142.81 ± 7.88	30.01 ± 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 20-07-21	148.32 ± 10.92	33.23 ± 7.20	0.05 ± 0.01
NSTP	Crawick	55.3783, -3.9313	V7-2x	75	23 (49)	18-38	16-04 to 23-04	30-06 to 07-07-21	138.70 ± 5.22	26.95 ± 2.33	0.06 ± 0.01
SM	Endrick	56.0492,-4.4399, 56.0085, -4.5897	V7-2x	75	50 (145)	18-38	15-04 to 03-05	29-06 to 17-07-21	143.08 ± 8.79	29.73 ± 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 08-07-21	149.26 ± 10.13	34.19 ± 6.66	0.05 ± 0.01
SM	Bann	54.9841, -6.5618	V7-2x	99	18 (59)	20-40	07-05 to 25-05	14-08 to 01-09-21	163 ± 15.53	44.83 ± 13.90	0.04 ± 0.01

Table 4.1. (continued) The number of smolts tagged with acoustic tags in England (Derwent), Scotland (Bladnoch, Nith, Crawick, Endrick, Gryffe), Northern Ireland (Bann, Agivey, Bush, Carey, Glendun, Roe, Faughan) and the Republic of Ireland (Burrishoole) by five different projects (SeaMonitor (SM); West Coast Tracking Project (WCTP); Nith Smolt Tracking Project (NSTP); Derwent Salmon Tracking Project (DTP)) during this study that successfully exited their natal river or estuary (No.) out of the total number tagged (n), as well as their date tagged (dd – mm; all smolts were tagged during 2021), tag expiry date (dd-mm-yy), mean fork length (Mean FL; mm ± SD) and Mean Mass; g ± SD). The format of this table was based upon that of Chapter 5. All smolts were wild, excluding River Burrishoole smolts tagged with V8-4x and V7-2x tags.

Partner	River	Release site (lat, long °)	Tag Type	Tag life (days)	No. (n)	Nom. Delay (sec)	Date Tagged	Tag expiry date	Mean FL (mm)	Mean Mass	Mean Tag Burden
	Agivey	54.9879, -6.6661	V7-2x	99	16 (41)	20-40	20-04	28-07-21	153.75 ± 9.31	37.69 ± 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	168.58 ± 8.59	48.04 ± 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 12-08-21	165 ± 6.20	45.33 ± 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 07-08-21	142.43 ± 7.48	31.10 ± 4.55	0.05 ± 0.01
SM	Roe	54.9710, -6.9253	V7-2x	94	9(11)	30-60	29-04	01-08-21	152 ± 3.87	36.44 ± 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 17-08-21	143.16 ± 4.19	-	-
SM	Burrishoole	53.9137, -9.5713	V8-4x	173	46(50)	40-80	05-05 to 07-05	25-10 to 27-10-21	195.72 ± 9.63	84.45 ± 13.50	0.02 ± 0.004
			V7D-2x	100	9(10)	30-90	07-05	15-08-21	205.78 ± 17.82	101.84 ± 28.50	0.02 ± 0.01
			V7-2x	120	19(25)	40-80	05-05 to 11-05	04-09 to 08-09-21	150.32 ± 7.10	31.96 ± 4.04	0.05 ± 0.01

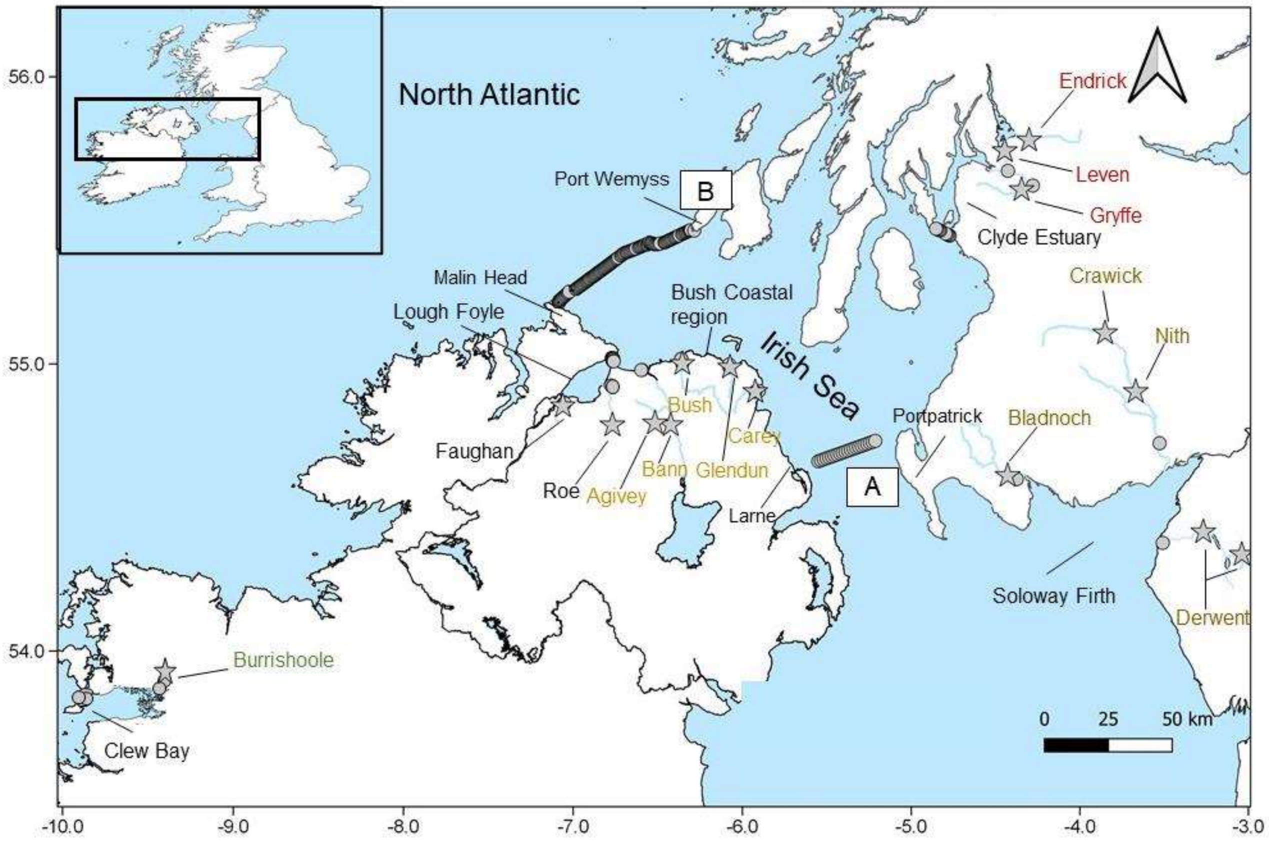


Figure 4.1 Map displaying the 14 rivers where Atlantic salmon smolts (*n* = 1068) were tagged in England, Scotland, Northern Ireland and the Republic of Ireland during this study. Rivers are colour coded based upon coastal regions (1-4) where: Region 1, the Solway Firth (Rivers Derwent, Nith, Bladnoch) is represented in brown; Region 2, the Clyde Sea (Rivers Endrick and Gryffe) is represented in red; Region 3, the Bush Coastal region (rivers Bann, Bush, Carey & Glendun) is represented in yellow; Region 4, Lough Foyle (rivers Roe and Faughan) is represented in black; Region 5, Clew Bay (River Burrishoole) is represented in green. Tagged fish release sites are represented by stars, and acoustic receivers (*n* = 182) are represented by grey dots. Marine monitoring lines in the Irish Sea are labeled in alphabetical order from south to north. This figure and caption were adapted from Chapter 5.

4.2.3 Acoustic receiver deployment

In total 182, 69 kHz acoustic receivers were deployed in this study (Table A3.1; Fig. 4.1). This included VR2W receivers (InnovaSea Ltd., Nova Scotia, Canada) deployed at the exit of rivers where smolts were tagged (*n* = 11; Fig. 4.1; Table A3.1). Consistent with a previous study (Chapter 5) only smolts that were detected on the final riverine receiver were included in the analysis. Additionally, three monitoring lines were deployed at the exit of estuaries and embayment's including the Clyde Estuary (*n* = 8; Fig. 4.1; Table A3.1), Lough Foyle (*n* = 10; Fig. 4.1; Table A3.1) and Clew Bay (*n* = 10; Fig. 4.1; Table A3.1). 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, p.915) and a coastal embayment as "an extension of the sea into an indentation of the coast" (Schwartz, 1982, p.442).

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 (Fig. 4.1; monitoring line A; distance ~ 36 km) and a line of 108 acoustic receivers extending from Malin Head, Ireland to Port Weymss, Scotland (Fig 4.1; monitoring line B; distance ~ 63 km). In both the riverine and estuarine environment, acoustic receivers have been reported to have a detection efficiency of 90% at 200 m (Honkanen et al., 2018). Unfortunately, no formal range testing of monitoring line A or B was carried out. In this study, 23 acoustic receivers could not be retrieved at the end of the study and were presumably 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 A3.1).

4.2.4 Statistical analysis

All analyses in this study were conducted using R versions 3.5.3 and 4.1.1 (R Core Team 2019, 2021).

4.2.4.1 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 tags minimum nominal delay (Table 4.1; Holbrook et al., 2018; Pincock, 2012). For a detailed description of false detection filtering see Lilly et al., 2022. Additionally, post-smolts that were detected at monitoring lines A and B and detected for multiple days beyond the date when 75% of post-smolts exited the Irish Sea, were removed from the analysis as this was likely a detected tag that was consumed by a predator. In this study only one post-smolt met this criterion. An Atlantic salmon post-smolt from the River Bann (ID: 46806) that was detected on monitoring line B from June 30th – July 6th and was removed from the analysis.

4.2.4.2 Migration success

Minimum migration success through the Irish Sea was defined as the proportion of post-smolts that entered the Irish Sea either from their natal river, or estuary (Clyde Estuary (River Endrick, River Gryffe), Lough Faughan (River Roe, River Faughan) that were detected on monitoring line B (Fig.4.1). In addition, the loss rate (%.km^{-1}) of post-smolts through the Irish Sea was calculated as the proportion of post-smolts that were not detected on monitoring line B, divided by the minimum distance travelled to reach monitoring line B (Fig. 4.1). Minimum migration success and loss rates could not be calculated for post-smolts entering the Solway Firth (from the rivers Derwent, Nith and Bladnoch) 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). Lastly, Spearman's correlation was used to test the relationship between the total distance travelled by a post-smolt from each river system through the Irish Sea and overall migration success.

4.2.4.3 Migration duration/speed

The mean duration of post-smolt migration through the Irish Sea was calculated as the time between their final detection on the last riverine receiver (rivers Derwent, Nith, Bladnoch, Carey, Glendun, Bush, Bann)/estuarine (rivers Endrick, Gryffe, Roe, Faughan)/coastal embayment (River Burrishoole) to monitoring line B (Chapter 5). In addition, the mean speed of post-smolts migrating through the Irish Sea was calculated in kilometres per day (km.day^{-1}) by dividing the minimum distance travelled by the total duration it took them to migrate to monitoring line B. The minimum distance travelled to reach monitoring line B was calculated as a straight-line distance (excluding land) using the Google Earth "Ruler" tool between the last riverine/estuarine receiver to monitor line B (*sensu* Barry et al., 2020).

4.2.4.4 Space use

To assess Atlantic salmon post-smolt distribution across monitoring lines A and B, post-smolts were grouped and compared amongst five regions defined based upon whether post-smolts had to navigate through the same coastal environment to reach the Irish Sea. Region 1 was defined as the Solway Firth (rivers Derwent, Nith, Bladnoch), Region 2 as the Clyde Sea (rivers Endrick & Gryffe), Region 3 as the Bush Coastal region (rivers Bann, Bush, Carey & Glendun), Region 4 as Lough Foyle (rivers Roe & Faughan) and lastly, Region 5 consisted of post-smolts that had to navigate through Clew Bay (River Burrishole; Chapter 5).

Pearson Chi-square tests (χ^2) were used to determine if detections of post-smolts from each region were equally distributed over receivers on monitoring lines A and B. Due to the large number of receivers in each monitoring line, monitoring line A was divided into 11 groups of two receivers and monitoring line D was divided into 12 groups of nine receivers. Additionally, to ensure that the number of post-smolts detected in a receiver group was not overestimated, duplicated detections of the same individual in the same receiver group were removed. Lastly, if post-smolts were detected in adjacent groups within less than their tag's nominal delay (Table 4.1) then the initial detection was kept.

The distribution of post-smolts on monitoring lines A and B was visualized by first creating a map of the study site using the get_google_map function in the R package *ggmap* (Kahle & Wickham, 2013). A heatmap of the number of post-smolts detected at each site was added to the map using the stat_density_2d function in the R package *ggplot2* (Wickham, 2016). Lastly, as we were mainly interested in the locations where post-smolts exit the Irish Sea, the locations where 50% (core area) and 90% (home range) of individuals per each region/river system were extracted.

4.2.4.5 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 were calculated for their final detection on the last riverine/estuarine/coastal embayment receiver and initial detection on monitoring line B, respectively (Bjerck et al., 2021). Exiting the Irish Sea was defined as their initial detection on monitoring line B, as at this point we knew they were travelling north from their natal river and into the North Atlantic.

4.2.4.6 Physiological factors influencing migration success

To examine the effects of biotic factors, Fork Length (FL; cm), mass (g), condition factor (k), tag burden (fraction of tag mass to body mass), and date of sea entry on Irish Sea migration survival, a general linear mixed model (GLMM) with a binomial error structure and logit link function was fit using the R package *lme4* (Bates et al., 2015) with river included as a random effect (Kessel et al., 2016). The dependent variable (Irish Sea survival) was coded as 1, if a post-smolt was detected on monitoring line B, and 0 if a post-smolt was detected on the final riverine/estuarine receiver but not on monitoring line B. The condition factor and tag burden of a smolt was calculated using the methods outlined in Barnham & Baxter (1998). Lastly, 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 as used in

Lilly et al. 2021. 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, and Julian day. Smolts that were not detected leaving their natal river but were detected on monitoring line B ($n = 19$) were removed from the analysis. In addition, River Faughan smolts were removed from the analysis as mass measurements were not available. This left 433 data points to include in the analysis (1 = 119, 0 = 314). 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 ΔAIC_c <2 were then compared using likelihood ratio tests using the function lrtest in the R package *lmtest* (Zeileis & Horthorn, 2002) to determine the significance of each explanatory variable and the final model. Lastly, once the final model was determined, the marginal R^2 (variation explained by fixed effects) and conditional R^2 (variation explained by both fixed and random effects) were calculated for that model (Matley et al., 2020).

Initial model:

Logit(Migration success ~ FL + Julian day + (1|River)

4.2.4.7 Environmental data

Modelled 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 Modelling 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 terrain-following sigma coordinate layers (total number of vertical layers) that follow the bathymetry, 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). In this study, ocean currents were derived from the closest NEA-ROMS nodes to each acoustic receiver.

Model temperature was derived from the Scottish Association for Marine Science's West *Scotland* Coastal Ocean Modelling System, (WeStCOMS) which is based on the open source Finite Volume Community Ocean Model (FVCOM; Chen et al., 2011; Aleynik et al., 2016). FVCOM is an unstructured grid, primitive-equation, free-surface, hydrostatic model with a varying horizontal resolution of 0.1 – 2.3 km (Chen et al., 2011; https://www.sams.ac.uk/facilities/thredds/). The WeStCOMS domain extends from the Isle of Man to the North Minch, and from the Scottish mainland to the Outer Hebrides archipelago. The model is one-way nested within the NEA-ROMS model described above (Aleynik et al., 2016). In this work, temperature series were taken from the closest WeStCOMS nodes to each acoustic receiver. The WeStCOMS temperature data were preferred here since this system includes a higher number of fresh water sources than its parent model. On the other hand, the WeStCOMS is restarted every week from a resting state, introducing a discontinuity in the ocean current time series that may have a negative impact in this research. Therefore, the currents were obtained from the NEA-ROMS model instead.

4.2.4.8 Environmental correlates of transition into North Atlantic

4.2.4.8.1 Temperature

To determine if 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 range in temperature on the median passage date (50% quantile) when post-smolts had their initial detection on monitoring line B was extracted from the WeStCOMS model.

4.2.4.9 Environmental cues of transition into North Atlantic

4.2.4.9.1 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 per hour 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 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). For this analysis and the analysis listed below, the initial detection of a post-smolt on monitoring line B was used, as we knew at this point post-smolts were travelling in a northward through the Irish Sea and into the North Atlantic.

4.2.4.9.2 Current direction

Hourly current direction data for each receiver location on monitoring line B was obtained from the WeStCOMS hydrodynamic model as described above, where currents travelling in the North East, South East, South, West and North West were represented by values ranging from 1° - 89°, 91° - 179°, 181° - 269° and 271° - 359°, respectively. Since the current direction data was 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).

Secondly, 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 five receivers where the highest number of initial post-smolt detections occurred.

4.3 Results

4.3.1 Migration metrics

In total, approximately 32% of all smolts (*n* = 148) that entered the Irish Sea (*n* = 460; Table A3.2) were detected at monitoring line B, thus indicating successful migration to the outer edge of the Irish Sea (Fig. 4.1). The Irish Sea loss rates of post-smolts ranged from 0.14 $\%.km^{-1}$ for River Faughan post-smolts to 1 $\%.km^{-1}$ for River Bush post-smolts (Table A3.2). The highest overall Irish Sea loss was observed for River Endrick post-smolts at 76% (Table A3.2). Overall loss was correlated with the minimum total distance travelled by a post-smolt through the Irish Sea (Spearman Rank Correlation: $r = -0.95$, $n = 11$, $p < 0.001$).

The time difference between the first date of entry of a tagged post-smolt into the Irish Sea and detection of the last individual to exit was 63 days. The median dates of entry and exit of post-smolts into and out of the Irish Sea were May 6th ± 8.12 days (± SD; range: April 18th – June 2nd) and May 14th ± 13.41 (range: April 21st to June 20th), respectively (Table A3.3) While most post-smolts entered the Irish Sea during the first two weeks in May, there appeared to be a difference between rivers in Northern Ireland and Great Britain in the date they exited the Irish Sea (Table A3.3; Fig. 4.2). 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 exited during the first week of June (Fig. 4.2; Table A3.3). One consistent finding amongst all rivers is that post-smolts underwent rapid migrations through the Irish Sea, with a mean (±SD) migration speed of 6.9 ± 1.71 km.day^{-1} for River Endrick post-smolts to 39.94 ± 12.04 km.day^{-1} for River Roe post-smolts. There were no post-smolts from the River Burrishoole detected in the Irish Sea receiver arrays, however, the median date of entry into the coastal zone west of Ireland for post-smolts from this river in 2021 was May 11th ± 2.04 days (Fig. 4.2; Table A3.3).

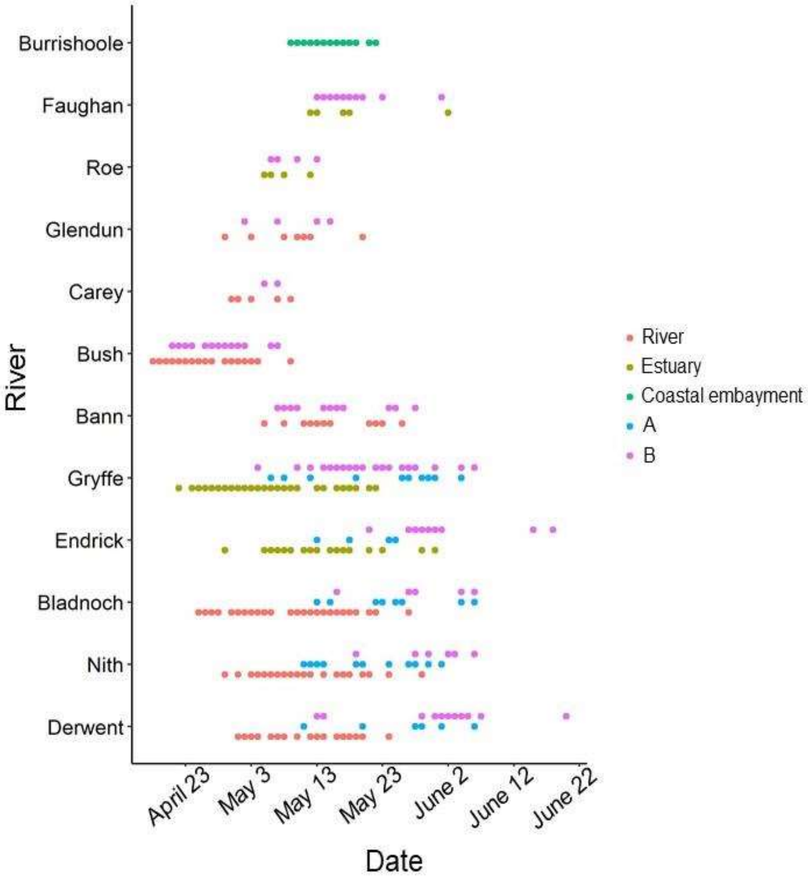


Figure 4.2. Abacus plot displaying the dates (mm-dd) when Atlantic salmon post-smolts (*n* = 509) were last detected in their natal river/estuary (rivers Endrick, Gryffe, Roe, Faughan) or coastal embayment (River Burrishoole) and entered the coastal zones of the Irish Sea or the west coast of Ireland (River Burrishoole; Fig. 4.1: Clew Bay) and were detected on monitoring lines A and B (excluding the River Burrishoole Fig. 4.1).

4.3.2 Predictors of migration success

Modelling migration success through the Irish Sea showed that only forklength (FL) successfully predicted survival (*p* = 0.005; Table 4.2). K (*p* = 0.50) and Julian day (*p* = 0.41) did not significantly improve the model (Table 4.2). However, only 3% of the variation in migration success was explained by FL (Table 4.2: Rm^2). The mean FL (± SD) for Atlantic salmon that did, and did not, complete a successful migration through the Irish Sea was 156.60 mm (± 13.90, range: 130.0 -194.0 mm) and 148.20 mm (± 12.50, range: 130.0 – 202.0 mm), respectively. The greatest amount of variation in post-smolt migration success through the Irish Sea was explained by their river of origin (Table 4.2; Rc^2 = 20%). The model predicted probability of successful migration by a post-smolt through the Irish Sea at the minimum (130.0 mm), mean (150.50 mm) and maximum (202.0 mm) FL of fish in this study was 18, 26 and 52%, respectively (Table 4.2; Fig. 4.3).

Table 4.2 Parameter values from the linear mixed models (LMM's) assessing the influence of the forklength (FL), condition factor (K) and julian day (see methods) on the successful migration of Atlantic salmon post-smolts through the Irish Sea. River location was included as a random effect in the model. The two last 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)).

Model	**Variable**	**Value**	**SE**	**z-value**	***p***	**R^2_M**	**R^2_C**
Initial	Intercept	-5.82	3.69	-1.58	0.11	0.02	0.20
	FL	0.24	0.13	1.88	0.06		
	K	-0.85	1.26	-0.68	0.50		
	Julian day	5.80	7.04	0.83	0.41		
Final	Intercept	-4.66	1.84	-2.53	0.01	0.03	0.19
	FL	0.24	0.12	1.98	0.05		

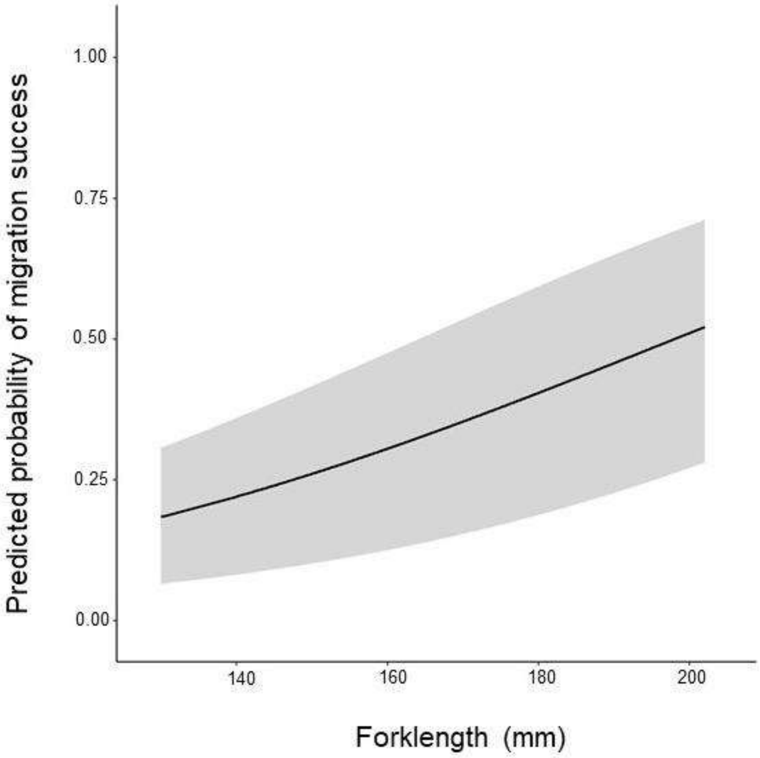


Figure 4.3 Results for mixed regression analysis. Plot displayed the predicted probability of Atlantic salmon post-smolt migration success through the Irish Sea with fork length. The shaded regions correspond to the 95% confidence interval of the final model.

4.3.3 Monitoring line passage

Post-smolts were detected on a mean number of 1.44 ± 0.91 (± SD; *n* = 43; range: 1-6) and 1.89 ± 1.12 (*n* = 148; range: 1-6) receivers on monitoring line A and B respectively. Only post-smolts migrating from Regions 1 (rivers Derwent, Nith, Bladnoch) and 2 (rivers Endrick, Gryffe) were detected at monitoring line A (Table A3.2; Fig. 4.4: a). Post-smolts from all river systems in Regions 1 to 4 were detected on monitoring line B (Table A2; Fig. 4.4: a). There were no post-smolts from Region 5 (River Burrishoole) detected on either monitoring line.

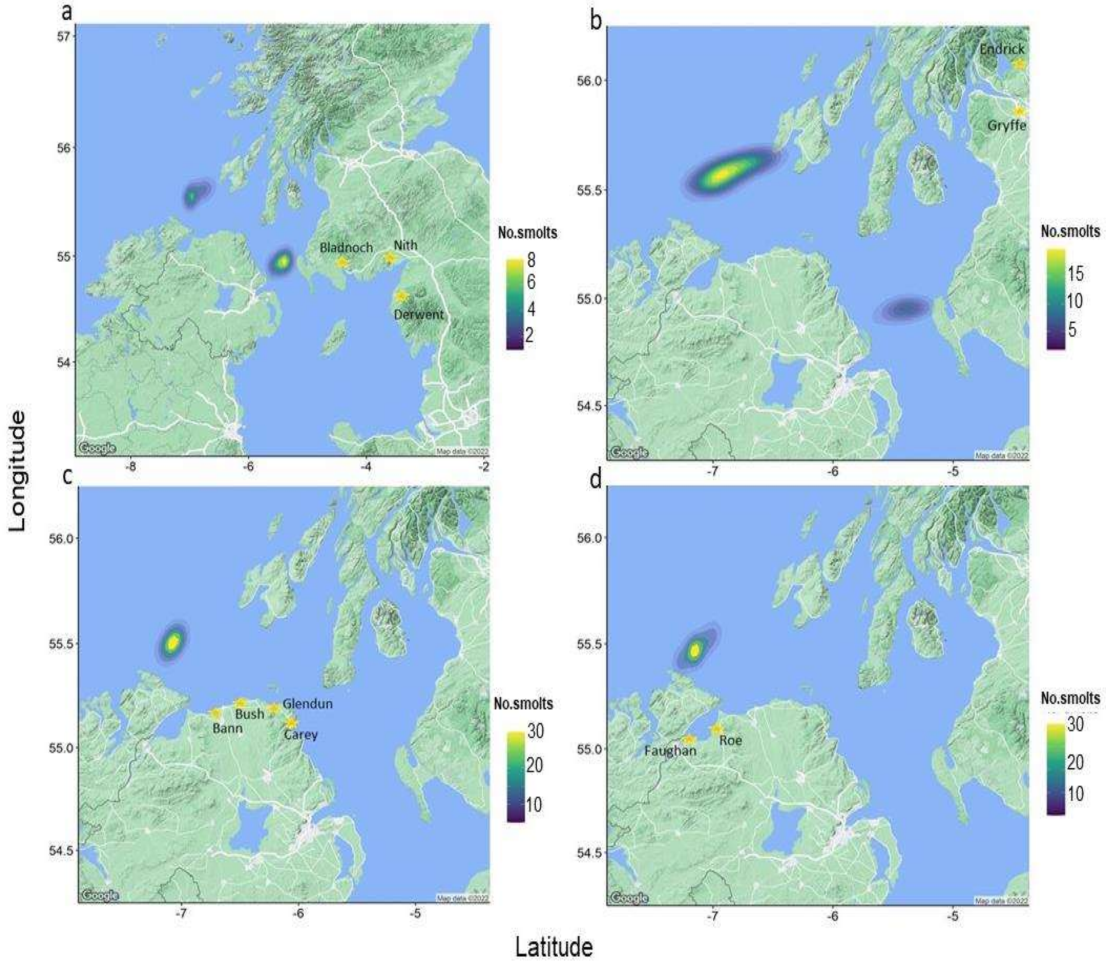


Figure 4.4 Heatmaps displaying the number of Atlantic post-smolts detected at each acoustic receiver on monitoring lines A and B (Fig. 4.1) during the period of this study. The orange stars represent the location of each river (n = 11) where Atlantic salmon post-smolts were tagged. Rivers were grouped together by coastal region where they entered the Irish Sea (Fig. 4.1, 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).

In this study, post-smolts migrating from the same coastal regions displayed similar passage position on monitoring lines A and B (Fig. A3.1). 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: χ^2_{10} = 14.56, p = 0.149; Region 2: χ^2_{10} = 12.71, p = 0.24; Fig. 4.4: a,b). However, 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: χ^2_{11} = 33.20, p = 4.88 × 10^{-4}; Region 2: χ^2_{11} = 35.44, p = 2.21 × 10^{-4}; Region 3: χ^2_{11} = 176.53, p = 2.20 × 10^{-16}; Region 4: χ^2_{11} = 40.46, p = 2.98 × 10^{-5}; Fig. 4.4).

In general, there appeared to be a relationship between where on the main array 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 (Fig. 4.4: a, b; Fig. A3.1:b-e) and England (Fig.4.4:a; Fig. A3.1:a) appeared to have a higher likelihood of being detected near the centre of monitoring line B, with the highest concentration (50% of individuals) of post-smolts migrating from Regions 1 and 2 being detected over a distance of approximately 20 km between receivers 49 – 75 (*n* = 11) and 47 – 78 (*n* = 20), respectively (Table 4.3; Fig. 4.4:a,b; Fig. A3.1:a-e). Whereas, post-smolts migrating from rivers in Northern Ireland appeared to remain close to the Irish coast, with the highest concentration (50% of individuals) of post-smolts migrating from regions 3 and 4 occurred over a distance of approximately 15 km between receivers 31 – 44 (*n* = 48) and 24 – 39 (*n* = 11), respectively (Table 4.3; Fig. 4.4:c,d; Fig. A3.1:f-k).

Table 4.3. Receiver locations (the range) on monitoring line B (Fig. 4.1) where 50% and 90% of post-smolts (No. smolts) from each coastal region (rivers combined in "Overall") and river were detected in this study, as well as the length of the line (km) over which fish were detected.

			50% of individuals monitoring line B				**90 % of individuals monitoring line B**			
Region	**River**	**No. smolts total**	**No smolts**	**range**	**distance (km)**	**% of line**	**No. smolts**	**range**	**distance (km)**	**% of line**
1	Overall	22	11	49 – 75	15.30	24.36	19	45 – 94	27.70	44.11
	Derwent	11	6	47 – 74	15.10	24.04	10	45 to 93	20.80	33.12
	Nith	6	3	50-63	7.65	12.18	5	44 to 82	21	33.44
	Bladnoch	5	2	54 - 80	14.40	22.93	4	47 to 93	25.80	41.08
2	Overall	36	20	47-78	17.60	28.03	32	38 – 102	36.40	57.96
	Endrick	9	6	41 – 71	17.80	29.34	8	35 to 93	22.50	35.83
	Gryffe	27	15	49 – 79	14.30	22.77	25	41 – 104	35.70	56.85
3	Overall	68	48	31 – 44	7.07	11.26	60	23 – 69	27.10	43.15
	Bann	21	13	27 – 37	5.95	9.47	17	15 – 37	14.80	23.57
	Bush	39	29	33 – 44	6.61	10.53	35	25 – 55	17.80	28.34
	Carey	3	2	47 - 74	25.48	25.48	3	38 – 87	27.50	43.79
	Glendun	5	3	34 – 45	6.03	9.60	5	14 – 67	32.70	52.07
4	Overall	23	11	24 – 39	8.91	14.19	22	12 – 51	24.90	39.65
	Roe	5	3	24 – 34	6.08	9.68	5	8-37	18.80	0.30
	Faughan	18	10	22 – 40	10.80	17.20	17	12 – 51	24.70	39.33
5	Burrishoole	0	0	-	-	-	-	-	-	-

4.3.4 Environmental correlates of migration

4.3.4.1 Temperature

Most (median value; Table A3.3) 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 9.12 to 9.88°C. In contrast, most (median value; Table A3.3) 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 10.33 to 11.01°C.

4.3.5 Environmental cues initiating migration

4.3.5.1 Time of day

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} = 0.11 ± 0.26 post-smolts/hour). The mean hour when post-smolts were initially detected on monitoring line B occurred at 11:36 am ± 2.24 hours (± SD; Fig. 4.5:a).

4.3.5.2 Current direction

In this study, the timing of exit of a post-smolt from the Irish Sea (first detection on monitoring line B receiver) was highly dependent on current direction ($z = 0.49$, $p < 0.001$). The mean current direction (circular mean degree) at the time of initial post-smolt detection (all rivers combined) occurred at 283.33 ± 1.11° (± SD; between west and north-west; range: 0 – 353°; Fig. 4.5: b). Furthermore, the highest proportion of post-smolts (n = 60; 40.27%;

Table 4.4) were initially detected on monitoring line B during ebb tide when currents were tracking westwards. During the timestamp 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 4.4). Lastly, most post-smolts exited the Irish Sea when currents were tracking in a westerly direction, as post-smolts detected at the five most common receivers were exposed to a variety of current directions with a high number of hourly currents tracking North East on the ebbing tide (Fig. A3.2).

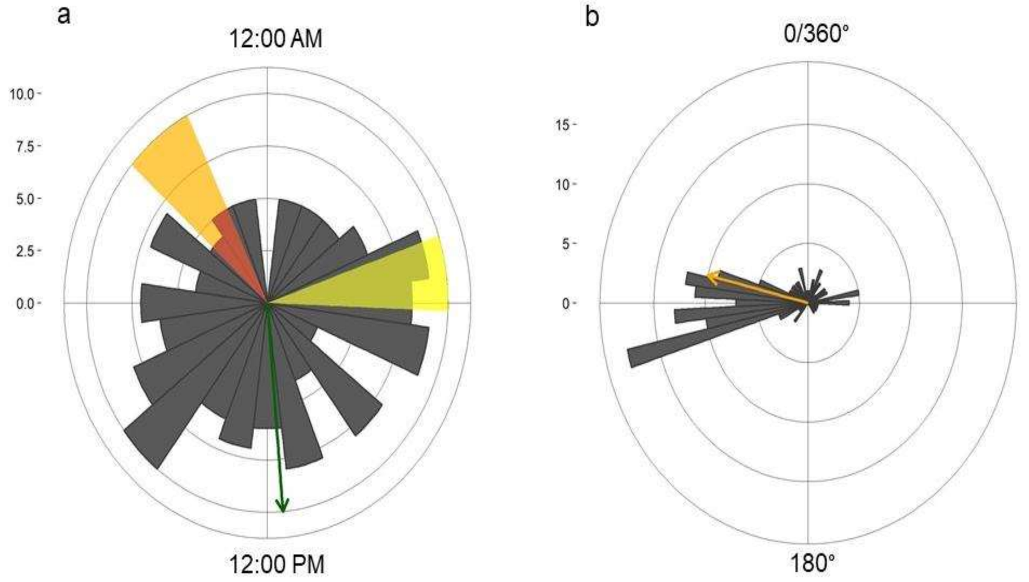


Figure 4.5 Rose diagrams depicting the hour of the day (a) and direction of currents (°; b) when post-smolts were initially detected at a unique acoustic receiver on monitoring line B. The green and orange hours reflect the mean hour and mean current direction when post-smolts were initially detected (Lilly et al., 2022). The orange and yellow bands in a reflect the variation in sunrise and sunset times for the total duration post-smolts were detected on monitoring line B (April 21st – June 20th).

Table 4.4. The proportion of post-smolts (%) initially detected on monitoring line B (*n* = 148) when averaged hourly modelled currents were travelling in a North East (1 - 89°), South East (91 - 179°), South West (181 - 269°) and North West (271 - 359°) direction. In addition, 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 (sum vertical and horizontal components; Mean speed; m/s).

Current direction	**Degree range**	**% of smolts (n)**	**Mean direction (°)**	**Mean u (m/s)**	**Mean v (m/s)**	**Mean speed (m/s)**
NE	1° - 89°	17.57 (26)	53.63 ±0.50 (0.002 – 89)	0.59 ± 0.45 (0.001 – 1.28)	0.28 ± 0.14 (0.002 – 0.46)	0.72 ± 0.36 (0.04 – 1.29)
SE	91° - 179°	5.37 (8)	108.97 ± 0.33 (91 – 147)	0.82 ± 0.40 (0.13 – 1.30)	0.27 ± 0.30 (0.002 – 0.81)	0.89 ± 0.43 (0.24 – 1.42)
SW	181° - 269	36.24 (54)	255.69 ± 0.18 (218 – 269)	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	40.27 (60)	291.42 ± 0.37 (271 – 353)	0.68 ± 0.41 (1.64 – 0.05)	0.17 ± 0.10 (0.01 – 0.48)	0.73 ± 0.37 (0.11 – 1.67)

4.4 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 studies provided valuable insights into the migratory patterns of post-smolts through the Irish Sea, our study highlights how the merging of resources and dissemination of results amongst multiple nations and projects as they cross jurisdictional boundaries during their early marine migration is needed to inform the conservation of Atlantic salmon (Flye et al., 2021).

4.4.1 Overall loss

Loss rates in this study were quite similar amongst post-smolts migrating from the same region. This is likely a result of fish encountering similar nearshore stressors (Table A3.2). However, when loss rates are multiplied by the minimum total distance travelled in the study reported here there appeared to a positive relationship between the total distance travelled by post-smolts and the overall loss rate. Overall loss rate ranged from a minimum of 5% for River Faughan post-smolts (38 km to reach Irish Sea exit) upwards to 76% for River Endrick (168 km to reach Irish Sea exit) post-smolts. Post-smolts migrating a greater distance through the Irish Sea spent a greater duration in this region (e.g. River Derwent: 278 km, 23 days versus River Roe: 38 km, 1.02 days) which would increase their likelihood of being exposed to any stressors acting upon migration success such as marine predators (Jepsen et al., 1998).

The loss of Atlantic salmon post-smolts in this study is likely related to natural threats such as predators. Harbour seals, cetaceans (e.g. the Bottlenose Dolphin (*Tursiops truncatus*)), piscivorous birds (e.g. the Cormorant (*Phalacrocorax carbo*)), and fishes (e.g. Atlantic cod (*Gaadus morhua*), Saithe (*Pollachias virens*)) have been reported to be present within river mouths and estuaries during the period when salmonids are present, suggesting that they may prey on post-smolts (Allegue et al., 2020; Arso Civil et al., 2019; Carter et al., 2001; Kennedy & Crozier, 2010; Thorstad et al., 2011a, 2012a,b ; Wilson et al., 1997). It is known that these species listed occupy 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). Additionally, while it was assumed that all tag detections used in this study were those of post-smolts because of the similarity of swim speeds and directional passage reported by previous studies (Chaput et al., 2019; Green et al., 2022) we were unable to determine with complete certainty if some detections were from a predator. Future studies should utilize predation tags and/or acoustically tag predators of post-smolts to get an accurate description of their behaviour (Gibson et al., 2015; Hanssen et al., 2022; Lennox et al., 2021; Nash et al., 2022). Furthermore, it important to note that the nominal tag delay varied substantially between river systems in this study ranging from 30 – 60 up to 40-80 seconds. The longer nominal tag delays may have prevented us from detecting smolts that were moving quickly past monitoring line's A and B. Lastly, in this study we can't rule out whether stress induced by the tagging procedure or expulsion of tags influenced loss estimates (Cooke et al., 2011; Klinard & Matley, 2020).

4.4.2 Morphological predictors of survival

Consistent with other estuarine and early marine migration studies, here we report that for post-smolts migrating through the Irish Sea there was a size effect on survival; with larger salmonid post-smolts having a higher likelihood of completing a successful migration (Dieperink et al., 2002; Futamura et al., 2022; Thompson & Beauchamp, 2014). Larger smolts are thought to undergo more efficient migrations, thus reducing their exposure to predators (Flávio et al., 2021). However, its important to note that FL only accounted for a small percentage of the variation explained in the model. In this study, the size of the smolt tagged was dependent on the size and mass of the tags used by each project to limit tag burden. In thisstudy tag burdens did not exceed 0.07, the value at which tags have been shown to negatively impact survival and the size of smolts tagged ranged from 13.0 to 21.50 cm (Brown et al.,2010). Future studies that vary the size of the tag used to target smaller individuals within a population would most likely find that the effect of body size on migration success is even greater than that shown here.

The sea entry date is thought to be a key factor linked to post-smolt growth and survival as it may dictate their likelihood of overlap with key prey items such as fish larvae and amphipods (Hvidsten et al., 2009; Thorstad, et al., 2012b; Utne, et al., 2021a). 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 date did vary by up to a month for some river systems included in this study (Table A3.3; River Endrick, 30 days) on average post-smolts spent a short period within the Irish Sea, ranging from 1.02 ± 0.71 to 22.81 ± 8.45 (mean ± SD; Table A3.2) days for River Roe and River Nith post-smolts, respectively. Research directed surface trawls targeting post-smolts are required to determine if post-smolts are consuming large amounts of prey while migrating through the Irish Sea, and if prey abundances vary throughout early-late spring. Due to their relatively efficient migration through the Irish Sea it can be speculated that post-smolts may not utilize the Irish Sea region for feeding, and instead upon exiting their natal rivers focus on reducing the time taken to reach their northern grounds located off the continental shelf (Table A3.2; Ounsley et al., 2020).

4.4.3 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 post-smolts from Northern Ireland were detected exiting the Irish Sea on the western half of monitoring line B.

Consistent with the findings of Barry et al. (2020) and Green et al. (2022) it appears that most post-smolts migrate in a north direction through the Irish Sea. When assessing the distribution of Atlantic salmon post-smolts on monitoring line B, most Atlantic salmon post-smolts in this study appeared to travel in a northwest direction upon exiting their natal river. 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 prior to two migrating back to monitoring line B (Table A3.2). The largest fresh water input into the Irish Sea originates from the Clyde Sea, which creates a southerly coastal current extending to the Mull of Galloway. This current is most notable during 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 were unaccounted for and it is possible that they may have migrated further south around the coast of Ireland, however, this 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 low. Most fisheries in this region operate nearshore, targeting invertebrates such as Norwegian lobster (*Nephrops norvegicus*) using demersal trawls (ICES, 2019a). During their coastal migration, Atlantic salmon post-smolts have been reported to remain within the top six metres of the water column, results from our study suggest that a majority of post-smolts migrate away from nearshore coastal areas (Davidsen et al., 2008).

There are currently two operational aquaculture sites located on the Antrim coast of Northern Ireland, within the boundaries of the Irish Sea (SeaFish, 2015). The main concern for wild salmon from salmon aquaculture is the high density of sea lice. Lice once they settle on salmonids feed on blood and mucus and, if present in high enough numbers of lice infections can lead to physiological impediments, behavioural changes and ultimately mortality (Bjørn et al., 2001; Skilbrei et al., 2013; Wooten et al., 1982). Prior to developing into the infectious adult stage, motile sea lice larvae are known to drift for up to 30 km prior to settling on to a host (Rees et al., 2015). For post-smolts to accumulate enough sea lice to lead to mortality (~ 1.6 lice larva/gram of smolt) some studies have suggested that they would have to spend more than a few weeks close to an aquaculture site (Bjørn & Finstad, 1997; Krkošek et al., 2009). However, its important to note that there is variation in what is considered a significant sea lice load with studies from Norway reporting a 100% lice-related marine mortality when the lice load is >0.3 lice g^{-1} (Taranger et al., 2012, 2015). While post-smolts from English and Scottish rivers did take between two to three weeks to migrate through the Irish Sea, all post-smolts were found to undergo relatively efficient (10 – 39 km.day^{-1}: Table A3.2) migrations, suggesting that their time spent near the aquaculture sites was minimal. The migration speeds in this study are similar to the results of Barry et al. (2020) and Green et al. (2022) who reported 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.

4.4.4 Environmental correlates of post-smolt transition

4.4.4.1 Temperature

The modelled water temperature experienced by post-smolts as they exited the Irish Sea ranged between 9 - 11°C. This is similar to temperatures reported during their offshore marine migration (Holm et al., 2006; Ounsley et al., 2020). Water temperatures been reported to be a critical factor associated with post-smolt growth and ultimately adult return rates (Friedland et al., 1998). While we did find that the temperature at Irish Sea exit varied amongst smolts from Northern Irish (~ 9 - 10°C) versus English/Scottish rivers (~ 10 - 11°C) this may be an artifact of the variation in tagging dates amongst river systems in this study. Future studies should further standardize tagging procedures by ensuring tagging dates occur throughout the entire smolt run to get an accurate representation of population level migration metrics.

4.4.5 Environmental cues of post-smolt transition

4.4.5.1 Time of Day

Contrary to our hypothesis, Atlantic salmon post-smolts were found to exit the Irish Sea regardless of the time of day with the mean migration time occurring just prior to noon. Some studies have noted that as post-smolts transition from the riverine to early marine environment, post-smolts 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 engaging in diurnal migrations is thought to be related to a trade off between the abundance of predators in a region 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 fishes are present (Hastie et al., 2016; Zamon, 2001). Migrating during the night may be beneficial to smolts and post-smolts navigating through rivers and estuaries, respectively, as they contain a higher number of migratory constriction points in comparison to the pelagic zone of the coastal marine environment (Lacroix et al., 2004b; Lefèvre et al., 2012). Post-smolts are visual predators that must feed during their early marine migration to cover the vast distances required to reach their northern feeding grounds (Utne et al., 2021b). Migrating during the day may be a strategy that increases their chances of capturing prey along their migratory route (Andreassen et al., 2001; Hedger et al., 2008; Kadri, 1997).

4.4.5.2 Current direction

Through combining actual post-smolt movement data with detailed current data in the Irish Sea, here we report that Atlantic salmon post-smolts appeared to be exiting the Irish Sea with the outgoing tide when currents were tracking in a northwest direction (towards the slope current). The main driver of the current in the Irish Sea are the M2 and S2 tidal constituents with the dominant flow directed northwards during the spring and winter, however, during the summer months dominant flow can reverse southward (2.50 $km^3.day^{-1}$; Howarth, 2005; Olbert et al., 2012; Olbert & Hartnett, 2010). Results from this study suggest that Atlantic salmon post-smolts may be utilizing the dominant northward current at the most opportune time to move quickly offshore and aid in their migration towards the slope current (Barry et al., 2020).

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 travelling 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 decipher the direction of the current limiting the ability to generalize the findings to multiple populations. The result from Barry et al., (2020) and this study contrasts with the predictions made by the particle tracking study conducted by Ounsley et al. (2020), which suggested that for post-smolts migrating from rivers in Northern Ireland and Scotland to reach the slope current they would have to deviate from local current patterns early on in their migration and travel in a northwest direction. While particle tracking studies provide a good indication of behaviours and environmental variables which could lead to a successful migration, they are unable to capture the complexity and decision making of actual post-smolts (Ounsley et al., 2020).

4.4.6 Conclusion

In conclusion, this study is the first to assess the early marine migration of post-smolts (*n* = 483) from four nations (England, Scotland, Northern Ireland, Ireland) in the British Isles (14 rivers) through the collaboration of four different projects (SeaMonitor; West Coast Tracking Project; COMPASS, Derwent Tracking Project) comprising six different organizations (SeaMonitor: Marine Institute, Agri-Food and Biosciences Institute, Loughs Agency, University of Glasgow; West Coast Tracking Project: Atlantic Salmon Trust; Derwent Tracking Project: Environment Agency). In this study we were able to obtain baseline information concerning the survival, timing, and basic drivers of post-smolt migration through the Irish Sea. Temporal repeatability of this project over multiple years is required to determine whether changes in ocean circulation patterns could modify migratory patterns and ultimately loss rates of post-smolts migrating through this region (Thorstad et al., 2012b; Chaput et al., 2018).

Chapter 5: The early phase of the marine migration pathways of Atlantic salmon post-smolts from multiple rivers in Scotland, England, Northern Ireland and Ireland.

Abstract

The early phase of the marine migration of Atlantic salmon (*Salmo salar*) post-smolts remains poorly documented for many populations. Previous trawling studies have shown European salmon post-smolts migrate towards the slope current over the Vøring plateau near Norway, however, the migration pathways that post-smolts take to reach this area are unknown. Therefore, this collaborative study investigated the migration pathways of post-smolts during the early phase of their marine migration, by drawing together acoustic telemetry data collected from seven projects. In total, 1806 salmon smolts were tagged in 23 rivers across four countries and detected by a network of 398 acoustic receivers deployed in marine waters and a submersible glider. This study demonstrated that post-smolts from different rivers, and individuals from the same river, utilise multiple pathways during the early phase of their marine migration. Overall, 34.7% of acoustically tagged post-smolts were detected on receivers in marine waters. The majority of these post-smolts migrated in a northerly or north-westerly direction once entering marine waters. A few post-smolts migrated south or in a north-easterly direction, which is contrary to what expected. The findings from this study have clear management implications as potential anthropogenic pressures, such as aquaculture and offshore renewables, could overlap with these migration pathways. This study provides an unprecedented insight into the early phase of the marine migration for post-smolts from across a broad geographic region.

5.1 Introduction

Anadromous Atlantic salmon (*Salmo salar*) post-smolts from populations in Europe make long-distance migrations from fresh water, through the coastal zones to feeding grounds in the north-east Atlantic (Friedland, 1998; Holm et al., 2000). The pathways they use to reach their feeding grounds, their migration behaviour and the cues that they use for navigation are, however, very poorly understood (Dadswell et al., 2010; Ounsley et al., 2020). For example, the roles of active swimming and passive, current-driven migration movements, in defining post-smolts pathways in the coastal zones are unclear. Findings from trawling studies have shown that post-smolt distribution during the first few months in the open ocean closely matches the slope current over the Vøring plateau (Holm et al., 2000; Gilbey et al., 2021). This is consistent with results from several studies which have linked post-smolt migration pathways and the prevailing currents. For example, Mork et al. (2012) found that the strength and direction of currents were likely drivers for migration pathways and that the inter-annual variation in currents affects the routes taken by post-smolts migrating in the northeast Atlantic. Dadswell et al. (2010) suggested that European stocks migrate using the North Atlantic Subpolar Gyre. However, during the early phase of the marine migration post-smolts may not be solely utilising current following behaviour. A particle tracking study by Ounsley et al. (2020) found that current-following behaviour alone would not be enough for post-smolts migrating from rivers on the west coast of Scotland to reach their feeding grounds. Modelling work by Moriarty et al. (2016) suggested that directed swimming led to the highest migration success rate for Atlantic salmon through the Gulf of Maine. Similarly, Newton et al. (2021), in a study combining acoustic telemetry and particle tracking, found that the actual post-smolt migration route of the fish, in their study, was best predicted by active swimming rather than simply following the current. Therefore, it may be that active navigation and swimming are required for most salmon post-smolts during early marine migration in the coastal zone. When post-smolts reach the better-defined and more consistent oceanic currents then a switch to current following is the main form of migration. Other factors are also likely to affect the migration pathways used. Holm et al. (2000) found that the majority of post-smolt captured during trawl netting were in salinities >35.0 ppt and at temperatures of 9-11ºC. Additionally, the distribution of post-smolts detected at sea is possibly linked with the presence and abundance of suitable prey items, suggesting that prey availability influences migration pathways (Gilbey et al., 2021; Utne et al., 2022).

Once salmon reach their presumed feeding area, studies have shown that fish from different populations aggregate (Hansen & Jacobsen, 2003; Gilbey et al., 2021). However, it is not known how early this aggregation takes place and, thus, whether different populations use the same migration pathways at the same time salmon from different populations enter the Atlantic Ocean at different points across a wide range of latitudes. Therefore, the environmental conditions and sea currents post-smolts encounter when they first enter the marine environment vary considerably, which makes it likely that there are population-specific, and possibly even individual, variation in the migration route taken and, in the cues, used to determine that pathway.

Information available to date on post-smolt marine migration patterns mostly comes from mark-recapture studies at sea and trawling studies that have used genetic markers to assign post-smolts back to their natal rivers (Harvey et al., 2019; Gilbey et al., 2021). These studies provide broad spatial coverage but are observational, providing only one data point at the point of capture, without any definitive information on the migration pathways or the speed of the migration before capture. However, telemetry methods have the capacity to provide spatially and temporally detailed information on salmon migration. The drawback of such studies is that they are usually dependent on strategically placed arrays of stationary receivers, of which, the number required, cost and the complexity of their deployment/recovery logistics increase geometrically with the distance from shore. As a result, acoustic studies to date have been largely conducted in estuarine and near coastal environments (but see Chaput et al., 2019). Satellite telemetry can provide tracks without the need for stationary receiver arrays, but the required tags are large and only suitable for studies on large adult salmon (Strom et al., 2018). Another approach that has been used to infer migration pathways is through simulation models using ocean current models. Modelling, using high-resolution oceanographic data has the potential to provide broad geographic coverage and high-resolution outputs. However, the nature and role of environmental cues used by salmon to navigate pathways are poorly understood and study results to date are somewhat contradictory (contrast: Mork et al., 2012;

Moriarty et al., 2016; Ounsley et al., 2020 & Newton et al., 2021) resulting in modelled migration pathways with high levels of uncertainty.

As marine coastal areas are subject to high levels of human activity, an understanding of salmon migration pathways through coastal areas has clear management importance to mitigate impacts. Coastal zones are increasingly used for renewable energy development including wind, tidal and wave energy. The impacts of generation and transmission infrastructure on migrating salmonids have not been investigated extensively but potential impacts could include migration delays and modified routes resulting from device avoidance and increased mortality due to predator aggregation around the devices (Wyman et al., 2018; Copping et al., 2021). Coastal waters are also used by the aquaculture industry for salmon farming in many areas of western Europe; negative interactions between wild migrating post-smolts and salmon aquaculture are of major concern (Finstad et al., 2001; Bohn et al., 2020; Johnsen et al., 2021). Salmon aquaculture is a particularly pervasive pressure in the area of the study presented here. Another potential anthropogenic threat is pelagic fisheries; there is evidence from the northeast Atlantic of post-smolts being caught as a by-catch in pelagic trawl fisheries (ICES, 2004, ICES, 2020).

Here we report a geographically extensive telemetry study, formed by merging data from seven separate projects and collaborations by 19 different research groups. The study presented here investigated the marine migration pathways of 1806 Atlantic salmon post-smolts from 23 rivers in Scotland, England, Northern Ireland and Ireland through coastal marine waters of the eastern Atlantic.

5.2 Materials and Methods

5.2.1 Study area

In 2021, seven acoustic telemetry studies were conducted in marine waters extending from the north of the island of Ireland, north-western England and Western Scotland (including the area of sea to the west of the Outer Hebrides (Fig. 5.1). Each project had somewhat separate objectives and were focussed on a range of species but used the same technology. Four of the seven projects aimed to determine the early phase of the marine migration of Atlantic salmon post-smolts. Five of the projects (the West Coast Tracking Project, SeaMonitor Project, Nith Smolt Tracking Project, Torridon Tracking Project and Derwent Tracking Project) acoustically tagged and/ or deployed acoustic receivers in the study area (See Table A4.1 for more detailed information about these projects including their objectives and aims). An additional three projects (the Collaborative Oceanography and Monitoring for Protected Areas and Species (COMPASS) Project, the Movement Ecology of the Flapper Skate (MEFS) project and Sar Altimetry Mode Studies and Applications (SAMOSAS Project), which were conducted in 2021, deployed acoustic receivers for their own projects which allowed opportunistic detections of post-smolts to be included in this study. Therefore, combined these projects covered a broad geographic area, covering a latitudinal distance of 400 km (Fig. 5.1).

5.2.2 Fish capture and tagging

During the months of April and May 2021, 1806 wild Atlantic salmon smolts were captured across 23 rivers in Scotland (n_{River} = 14; n_{Tags} = 1294), England (n_{River} = 1; n_{Tags} =150), Northern Ireland (n_{River} = 7; n_{Tags} = 362) and Ireland (n_{River} = 1; n_{Tags} = 85) using 1.5 m diameter rotary screw traps, fyke nets and Wolf-type downstream traps (Fig. 5.1; Table 5.1). In addition, 60 hatchery reared Atlantic salmon smolts of a ranching strain were released in Ireland (n_{River} = 1). The smolts were tagged with acoustic tags and released in their natal river or lake. Almost all rivers included in the study had one fish release site, however, the Rivers Derwent and Endrick each had two release sites in the river (Table 5.1; Fig. 5.1).

In general, only salmon smolts with a fork length ≥ 130 mm and weighing ≥ 20 g were tagged with V7-2x, V7-4x, V7-4L and ID-LP6 acoustic tags and smolts with a fork length ≥ 140 mm were tagged with V8-4x, V7D-2x and ID-LP7 acoustic tags, all details of tag specifications (length (mm), weight (g), nominal delay) are included in Table 5.1. The majority of smolts were tagged with V7-2x acoustic tags (Table 5.1; InnovaSea, Bedford, Nova Scotia, Canada). However, smolts from the River Bush were tagged with V7-4L acoustic tags (Table 5.1; InnovaSea, Bedford, Nova Scotia, Canada) and ranched smolts from the River Burrishoole were tagged with V8 – 4x (Table 5.1; InnovaSea, Bedford, Nova Scotia, Canada) and V7D-2x acoustic tags (Table 5.1; InnovaSea, Bedford, Nova Scotia, Canada).

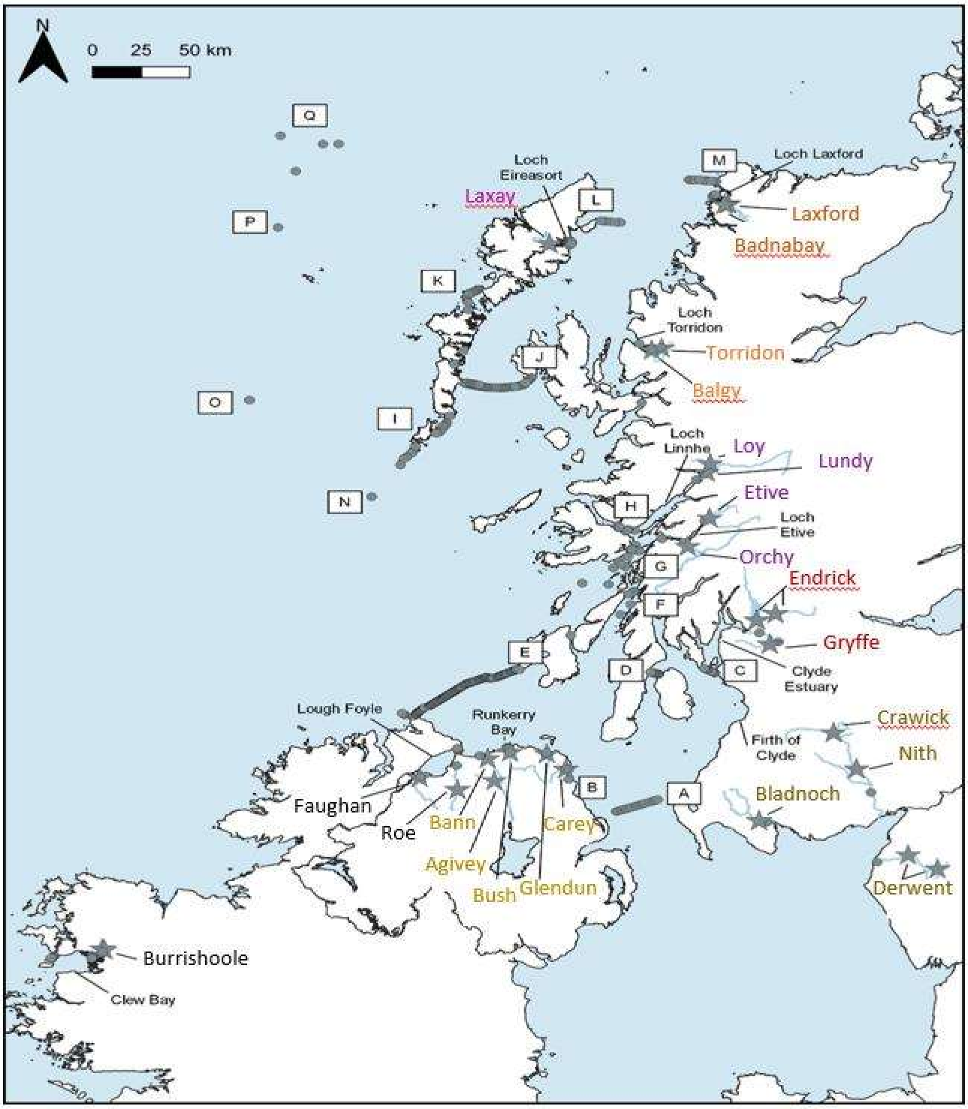


Figure 5.1. Map displaying the rivers (and their tributaries; *n* = 23) where smolts (*n* = 1806) were tagged in Scotland, England, Northern Ireland and the Ireland for this study. Release sites are represented by stars and acoustic receivers (*n* = 398) are represented by grey dots. Marine monitoring lines and points (*n* = 17) for this project are labeled in alphabetical order from south to north (A-Q). Lastly, monitoring regions 1-9 are represented by the colour of the text where: Region 1, the Solway Firth (Rivers Derwent, Nith, Bladnoch) is represented in brown; Region 2, the Clyde Sea (Rivers Endrick and Gryffe) is represented in red; Region 3, Loch Linnhe (Rivers Etive, Orchy and Lochy) is represented in purple; Region 4, Loch Torridon (Rivers Balgy and Torridon) is represented in orange; Region 5, Loch Eireasort (River Laxay) is represented in pink; Region 6, Loch Laxford (Rivers Laxford and Badnabay) is represented in dark orange; Region 7, Bush coastal region (Rivers Bann, Bush, Carey and Glendun) is represented in yellow; Region 8, Lough Foyle (Rivers Roe and Faughan) is represented in black; Region 9, Clew Bay (River Burrishoole) is represented in green.

Wild salmon smolts from the rivers Balgy and Torridon were tagged using ID-LP7 (Table 5.1; Thelma Biotel, Trondheim, Norway) and ID-LP6 acoustic tags (Table 5.1; Thelma Biotel, Trondheim, Norway). All tag types operated on the 69 kHz acoustic frequency and code map 114 or 115 and thus were compatible with all receivers deployed by the eight projects involved in this study.

Acoustic tagging followed standard surgical tagging methods, however, there were slight differences between projects. In general, once anaesthetised, smolts were measured for fork length and weight to the nearest 0.1 mm and 0.1 g, respectively. The acoustic tag was then inserted into the abdominal cavity through an ~10 mm incision anterior to the pelvic girdle. The incision was then sutured closed using one or two interrupted surgeon knots. The smolts were then placed in aerated water post-surgery and released once fully recovered (see Lilly et al., 2021 for details). In the River Burrishole fish were held overnight in flow through containers within the river before release the following day. All acoustic tagging was conducted under licence by appropriate national authorities (UK Home Office licence PP0483054; UK Home Office licence PPL2869; HPRA Licence AE19121/P003 Case No. 7028960).

Table 5.1. The number (No.) of salmon smolts that were fitted with acoustic tags during this study, that were detected successfully exiting each river. The tagged fish release site (Latitude and Longitude), the tag type, tag life, nominal delay between acoustic transmissions, the date fish were tagged, tag expiry date, mean fork length (mm ± SD) and mean weight (g ± SD) are only provided for those smolts that were successfully detected on the final riverine receiver and included in this study. Note for the River Burrishoole ranched smolts, which are on average larger than wild smolts, were tagged with V8-4x and V7D-2x tags, whereas, wild smolts were tagged with V7-2x tags. The solid lines separate smolts tagged in Scotland, England, Northern Ireland and Ireland.

River	**Release site (lat, long º)**	**Tag Type**	**Tag life (days)**	**Nom. Delay (sec)**	**Power output 1µPa @ 1m**	**No. (Total no. tagged)**	**Date Tagged**	**Tag expiry date**	**Median fork length (mm ± SD)**	**Median Weight (g ± SD)**	**Median Tag Burden (± SD)**
Endrick	56.0492, - 4.4399 56.0085, -4.5897	V7-2x	75	18-38	137	50 (145)	15-04 to 03-05	29-06 to 17-07	141.50 ± 8.79	29.05 ± 5.61	0.06 ± 0.01
Gryffe	55.8693, -4.4942	V7-2x	75	18-38	137	93 (102)	12-04 to 24-04	26-06 to 08-07	148.0 ± 10.13	33.40 ± 6.66	0.05 ± 0.01
Bladnoch	54.8672, -4.4989	V7-2x	75	18-38	137	53 (130)	20-04 to 14-05	04-07 to 28-07	141.0 ± 7.88	29.50 ± 5.05	0.06 ± 0.01
Nith	55.3783, -3.9313	V7-2x	75	18-38	137	66 (130)	23-04 to 06-05	07-07 to 20-07	147.50 ± 10.92	32.80 ± 7.20	0.05 ± 0.01
Etive	56.5852, -5.0233	V7-2x	75	18-38	137	66 (87)	19-04 to 14-05	03-07 to 28-07	137.0 ± 7.12	24.0 ± 3.72	0.07 ± 0.01
Orchy	56.4166, -5.1921	V7-2x	75	18-38	137	105 (113)	16-04 to 09-05	05-07 to 23-07	137.0 ± 6.91	24.0 ± 3.80	0.07 ± 0.01
Lundy	56.8420, -5.0688	V7-2x	75	18-38	137	53 (75)	12-04 to 18-05	26-06 to 01-08	135.0 ± 5.64	22.95 ± 3.46	0.07 ± 0.01
Loy	56.8907, -5.0347	V7-2x	75	18-38	137	96 (170)	19-04 to 10-05	03-07-24-07	134.0 ± 4.99	22.15 ± 2.79	0.07 ± 0.01
Badnabay	58.3722, -5.0450	V7-2x	75	18-38	137	9 (9)	29-04	13-07	133.0 ± 11.61	25.30 ± 8.84	0.06 ± 0.01
Laxford	58.3760, -5.0101	V7-2x	75	18-38	137	77 (91)	28-04 to 05-05	01-07 to 19-07	140.50 ± 8.88	26.60 ± 5.90	0.06 ± 0.01
Laxay	58.1041, -6.5480	V7-2x	75	18-38	137	103 (119)	19-04 to 05-05	03-07 to 19-07	146.0 ± 13.46	31.83± 8.75	0.05 ± 0.01
Crawick	55.3783, -3.9313	V7-2x	75	18-38	137	24 (50)	16-04 to 23-04	30-06 to 07-07	139.0 ± 5.10	27.20 ± 2.31	0.06 ± 0.01
Balgy	-	ID-LP6	70	30	137	5 (7)	20-04 to 12-05	29-07 to 19-08	135.0 ± 4.06	24.70 ± 1.93	0.05 ± 0.009
		ID-LP7	101	30	139	3 (3)	30-04	22-09	139.0 ± 3.51	26.50 ± 1.66	0.07 ± 0.004
Torridon	-	ID-LP6	70	30	137	11 (12)	28-04 to 21-05	06-08 to 30-08	149.0 ± 11.86	31.60 ± 7.28	0.05 ± 0.01
		ID-LP7	101	30	139	39 (51)	20-04 to 18-05	10-09 to 07-10	153.0 ± 14.68	35.80 ± 10.45	0.05 ± 0.01
Derwent	54.6105, -3.0616 54.6876, -3.2978	V7-2x	75	18-38	137	41 (150)	29-04 to 03-05	13-07 to 17-07	140.0 ± 7.33	29.30 ± 5.02	0.05 ± 0.01
Bush	55.2029, -6.5233	V7-4x	522	30-60	137	73 (80)	13-04 to 26-04	17-09 to 30-09	168.0 ± 8.59	47.34 ± 7.99	0.04 ± 0.01
Glendun	55.1215, -6.0663	V7-2x	99	20-40	137	21 (24)	16-04 to 30-04	07-24 to 07-08	142.18 ± 7.48	32.0 ± 4.55	0.05 ± 0.01
Bann	54.9841, -6.5618	V7-2x	99	20-40	137	18 (59)	07-05 to 25-05	14-08 to 01-09	161 ± 15.53	43.0 ± 13.90	0.04 ± 0.01
Agivey	54.9879, -6.6661	V7-2x	99	20-40	137	16 (41)	20-04	28-07	153 ± 9.31	37.0 ± 7.1	0.04 ± 0.01
Carey	55.2010, -6.2292	V7-2x	99	20-40	137	7 (9)	29-04 to 05-05	06-08 to 12-08	163.0 ± 4.79	43.0 ± 3.46	0.03 ± 0.003
Roe	54.9710, -6.9253	V7-2x	94	30-60	137	9 (11)	29-04	01-08	152.0 ± 3.87	36.0 ± 3.32	0.04 ± 0.004
Faughan	55.0251, -7.2359	V7-2x	94	30-60	137	38 (53)	07-05 to 15-05	09-08 to 17-08	144.0 ± 4.19	-	-
Burrishoole	53.9137, -9.5713	V8-4x	173	40-80	144	46 (50)	05-05 to 07-05	25-10 to 27-10	195.50 ± 9.63	85.40 ± 13.50	0.02 ± 0.004
		V7D-2x	100	30-90	137	9 (10)	07-05	15-08	205.0 ± 17.82	109.70 ± 28.50	0.02 ± 0.01
		V7-2x	120	40-80	137	19 (25)	05-05 to 11-05	04-09 to 08-09	148.0 ± 7.10	30.80 ± 4.04	0.05 ± 0.01

5.2.3 Acoustic receiver deployment

In total, 398 69 kHz acoustic receivers (VR2W, VR2Tx, and VR2AR models Innovasea, Canada) were deployed in this study, of which 339 were recovered (Table 5.2; Fig. 5.1; see Table A4.2 for more detailed information). Multiple acoustic receivers which were located adjacent to one another in a continuous detection line, are henceforth described as a monitoring line; a single acoustic receiver is referred to as a monitoring point (Fig. 5.1). In addition, to stationary acoustic receivers deployed for this project, a submersible glider (Slocum G3 Glider, Teledyne Marine, US) was deployed at the slope of the continental shelf, west of the Hebrides (Fig. 5.1, point Q). The glider was deployed from the MRV Celtic Explorer on April 16th, 2021 at coordinates 58.29693°N, -9.11746°W. Waypoints for the glider transect were selected based on areas of smolt congregation on the shelf edge which were identified during the SALSEA MERGE research project (Utne et al., 2021). Though fitted with a deep-water engine (up to 1000 m depth), glider dive depth was restricted to 300 m when within the shelf edge transect area to ensure that it would be within detection range of smolts moving within surface waters. The submersible glider had a VMT acoustic receiver (Innovasea, Canada) mounted which operated on an acoustic frequency of 69 kHz and thus able to detect the acoustic tags used in this study. The submersible glider covered a total of 1200 km over 57 days. The initial transects ran from WSW to ENE along the shelf edge with the glider then moving northwards off the shelf edge into deeper water. Strong off-shelf currents meant that the glider could only rejoin the shelf after moving back west towards the start of the initial transect location. The glider then completed another transect before travelling into shallow coastal waters to the west of the Isle of Harris for recovery.

At the exit of all river systems, monitoring points were deployed to detect the transition of smolts from the riverine to the early marine environment, and thus entering the study area (Table A4.2; Fig. 5.1). Monitoring lines were deployed at the exit or entrance of estuaries, sea lochs and coastal embayments (the Firth of Clyde, Loch Etive, Loch Linnhe, Loch Eireasort, Loch Laxford, Loch Torridon, Lough Foyle, Runkerry Bay and Clew Bay) as well as, in key locations in coastal waters (Fig. 5.1; Table 5.2). This includes monitoring points and lines that were included in Chapter 4 (Fig. 4.1).

Table 5.2. Summary of receiver deployment, including the mid point latitude and longitude for each monitoring line or point; the number of receivers deployed and recovered, approximate distance (km) covered by monitoring line and mean distance (km) between receivers in each monitoring line. A – refers to this information being unavailable from project partners.

ID	Description of location	Latitude	Longitude	Number of receivers recovered (number of receivers deployed)	Approximate distance (km) covered by monitoring line	Mean distance (km) between receivers in monitoring line
A	Larne to Portpartrick	55.931	-5.477	20 (22)	23	1 km
B	Waterfoot, NI	55.064	-6.041	1 (1)	-	-
C	Isle of Cumbrae	55.725	-5.000	6 (8)	5.5	0.6
D	Isle of Arran	55.694	-5.437	6 (8)	6	0.65
E	Malinhead to Isle of Islay	55.494	-6.886	99 (108)	63	0.6
F	Isle of Jura to mainland Scotland	55.883	-6.108	7 (11)	7.5	0.7
G	Firth of Lorne	56.383	-5.620	10 (12)	5	0.7
H	Sound of Mull	56.512	-5.767	7 (8)	2.5	0.7
I	Southern Hebridean Islands	56.989	-7.371	18 (26)	15	0.7
J	Isle of South Uist to mainland Scotland	57.269	-6.863	59 (71)	40	0.7
K	Northern Hebridean Islands	57.741	-7.204	18 (18)	13	0.7
L	Isle of Lewis	58.249	-6.047	8 (12)	12	1
M	Sutherland	58.506	-5.248	17 (18)	14.5	1
N	North Atlantic Ocean (south of Hebridean Islands)	56.604	-7.855	1 (1)	-	-
O	North Atlantic Ocean (west of Hebridean Islands)	58.092	-8.913	1 (1)	-	-
P	North Atlantic (Continental Shelf)	58.0918	-8.913433	1 (1)	-	-
Q	North Atlantic (Continental Shelf – submersible glider)	58.584	-8.614	1 (1)	-	-

The continuous distance covered by marine monitoring lines ranged from 5 to 63 km and the spacing between receivers ranged from 0.6 to 1 km (Table 5.2). The detectability of acoustic tags varies depending on the type of water (i.e. fresh water versus saltwater) and local environment (for example, noise reduces the detection range of Tags (Reubens et al., 2019). Previous studies conducted in coastal marine waters, similar to those in this study, demonstrated a detection range from 190 to 350 m (Main, 2021*;* Newton et al., 2021; Thambithurai et al., 2022).

5.2.4 Statistical analysis

The objective of this study was to examine large scale fish movements beyond the immediate coastal environment. Therefore, for this analysis post-smolts migrating from tributaries or multiple release sites in the same river system were combined into one group. This included smolts from the Rivers Nith (mainstem) and Crawick which were combined as River Nith origin fish. Similarly, for the River Lochy (Rivers Lundy and Loy fish were combined), River Bann (Rivers Agivey and River Bann fish were combined). Also combined were the multiple release sites on the Rivers Endrick and Derwent.

For river systems with estuaries and costal embayments, only post-smolts that were detected on a receiver at the mouth of each river or on a receiver in the coastal marine environment were included in the analysis. For river systems with sea lochs, only post-smolts which were detected on the final monitoring line at the exit of the sea loch or on a receiver in the coastal marine environment were included in the analysis. Thus, these post-smolts were deemed to have entered the study area (Table 5.1). To remove possible false detections caused by tag collisions or environmental noise, the raw data was filtered using the *false_detections* function in the R package *Glatos* (Holbrook et al., 2018). Summary statistics for tagged smolts at each tagging site (Table 5.1), were calculated and included mean fork length (mm), mean weight (g) and mean tag burden. Tag burden was defined as the ratio between the weight of the acoustic tag in air (g) and fish weight (g).

5.2.4.1 Migration pathways

Migratory pathways of Atlantic salmon post-smolts in this study were reconstructed based on the movements of post-smolts between combinations of monitoring points and lines. These movements were determined for each post-smolt using the *RunResidence* extraction function in the *VTrack* package in R (Campbell, 2013). Migratory pathways were then overlayed on a map of the Irish Sea and West Coast of Scotland using the QGIS v.3.14 function Points to Paths (https://qgis.org/en/site/). Reconstructed pathways represent the minimum (straight line) distance travelled by a post-smolt between successive detection points. These pathways are a simplified illustration of the broad migratory routes of salmon post-smolts and do not represent the true pathway taken. In instances where post-smolts passed an array undetected but were detected on a subsequent marine array, the receiver that detected the largest number of fish was used as a surrogate. Lastly, the migratory pathways were grouped into eight monitoring regions which consist of river systems which drain into the same coastal area. Regions 1 - 9 consisted of: Region 1, the Solway Firth (Rivers Derwent, Nith, Bladnoch); Region 2, the Clyde sea (Rivers Endrick and Gryffe); Region 3, Loch Linnhe (Rivers Etive, Orchy and Lochy); Region 4, Loch Torridon (Rivers Balgy and Torridon); Region 5, Loch Eireasort (River Laxay); Region 6, Loch Laxford (Rivers Laxford and Badnabay); Region 7, Bush coastal region (Rivers Bann, Bush, Carey and Glendun); Region 8, Lough Foyle (Rivers Roe and Faughan); Region 9, Clew Bay (River Burrishole) (Fig. 5.1).

5.2.4.2. Migration success

Minimum migration success was defined as the percentage of post-smolts detected on a marine array from the total number which entered the study area (i.e. detected leaving each river system, sea loch or coastal embayment) after taking into account individuals that were detected on subsequent arrays. This was calculated for each monitoring line included in the study.

Loss rates were only calculated for post-smolts migrating through estuaries, coastal embayments (Lough Foyle, Runkerry Bay, Clyde Estuary and Clew Bay) and the Irish Sea (monitoring line E). The loss rate of post-smolts through estuaries, coastal embayments and the Irish sea were calculated as the percentage of post-smolts detected at the final riverine receiver that were later detected on a following monitoring line, divided by the minimum (straight line) distance between the two arrays.

5.2.4.3 Migration duration/speed

The mean time (days) taken to travel between monitoring lines/points was calculated as the duration between the final detection at one monitoring line/point to the first detection at a subsequent monitoring line/point.

The mean speed of post-smolts migrating to monitoring points/lines was calculated both as body lengths per second ($L_F.s^{-1}$ (L_F (fork length)) and kilometers per day ($km.day^{-1}$). The distance used for these calculations was determined as the minimum (straight line) distance between the final river/tidal coastal limit receiver and the monitoring line/point of interest.

5.3 Results

In total, 1150 (64% of the total number tagged) post-smolts successfully migrated out of their natal rivers and were thus included in this study (Table 5.1). For these wild and ranched post-smolts the median (± SD) fork length was 144.0 ±17.10 mm and the median weight 29.30 ± 16.27 g. The mean tag burden was 0.05 ± 0.01 (Table 5.1).

In this study, 81.2% (*n* = 680) of salmon post-smolts (*n* = 837) were detected exiting estuaries and coastal embayments to reach coastal waters (Table 5.3). Migration success through coastal embayments and estuaries varied from 56.8% of post-smolts successfully migrating out of the

Lough Foyle to 87.67% of post-smolts successfully migrating out of Runkerry Bay (Table 5.3).

Table 5.3 Description of estuaries and coastal embayments included in this study, as well as mean distance (km) between the riverine receiver at river mouth to the exit, mean migration success (%), loss rate (%.km^{-1}), rate of movement (ROM) (km.day^{-1}) and the duration (days) spent in each estuary/coastal embayment. For detailed information see Table A4.3.

Tidal coastal inlet	Description of inlet	Mean distance (km)	Mean Migration success % (no.)	Mean Loss Rate (%.km^{-1})	Mean ROM (km.day^{-1}) ± SD	Mean Duration (days) ± SD
Clyde Estuary	Extended estuary giving way to a fjord	52.55	82.52 (118)	0.38	13.66 ± 5.66	5.04 ± 2.87
Runkerry Bay	Open tidal embayment	1.81	87.67 (64)	6.81	35.22 ± 30.75	0.19 ± 0.36
Lough Foyle	Estuary	24.0	56.82 (44)	2.05	11.95 ± 5.64	2.65 ± 1.96
Clew Bay	Sheltered tidal embayment	20.20	42.31 (22)	2.87	29.93 ± 16.71	1.33 ± 1.88

In coastal waters, 34.7% (*n* = 416) of post-smolts that left their natal river (*n* = 1200) were detected on marine arrays (Table 5.4). A total of 16.1% (*n* = 131) of post-smolts from Regions 1, 2, 7 and 8 (*n* = 813) were detected on monitoring line E, and 24.7% (*n* = 79) of Region 3 post-smolts (*n* = 320) were detected on monitoring lines G and H. A smaller percentage (8.1%) of Regions 4 and 5 post-smolts (*n* = 161) were detected on monitoring line L. Finally, 19.0% (*n* = 47) of Region 4,5,6 post-smolts (*n* = 247) were detected leaving monitoring line M (Table 5.4). As monitoring lines were in nearshore marine waters, which could result in varying detection efficiency throughout the study, and monitoring lines here did not always cover the entire channel, therefore, this was a minimum estimate of post-smolts migration success through these areas.

Table 5.4. Summary statistics for each monitoring line and point, including the number of post-smolts which passed each monitoring line / point (Number of individuals used to calculate ROM); regions of origin of those post-smolts; range of dates post-smolts were detected and the mean Rate of Movement of post-smolts as they migrate to the monitoring line / point from the river mouth or tidal coastal inlet exit. River Endrick and Gryffe smolts were excluded from Monitoring Line A calculation as this served as their exit from their natal estuary.

Monitoring Line / Point	No. passed array (No. used to calculated ROM)	Regions of origin	Date range detected	Mean RoM (LF s^{-1}) ± SD (range)	Mean RoM ($km.day^{-1}$) ± SD (range)
A	57 (38)	1 & 2	11-05 to 06-06	1.01 ± 0.47 (0.18 - 2.01)	12.57 ± 5.87 (2.38 - 25.34)
B	1 (1)	2	15-05	0.40	6.77
C	1 (1)	2	11-06	0.72	9.10
D	7 (6)	1 & 2	28-04 to 15-07	0.43 ± 0.21 (0.16-0.70)	0.06 ± 0.03 (0.02 to 1.0)
E	131 (112)	1, 2, 3, 7 & 8	21-04 to 20-06	1.61 ± 0.90 (0.33 - 4.45)	21.68 ± 12.65 (3.87 - 59.81)
G	79 (72)	3	23-04 to 21-07	1.47 ± 0.68 (0.38 - 3.36)	17.47 ± 7.89 (4.29 - 38.05)
H	71 (62)	3	21-04 to 20-07	1.86 ± 0.83 (0.56 - 4.18)	22.05 ± 9.64 (6.43-46.96)
I	3 (1)	3 & 7	11-05 to 05-06	1.0	11.62
J	4 (3)	3	02-05 to 27-05	1.20 ± 0.47 (0.73 - 1.68)	14.40 ± 4.99 (9.61- 19.56)
L	13 (7)	4 & 5	22-04 to 17-05	1.41 ± 0.38 (0.63 - 1.72)	16.93 ± 5.32 (7.20 - 21.19)
M	47 (40)	4, 5 & 6	01-05 to 17-05	1.93 ± 1.05 (0.46 - 4.44)	23.89 ± 13.06 (6.75 - 53.38)
N	2 (1)	3 & 9	27-05	1.11	13.79
O	2 (2)	9	08-06	3.03 ± 4.04 (0.18 – 5.89)	64.31 ± 85.36 (3.95 – 124.67)
P	2 (1)	1 & 9	19-05 to 08-06	1.93	25.87
Q	4 (3)	2, 3, 7 & 9	23-05 to 06-04	1.56	20.92
Clew Bay 1	52 (49)	9	06-05 to 05-06	24.17 ± 23.97 (0.16 – 72.59)	2.58 ± 6.05 (0.07 – 30.27)
Clew Bay 2	22 (19)	9	09-05 to 22-05	29.93 ± 16.71 (2.35 – 55.51)	1.33 ± 1.88 (0.36-8.58)

5.3.1 Migration pathways

Atlantic salmon post-smolts migrated in multiple and complex directions through coastal waters. These migration pathways are summarised below for each region included in the study (Fig. 5.2; Fig. A4.1):

5.3.1.1 Region 1: Rivers Derwent, Nith and Bladnoch (Fig. A4.1, a)

Salmon post-smolts (*n* = 47) from all four rivers in this region were detected on two of the most southerly monitoring lines in this study (monitoring lines A and E). Post-smolts from Region 1 were detected on monitoring line A between the 11th May and 6th June and detected on monitoring line E between 13th May and 20th June. Interestingly, four post-smolts from the River Derwent, England were detected within the Firth of Clyde on monitoring lines C and D between the 6th June and 13th July. Of these four post-smolts, one was subsequently detected leaving the Firth of Clyde and detected on monitoring line E. Finally, one post-smolt from the River Derwent was detected to the west of the Hebrides at monitoring point P on the 8th June.

5.3.1.2 Region 2: Rivers Endrick and Gryffe (Fig. A4.1, b)

Salmon post-smolts from the rivers Endrick and Gryffe exited the Clyde estuary and Firth of Clyde utilising multiple routes. Post-smolts migrated both east (*n* = 5) and west (n = 113) around the Isle of Cumbrae (monitoring line C), as well as east of the island of Arran (*n* = 39; assumed to travel east around the island if not detected on monitoring line D) and west (*n* = 4) around Arran (monitoring line D). Once post-smolts exited the Firth of Clyde, 36 were detected on monitoring line E between 4th May and 18th June. Counterintuitively, a small number (*n* = 10) of post-smolts migrated south and were detected on monitoring line A, between 6th May and 4th June. The majority of these post-smolts were not detected again, however, three of these post-smolts did subsequently migrate north to be detected on monitoring line E. One post-smolt from the River Gryffe was detected approximately 548 km from its natal river at the continental shelf by a Slocum glider (monitoring point Q) on the 23rd May. Finally, one post-smolt from the River Gryffe exited the Firth of Clyde and migrated west to be detected in a coastal embayment (monitoring point B), in Northern Ireland on 15th May. This post-smolt was then detected on monitoring line A on 4th June before migrating north again to be detected at monitoring point E on 6th June.

5.3.1.3 Region 3: Rivers Loy, Lundy, Etive and Orchy (Fig. A4.1, c)

Salmon post-smolts from Region 3 could exit Loch Linnhe and Loch Etive and migrate either through the Firth of Lorne (monitoring line G) or the Sound of Mull (monitoring line H). An approximately equal number of post-smolts from this region were detected using these two routes and were detected in the Firth of Lorne (*n* = 79) between 23rd April and 21st July and in the Sound of Mull (*n* = 71) between 21st April and 20th July. Four post-smolts detected on monitoring line J between 2nd May and 27th May thus appearing to pass through the Minch; two were detected in the waters between the southern Hebridean islands (monitoring line I) between 11th May and 13th May; one post-smolt migrated south to be detected at monitoring line E on the 15th May and one post-smolt was detected at monitoring point N on the 27th May. Finally, one post-smolt from the River Orchy was detected at monitoring point Q around 100 km to the west of the Isle of Lewis and approximately 362 km from its natal river on the 29th May.

5.3.1.4 Region 4: Rivers Balgy and Torridon (Fig. A4.1, d)

Salmon post-smolts from Region 4 exited Loch Torridon and were detected on two monitoring lines. Post-smolts from the Rivery Balgy (*n* = 1) were detected on monitoring line L off the east coast of the Isle of Lewis on 1st May. Furthermore, post-smolts from the Rivery Balgy and Torridon (*n* = 6) were detected off the west coast of the northern tip of mainland Scotland between 6th May and 13th May.

5.3.1.5 Region 5: River Laxay (Fig. A4.1, e)

Salmon post-smolts from region 5 exited Loch Eireasort and were detected on two monitoring lines. Post-smolts were detected on monitoring line L off the east coast of the Isle of Lewis ($n = 12$) between 22nd April and 17th May and on monitoring line M off the west coast of the northern tip of mainland Scotland ($n = 13$) between 2nd May and 17th May.

5.3.1.6 Region 6: Rivers Laxford and Badnabay (Fig. A4.1, f)

Post-smolts from Region 6 were detected on monitoring line M of the north west coast of mainland Scotland ($n = 29$) between 1st May and 17th May.

5.3.1.7 Region 7: Rivers Bann, Agivey, Bush, Carey and Glendun (Fig. A4.1,g)

Post-smolts from Region 7 were detected on monitoring line E between Ireland and Scotland ($n = 68$) between 2nd May and 29th May. One post-smolt from the River Glendun was detected between the southern Hebridean Islands (monitoring line I) on 5th June. Two post-smolts (rivers Glendun and Bush) migrated east and were detected in the Firth of Lorne (monitoring line G) on the 28th April and 26th May. One post-smolt from the River Glendun was detected at monitoring point O on the 19th May. Finally, one post-smolt from the River Bann was detected approximately 402 km from its natal river by the Slocum glider at monitoring point Q on the 31st May.

5.3.1.8 Region 8: Rivers Faughan and Roe (Fig. A4.1,h)

Salmon post-smolts from Region 8 ($n = 23$) were detected on monitoring line E between 6th May and 1st June.

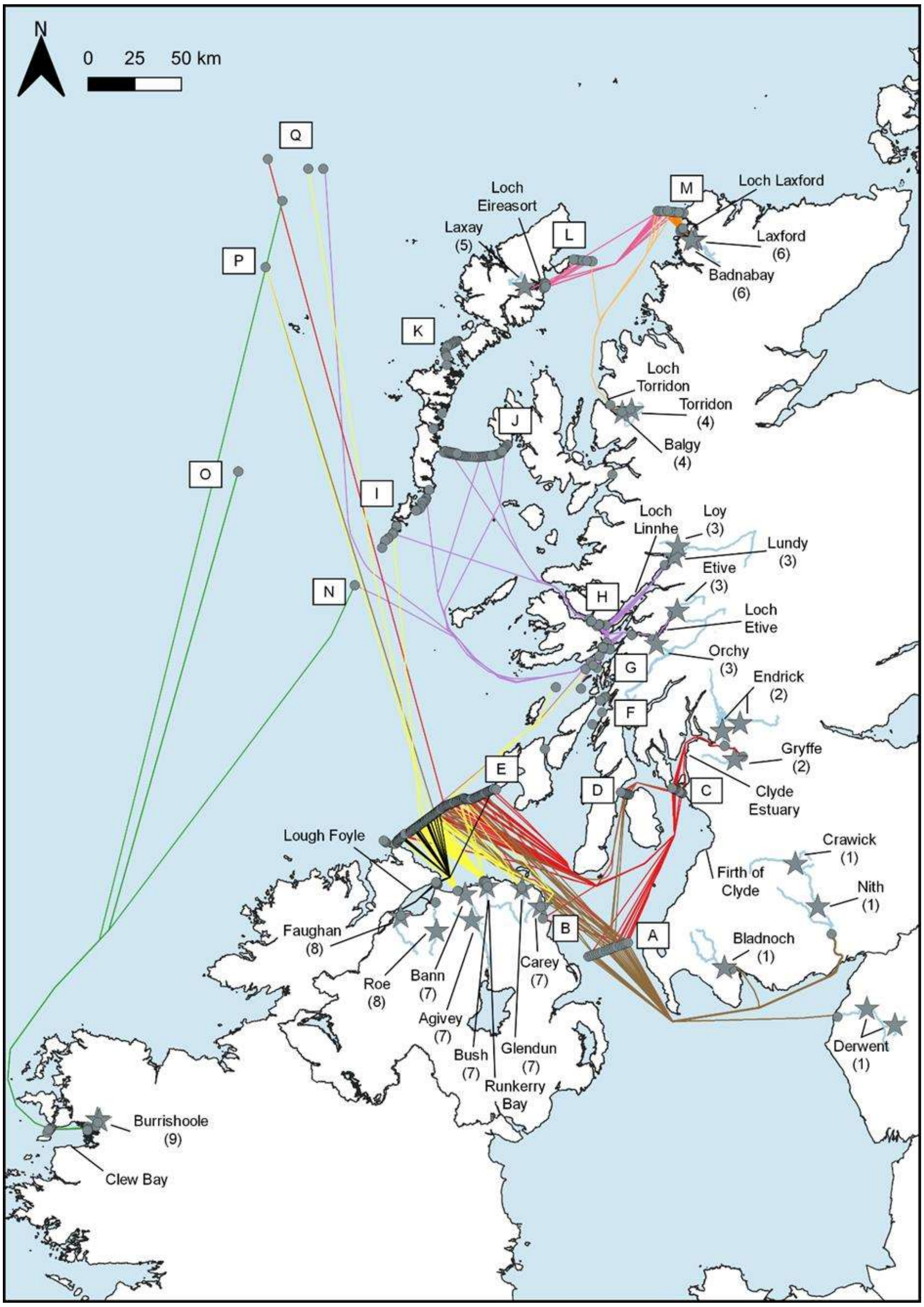


Figure 5.2. Map illustrating the estimated migratory pathways of Atlantic salmon post-smolts as they migrate from their natal rivers (*n* = 23) in Scotland, England, Northern Ireland and

Ireland, from detections on monitoring points/lines A-Q, (see Fig. 5.1 and Table 5.2 for more detail). The pathways of post-smolts from each region are represented by a unique color and each line represents an individual post-smolts pathway. The pathways illustrated are simplified representations and do not represent the true migratory pathways post-smolts undertook.

5.3.1.9 Region 9: River Burrishoole (Fig. A4.1,i)

Post-smolts from Region 9 were detected on several marine monitoring points which include monitoring point N (*n* = 1), O (*n* = 2) and Q (*n* = 1) to the south and west of the Hebrides, on the 24th May, 5th June and 4th June respectively. All post-smolts detected on marine monitoring points were of ranched origin.

5.3.2 Migration speed

The time taken to reach monitoring lines varied between rivers and regions. For example, it took post-post-smolts from the River Lochy an average of 12.74 days to migrate 203 km to monitoring line J, whereas it took post-smolts from the River Etive 14.16 days to migrate 172 km to monitoring line J. Furthermore, post-smolts from the River Glendun took on average 2.52 days and post-smolts from the River Bann took on average 1.31 days to migrate to monitoring line E despite covering similar distances (47.1 and 45.6 km respectively).

In this study, the furthest tracked post-smolt covered 564 km and originated from the River Burrishoole (Table A4.3). This post-smolt took approximately 26.09 days to migrate from the exit of Clew Bay (Clew Bay 2; ~541 km) to monitoring point Q (Table A4.3).

5.4 Discussion

Prior to this synthesis, our understanding of Atlantic salmon post-smolt migration through marine waters in the UK and Ireland was limited to data obtained through research directed surface trawling and particle tracking studies (NASCO, 2011; Barry et al., 2020; Ounsley et al., 2020; Gilbey et al., 2021). There have been very few acoustic telemetry studies conducted in this region, which have focussed on post-smolt migration through the Irish Sea or the seas west of mainland Scotland. Those that have been conducted have comprised relatively small sample sizes and few rivers (Barry et al., 2020, Green et al., 2022). Using data from 17 monitoring lines/ points deployed by five related projects (SeaMonitor, the West Coast Tracking project, COMPASS, MEFS MPA project and SAMOSAS project) we were able to detect Atlantic salmon post-smolts emigrating from a total of 23 rivers located in four countries (Scotland, England, Northern Ireland and Ireland) for a maximum duration and estimated minimum migration distance of approximately 100 days and 575 km. These data provide an unprecedented insight into the use of European coastal zones by sea migrating salmon post-smolts from across a broad geographic region (approximately 107,620 km^2).

5.4.1 Migration pathways

Empirical data collected in this study has enabled, for the first time, salmon post-smolt migration pathways in nearshore coastal waters to the west of the British Isles to be determined. This study has demonstrated that post-smolts take multiple migratory routes through marine waters from the mouth of their natal rivers towards the slope current at the continental shelf, with variation seen both within and between rivers. Post-smolts from Regions 1, 2, 7, and 8 tended to migrate in a northerly direction, as they were detected leaving the Irish Sea on monitoring line E (Fig. 5.2). However, there were a few exceptions with ten post-smolts from Region 2 migrating in a southerly direction (detected on monitoring line A), prior to three migrating back to monitoring line E (Fig 5.2). The remaining seven individuals were not detected, and we don't know which route they eventually took. These post-smolts may have been diverted by the southerly coastal flows generated by the large fresh water input from the Clyde sea that extends towards the Mull of Galloway (Kasai et al., 1999; Young et al., 2000). Once post-smolts left the Irish Sea (monitoring line E), the majority were not detected again, except for six post-smolts from Regions 1, 2 and 7 which were detected on monitoring lines I and G, and monitoring points O, P and Q. As not all migratory routes were covered by the monitoring lines and points included in this study and no fish from Regions 1, 2, 7 & 8 were detected on monitoring line J, this suggests once post-smolts left the Irish Sea they may have migrated west in the waters between the Hebridean islands and the island of Ireland and did not migrate through the Minch waters (between mainland Scotland and the Outer Hebrides). This possibility is further supported by data from salmon post-smolts from Region 3 whereby, only six out of the 150 salmon post-smolts which left the waters around the Island of Mull were detected migrating through the Minch waters and between the southern islands of the Outer Hebrides. Therefore, this further supports the possibility that post-smolts from regions sampled in this study are likely to have migrated west in the waters between the Hebridean Islands and the Island of Ireland. Post-smolts from the River Burrishoole (Region 9) were detected migrating northwards towards the continental shelf as they were detected on monitoring points O, P and Q but not monitoring line J. This suggests that these fish migrated northwards to the west of the Hebrides. Finally, detections of post-smolts from Regions 4, 5 and 6 on monitoring lines L and M, but not J, indicated a northerly migration route.

There appears to be within-river variation in the migratory routes taken by individual salmon post-smolts. For example, post-smolts from the rivers Derwent and Orchy adopted several different migratory pathways. River Derwent post-smolts tended to migrate north (detected on monitoring lines A and E), but surprisingly four of the post-smolts migrated into the Clyde estuary and were detected on monitoring lines C and D. Post-smolts from the River Orchy migrated in several directions, including through the Minch waters (monitoring line J), between the southern islands of the Outer Hebrides (monitoring line I), south towards Northern Ireland (monitoring line E) and west towards the continental shelf (monitoring point Q). The study presented here does not allow us to determine if this spatial variation is also matched with significant temporal variation in these migratory pathways. Future studies are needed to determine the scope and scale of any temporal variation in pathway use.

As previously mentioned, trawling studies have shown post-smolts from the United Kingdom and Ireland migrate towards the continental shelf, west of the Hebridean islands once they leave their natal river (Gibley et al., 2021). A particle tracking study by Ounsley et al. 2020, indicated that post-smolts emanating from rivers on the west coast of Scotland, would need to undertake active swimming behaviour to reach the North Atlantic Current, as opposed to simply following surface currents. It was also shown that populations across Scotland would need to adopt different, locally adapted migratory strategies to make successful migrations to reach the Norwegian Sea (Ounsley et al., 2020). The results from this study would suggest that different Regions do indeed adopt different migration pathways (Fig. 5.2). However, we have also shown that there is much within-population variation, with individuals from the same river adopting differing migratory pathways.

5.4.2 Migration Success

In this study, mean loss rates through coastal tidal inlets ranged between 0.38 to 2.05 %. km^{-1} through estuaries and 2.87 to 6.81 %.km^{-1} through coastal embayments. It is difficult to directly compare loss rates amongst tidal coastal inlets in this study as previous research has shown that loss rates are not solely dependent on the geography and/or physical properties of a system, and instead are most likely the result of an interaction between these two properties and natural and anthropogenic stressors (Dempson et al., 2011; Thorstad et al., 2012b; Chaput et al., 2019). For example, in this study we found that the loss rate was highest for River Bush post-smolts (the River Bush has no estuary and post-smolts transition directly from fresh water into full strength sea water) as they migrate approximately 2 km through the relatively open Runkerry Bay (6.12 %.km^{-1}; Table A4.3) (Flávio et al., 2020). In comparison, loss rates were the lowest for River Gryffe post-smolts (0.24 %.km^{-1}; Table A4.3) which had to migrate approximately 30 km through a narrow sea loch characterized by multiple shallow sills and gradually increasing salinity (Inall et al., 2004). In contrast to our results, Chaput et al. (2019) compared the survival of Atlantic salmon post-smolts migrating through two distinctly different estuaries draining into the Gulf of St. Lawrence, Canada over a period of 14 years and reported that loss rates for smolts migrating from river systems draining into the wide open Chaleur Bay were higher compared with the more enclosed Mirimachi Bay (Chaput et al., 2019).

In agreement with the results from other studies and Chapter 4, we show that the loss rates through coastal marine waters are lower than in tidal coastal inlets (Chaput et al., 2019; Kocik et al., 2009; Thorstad et al., 2012b). In this study, we were able to assess the loss rate of post-smolts through the Irish Sea (monitoring line E) emanating from Regions 1, 2, 7 & 8 (Table A4.3). The loss rate of post-smolts migrating through the Irish Sea ranged from 0.14 to 0.95 $\%.km^{-1}$. Focusing only on rivers in these regions which have a coastal embayments or estuaries, the estimated loss rate through the Irish Sea was lower than that of coastal embayments or estuaries, with loss rates ranging from 0.14 $\%.km^{-1}$ for River Faughan post-smolts (loss rate in Lough Foyle was 1.85 $\%.km^{-1}$) to 0.86 $\%.km^{-1}$ for River Bush post-smolts (loss rate through Runkerry Bay was 6.81 $\%.km^{-1}$) (Table S3). However, while these estimates of loss may seem low, if the loss rates are multiplied by the total distance travelled through the Irish Sea (range: 37.8 – 278 km) this indicates that substantial absolute loss (range 5 – 93%) may still occur through the Irish Sea (Table S3). However, it important to note that the nominal tag delay varied substantially between river systems in this study ranging from 30 – 60 up to 40-80 seconds. The longer nominal tag delays may have prevented us from detecting smolts that were moving quickly through coastal embayment/estuaries and the Irish sea. Lastly, in this study we can't rule out whether stress induced by the tagging procedure or expulsion of tags influenced loss estimates (Cooke et al., 2011; Klinard & Matley, 2020).

5.4.3 Speed and duration of migration

Similar to other studies, we found that salmon post-smolts spent differing periods of time migrating through estuaries and coastal embayments, with the difference primarily being driven by the variation in basin shapes (Dempson et al., 2011; Thorstad et al., 2012b; Chaput et al., 2019). Post-smolts took on average 0.19 days to migrate through Runkerry Bay, whereas post-smolts took on average 5.18 days to migrate through the Clyde estuary (Table 5.3). This variation in the time taken to migrate through coastal waters was also evident, which primarily reflects the different distances travelled by post-smolts. However, when examining the time taken for post-smolts to migrate through the same waterbody, i.e. the Irish Sea between monitoring lines A and E, differences can be seen. For example, post-smolts from the rivers Bladnoch and Nith took on average 2.7 and 3.6 days, respectively, to travel through the same area of the Irish Sea (Table A4.3).

In this study the mean speed of post-smolts migrating through estuaries and coastal embayments ranged from 0.06 ± 0.04 LF.s^{-1} for River Roe post-smolts migrating through Lough Foyle to 2.43 ± 2.14 LF.s^{-1} for River Bush post-smolts migrating through Runkerry Bay (Table A4.3). The mean speed of post-smolts migrating through coastal waters was much quicker than through estuaries and coastal embayments and ranged from 4.32 to 53.8 km.day^{-1} (Table A4.3).

5.4.4 Management implications

The migration pathways established in this study, will allow us to make linkages between these migration pathways and putative pressures. Currently, the main threats to Atlantic salmon in the early marine environment are thought to include predation, by-catch in fisheries, aquaculture and offshore renewables (Scottish Government, 2022). For example, loss rates of Atlantic salmon during their early marine migration may be attributed to the inability of post-smolts to detect and avoid predators that were not present in their riverine/estuarine environment (Leduc et al., 2007). Atlantic salmon adults and post-smolts may become by-catch in pelagic trawl fisheries mainly targeting mackerel, *Scomber scombrus* and herring, *Clupea harengus* (ICES, 2004, 2020). Some of the pathways identified in this study could overlap with these seasonal pelagic fisheries. One of the potential threats to post-smolts is the aquaculture industry with a high prevalence of the parasitic sea louse *Lepeophtheirus salmonis* in Scottish waters being associated with Atlantic salmon farms (Murray & Moriarty, 2021). Particle tracking studies conducted along the west coast of Scotland have predicted that sea lice drift northwards from farms with the Scottish Coastal Current (Scanlon et al., 2021). The results from this study suggest that the pathways of sea lice may overlap with the trajectories of post-smolts migrating from some rivers and regions in the United Kingdom (Scanlon et al., 2021). These are just a few of the potential pressures which could intersect the migration pathways of Atlantic salmon post-smolts.

5.4.5 Collaborations

This study highlights the importance of engaging in cross-organisation and jurisdictional collaboration to better understand the early marine migration of Atlantic salmon post- smolts from rivers in the United Kingdom and Ireland. This large-scale acoustic telemetry study would not have been possible without extensive collaboration between organisations and projects due to the cost of running a telemetry project over a wide geographic area, and the resources and staff time needed. It is estimated that the combined cost of the projects included in this study was in the region of £2.74 million and required a team of approximately 70 individuals to deliver this study.

5.4.6 Conclusion

In conclusion, this study has provided valuable empirical information concerning the migratory pathways of Atlantic salmon post-smolts migrating from four separate countries (Scotland, England, Northern Ireland and the Ireland). A future development might include combining the data collected in this study with particle tracking models to further improve predictions of the migratory routes of salmon post-smolts. Consistent with previous literature this study has confirmed that the early marine environment (particularly estuarine) migration is high risk for Atlantic salmon post-smolts (Thorstad et al., 2012b). However, we highlight that although losses within early marine migration waters are lower than in estuaries and coastal embayments the loss is still significant. Post-smolts appear to take multiple migratory pathways in coastal marine waters, however, we have shown that although a few (*n*=4) smolts were detecting migrating through the Minch waters, the majority of salmon smolts would appear to be migrating west in the waters between the southern tip of the Outer Hebrides and the Island of Ireland. The migratory pathways identified in this study do overlap with known pressures, such as climate change, offshore renewables, aquaculture and trawling by-catch in commercial fisheries (Foresth et al., 2017; Gilson et al., 2022), however, the risk is likely to vary between rivers and regions. Therefore, the results of this study highlight the importance of prioritising research directed at better understanding the potential impact of natural and anthropogenic stressors on post-smolts from the United Kingdom and Ireland.

6. General Discussion

Prior to the 1980's adult salmon return abundances followed cyclic patterns and unusual declines could most often be attributed to specific natural and anthropogenic disturbances such as riverine pollution (e.g. industrial and agricultural runoff), blockage of access to habitat (e.g. formation of canals, development of hydroelectric dams) or over-fishing (Dadswell et al., 2022; Lenders et al., 2016; van Dijk et al., 1995).

Over the last few decades management efforts in the fresh water environment has largely focussed on the removal of migratory barriers, improvements in water quality and reduced exploitation (Forseth et al., 2013, 2017; Thorstad et al., 2012b, 2021). For example, in many river systems, weirs and dams have now been deconstructed and/or fish ladders added to aid in access to upstream spawning habitat (Fjeldstad et al., 2012; Holbrook et al., 2011). In addition, pollution in many river systems draining into the North Atlantic has now been reduced due to increased regulation of both industrial and agricultural runoff (Dodd & Adams, 2014; Evans et al., 2001; Mawle & Milner, 2003). Lastly, in the North Atlantic non-recreational catches of Atlantic salmon in the riverine environment has largely been limited to recreational catch and release if populations fall below their conservation limits (ICES, 2021; Kennedy et al., 2019; Marine Scotland, 2022b).

In comparison, less emphasis has been put on managing Atlantic salmon in the marine environment. Management efforts in this region have largely focussed on reducing inshore and offshore fishery landings (Thorstad et al., 2012b, 2021). For example, since 2012 and 2014, all retention of Atlantic salmon in the Northern Irish Loughs Agency and DEARA regions have ceased, respectively (JNCC, 2018). In addition, the mixed stock drift net fishery off the west coast of Ireland has been closed since 2007 (Niven & McCauley, 2016). Furthermore, since 2015, all coastal fisheries for Atlantic salmon in Scotland are banned (Marine Scotland, 2019). Lastly, the two main offshore fisheries for Atlantic salmon from populations in the North Atlantic include Greenland, and Faroese fishery; during 2018 – 2020 the Government of

Greenland set a 30 t quota for Atlantic salmon landings, since 1991 commercial fishing for Atlantic salmon off the coast of the Faroes has been banned (Jacobsen et al., 2012; Niven & McCauley, 2016; West Greenland Commission, 2018).

However, despite these management efforts, adult returns continue to decline, with many populations in the North Atlantic now extirpated (Chaput, 2012; Dadswell et al., 2022; Lehnert et al., 2019; Olmos et al., 2019). For example, over the last four decades the total estimated number of maturing 1SW and MSW Atlantic salmon returning to their natal rivers in the North East Atlantic (N-EAC) has declined by approximately 68 and 22%, respectively (ICES, 2021; Figure 1.2). This suggests that conservation efforts aimed at significantly improving fresh water habitat and reducing fisheries landings is not enough to reverse population level decline (Thorstad et al., 2021). Therefore, due to the large emphasis on improving the fresh water environment, it is speculated that declines in Atlantic salmon populations over the last few decades is associated with lesser-known stressors encountered at sea, particularly during their early marine migration (Chaput, 2012; Dadswell et al., 2022; Thorstad et al., 2021).

Today, in the North East Atlantic, the two main threats to Atlantic salmon are thought to include the rapid expansion of the salmon farm industry, and climate change (Forseth et al., 2017; Thorstad et al., 2021). Since the early 1990's the salmon aquaculture industry has experienced rapid growth in Europe, with Norway and Scotland being the first and third top producers of farmed salmon in the world, respectively (Gargan et al., 2012; McIntosh et al., 2022). The two main concerns with the rapid expansion of salmon farms are the proliferation of pathogens that can be transmitted from farmed to wild salmon and genetic introgression from farmed escapees (Forseth et al., 2013). Firstly, increased density of salmon lice (*Lepeophtheirus salmonis*, Krøyer, 1837) can be found in coastal regions with aquaculture development, which in high enough densities can reduce salmonid populations (Thorstad et al., 2015; Vollset et al., 2016). For example, Gargan et al. (2012) compared the adult return rates of ranched Atlantic salmon smolts treated with and without emamectin (preventative sea lice treatment) and noted that the likelihood of treated post-smolts returning to their natal rivers as adults was 1.8 times higher. Furthermore, another pathogen that can easily proliferate at aquaculture sites and spread to the wild population are viral diseases (Johansen et al., 2011a). The most common viruses found at aquaculture sites (e.g infectious salmon anemia virus (ISAv)) can harm organs of farmed salmonids and lead to mortality, however, their effects on the wild population are currently unknown and requires further investigation (Barker et al., 2019; Johansen et al., 2011a; Vollset et al., 2021).

Secondly, there have been numerous reports of genetic introgression of escaped farmed Atlantic salmon into wild populations in the North Atlantic (Bourret et al., 2011; Diserud et al., 2019; Karlsson et al., 2016; Vollset et al., 2021). Mating with farmed fish may lead to population level declines due to a decreased likelihood of local adaptation as well as evolving genes that have fitness benefits, such as an increased ability to avoid predators or an ability to adapt to warming ocean temperatures (Bourret, et al., 2011; McGinnity et al., 2009; Thorstad et al., 2021; Vollset et al., 2021).

Over the last decade the North Atlantic has experienced rapid increases in temperature due to greenhouse gas emissions (Chemke et al., 2020). The age of smoltification has been shown to be negatively correlated with water temperature and studies have reported that in response to warming river temperatures smolts are transitioning into the North Atlantic approximately 2.5 days earlier per decade (Otero et al., 2014; Thorstad et al., 2021). The transition of post-smolts into the marine environment earlier in the spring may lead to a temporal and spatial mismatch of adults and their prey in northern feeding grounds (Kennedy & Crozier, 2010; McCormick, 1998; Otero et al., 2014; Thorstad et al., 2021).

6.1 Furthering our understanding

Prior to understanding the risk of natural and anthropogenic stressors on Atlantic salmon populations, we must first obtain baseline information concerning the migratory routes and the environmental drivers of migration. This thesis fills in knowledge gaps on the life history of Atlantic salmon post-smolts from multiple rivers in the British Isles as they transition from the fresh water to the early marine environment and highlight the importance of transboundary collaboration to improve species management. This is focussed on the smolt and post-smolt stages of the Atlantic salmon life cycle as there is limited knowledge around the strategies smolts may use to navigate through fresh water standing bodies of water as well as the migratory routes taken by post-smolts to reach their northern feeding grounds. Furthermore, any impediments to post-smolt migration is likely to decrease adult returns (Forseth et al., 2017).

Acoustic telemetry is now being used worldwide by researchers and governmental organizations to remotely track aquatic animals through environments ranging from rivers to offshore and even deep-sea marine environments (Daley et al., 2015; Hays et al., 2019; Lennox et al., 2017; Matley et al., 2022). Furthermore, this technology has provided valuable information on how natural and anthropogenic stressors can alter the life history of aquatic species and ultimately bolster conservation efforts (Hays et al., 2019; Hussey et al., 2015; Lennox et al., 2017). Due to their economic and cultural importance, over the last decade most finfish telemetry studies have focussed on salmonids (Matley et al., 2022). Furthermore, a high proportion of salmonid telemetry studies seem to focus on the smolt stage of their life cycle particularly within the fresh water environment, this is likely related to the relative ease of capturing and acoustically tagging individuals and deploying acoustic receivers in rivers. However, one aspect of their fresh water migration that has received limited attention is their migration through standing bodies of water.

The few studies assessing Atlantic salmon smolt migration through lakes have indicate that smolts display non-directional movements (Hanssen et al., 2021; Honkanen et al., 2018, 2021). However, these studies had a limited number of receivers, which prevented the researchers from studying lake migration in detail. The objective of this thesis (Chapter two) was to expand on previous studies through utilizing a large acoustic telemetry array (n = 38) in Scotlands largest lake to identify factors that could increase lake migration success. This chapter had three main hypotheses, 1) larger smolts would have a greater likelihood of completing a successful migration through the loch, 2) that successful individuals would exhibit more directed pathways towards the lake outlet, and 3) once near the lake outlet Atlantic salmon smolts would make a direct exit.

After testing multiple morphological and behavioural characteristics I could not identify characteristics unique to successful migrants. Furthermore, the migratory patterns of smolts closely resembled those of a correlated random walk model. Thus, results from Chapter two suggest that successful smolt migration through lakes may be due to chance. However, once a smolt came near the lake outlet there was a distinctive shift in their behaviour, tending to remain within a small area near the lake outlet prior to completing a successful migration. While this study provides valuable information concerning the behaviour of smolts through lakes it did not incorporate any environmental variables. Migration of smolts through lakes is thought to be partially dependent on the direction and speed of wind driven surface currents (Thorpe et al., 1981). The change in behaviour from random migrations in the main body of the lake to directed movements near the lake outlet is likely due to a shift in flow direction as they approach the lake outlet. Due to the high loss of smolts observed in this study, assessing whether flow direction drives movement warrants future investigation. While it is difficult to modify flow patterns in natural lakes, it would be possible to use this information to modify currents in impounded reservoirs (e.g. containing dams) to aid in successful smolt migration (Honkanen et al., 2021).

Once smolts successfully migrate out of their fresh water environment, many must first transit through an estuary prior to reaching the coastal marine environment. For example, in Great Britain alone there are 155 estuaries (Davidson, 2018). Previous studies have indicated that Atlantic salmon experience high rates of mortality during their first few months at sea due to exposure to novel natural and anthropogenic stressors. However, despite this there is still very little known about the migratory behaviour of Atlantic salmon smolts in British estuaries which includes the Clyde estuary, Scotland. In Chapter three, I used acoustic telemetry to provide valuable information concerning the loss rates and behaviour of Atlantic salmon smolts migrating from two distinctively different river systems through the Clyde estuary. Upon entering the estuary approximately 1/3 of tagged smolts were found to undergo passive reversal movements with the tide which is thought to allow them to adapt to increases in salinity. However, contrary to most estuarine studies and despite engaging in passive reversal movements there was high overall survival for smolts from both river systems in comparison to the fresh water environment. Smolts were found to undergo rapid migrations through the estuary and appeared to be engaging in active migration with the outgoing tide. Results from this thesis chapter are being incorporated into models developed by the Scottish Environment Protection Agency (SEPA) to assess the potential interaction of sea lice from farmed Atlantic salmon with wild populations. Due to the lack of migratory constriction points in the Clyde estuary and efficient migrations through this region post-smolts may have decreased their likelihood of encountering predators as well as experiencing spatial and temporal overlap with aquaculture sites. This study highlights the inability to generalize estuarine studies across different systems as the loss of smolts in estuaries is likely due to an interaction between the geography of the system and presence of threats.

Once smolts from rivers along the western coast of the British Isles exit their natal rivers/estuaries, many are thought to migrate through the Irish sea to reach the slope current located along the western coast of the Outer Hebrides. However, prior to Chapter four of this thesis, the potential migratory pathways, and environmental drivers of smolt movement through the Irish sea region were mainly inferred from particle tracking studies (Ounsley et al., 2020). The results of Chapter four are the result of an overarching project called Project SeaMonitor. The main aim of Project SeaMonitor was to understand aspects of the early marine migratory behaviour of Atlantic salmon migrating from rivers in the British Isles by undertaking a large-scale acoustic telemetry study in the Irish Sea Region. Results from this study indicated that in comparison with the estuarine environment, loss rates of post smolts through the Irish sea were low (< 1 %.km^{-1}). However, overall loss was dependent on the duration spent in the Irish sea with Scottish rivers experiencing higher overall loss in comparison to rivers in Northern Ireland. Furthermore, smolts transition into the North Atlantic appeared to be correlated with the water temperatures experienced by smolts and post smolts during their riverine and offshore marine migration, respectively. With most post smolts exiting the Irish sea within a temperature range of 9-11 °C. Exiting the Irish sea within a narrow temperature range may ensure that smolts reach their northern feeding grounds during periods of high prey abundance. However, while we know that river temperature is one of the main environmental parameters initiating Atlantic salmon smolt downstream migration in their natal rivers, we can't rule out whether similar temperatures experienced by post-smolts at sea is purely coincidental and this requires further investigation (McCormick, 2013a; Zydlewski et al., 2005). Lastly, the exit of post-smolts from the Irish sea appeared to be dependent on current direction, with most post-smolts exiting this region when currents were travelling in a westerly direction. Post-smolts are known to enter the slope current that extends from the west coast of Ireland to the Hebrides, travelling in a westerly current would reduce the time it would take smolts to exit the coastal environment and reach their target destination.

Building upon Chapter four, during the same period when project SeaMonitor was taking place, the Atlantic Salmon Trust was deploying acoustic receiver arrays and tagging Atlantic salmon smolts along the West Coast of Scotland. To better our understanding of smolt movement along the West Coast of Scotland, in Chapter five, I collaborated with a colleague from the Atlantic Salmon Trust to investigate the migratory pathways of smolts migrating past acoustic receiver lines (n = 17) deployed from the entrance to the Irish sea to the northern tip of mainland Scotland, as well as a submersible glider deployed off the west coast of Uist, Scotland. In total this study incorporated data from 23 Atlantic salmon rivers and four nations. The results from this study indicated that while there was variability in migratory pathways amongst river systems, upon exiting their natal river most post-smolts from rivers south of the Outer Hebrides travelled rapidly in a north westerly direction avoiding a region referred to as the Minch. This supports the observations made in Chapter four, and the predictions of particle tracking studies conducted along the west coast of Scotland. Currently, the highest density of aquaculture sites is located to the east of the Outer Hebrides in a region known as the Minch. Additionally, tidal turbines developments occur along the coast of Scotland's northern Irelands, specifically Shetland and Orkney where the European Marine Energy Centre (EMEC) resides (Neill et al., 2017). The findings of the studies have clear management implications, as smolts travelling from rivers draining into the Minch could experience high temporal and spatial overlap with anthropogenic stressors. Lastly, future studies should expand on this work and utilize hydrodynamic models as discussed in the previous chapter to identify whether smolts are following environmental cues during their migration along the west coast of Scotland.

6.2 Limitations of the work presented in this thesis

Originally the plan for my PhD thesis was to repeat the methods outlined in Chapters three and four over three years. Unfortunately, during the Covid-19 pandemic we were unable to hire vessels to deploy the estuarine/marine equiptment required for these projects during 2020. Therefore, due to the time sensitive nature of my PhD I had to limit my thesis chapters to include data from a single year. While in this thesis we were able to obtain baseline information concerning the survival, timing, and basic drivers of smolt migration through their estuarine and coastal marine environment, temporal repeatability of these study over multiple years is required to ground truth these results.

In addition, for acoustic receiver arrays where loss rates are provided, we assumed that these receivers/arrays had complete land to land coverage. This was based upon receiver range estimates provided by published studies conducted in the fresh water, estuarine, and coastal marine environment. However, detection range is often not consistent across different habitats and time (Huveneers et al., 2016). Prior to conducting and during an acoustic telemetry study range testing should be conducted as environmental conditions unique to each system can impede the (e.g. variation in wind, salinity, temperature) detection range of a receiver (Kessel et al., 2014). Range testing involves deploying an acoustic tag at a fixed location/depth and deploying acoustic receivers at varying spatial distances away from the tag (e.g. 50m intervals). Another alternative to range testing would be to evaluate the proportion of subsequent detections that occurred between two monitoring points/lines as illustrated in Chapter 3. For example, in Chapter 4, a line of acoustic receivers could have been deployed beyond monitoring line B to improve the accuracy of the estimated number of post-smolts migrating through the Irish Sea. Therefore, in all chapters where estimated loss rates are provided, they should be interpreted as maximum estimates as there is a chance that smolts travelled through arrays without being detected.

6.3 Conclusion

In conclusion, this thesis has provided valuable baseline information concerning the migratory pathways and loss rates of smolts from multiple populations in the British Isles as they transit into the North Atlantic. Prior to this study very little was known about the early marine migration of smolts along the west coast of Scotland. With the rapid decline in Atlantic salmon populations across the North East Atlantic and rapid increase in natural (e.g. increasing SST) and anthropogenic stressors (e.g. aquaculture, renewable energy development), future research should use the results of this thesis to focus on identifying the potential causes of river specific decline in both the fresh water and early marine environment. This would include deploying a higher density of acoustic receivers along the west coast of Scotland to pinpoint migratory constriction points and/or using novel tagging methods such as predation tags to determine potential causes of mortality (Hanssen et al., 2021). In addition, once stressors are identified researchers need to collaborate with governmental organizations to develop strategic plans to mitigate their effects.

Appendix 1: Supplementary Information for Chapter 2

(Combining acoustic telemetry with a mechanistic model to investigate characteristics unique to successful Atlantic salmon smolt migrants through a standing body of water)

** Note this chapter and supplementary materials are published in Environmental Biology of Fishes*

The following supplementary information provides examples of the migratory trajectories of acoustically tagged Atlantic salmon smolts (successful versus unsuccessful migrants) migrating through Loch Lomond during 2020.

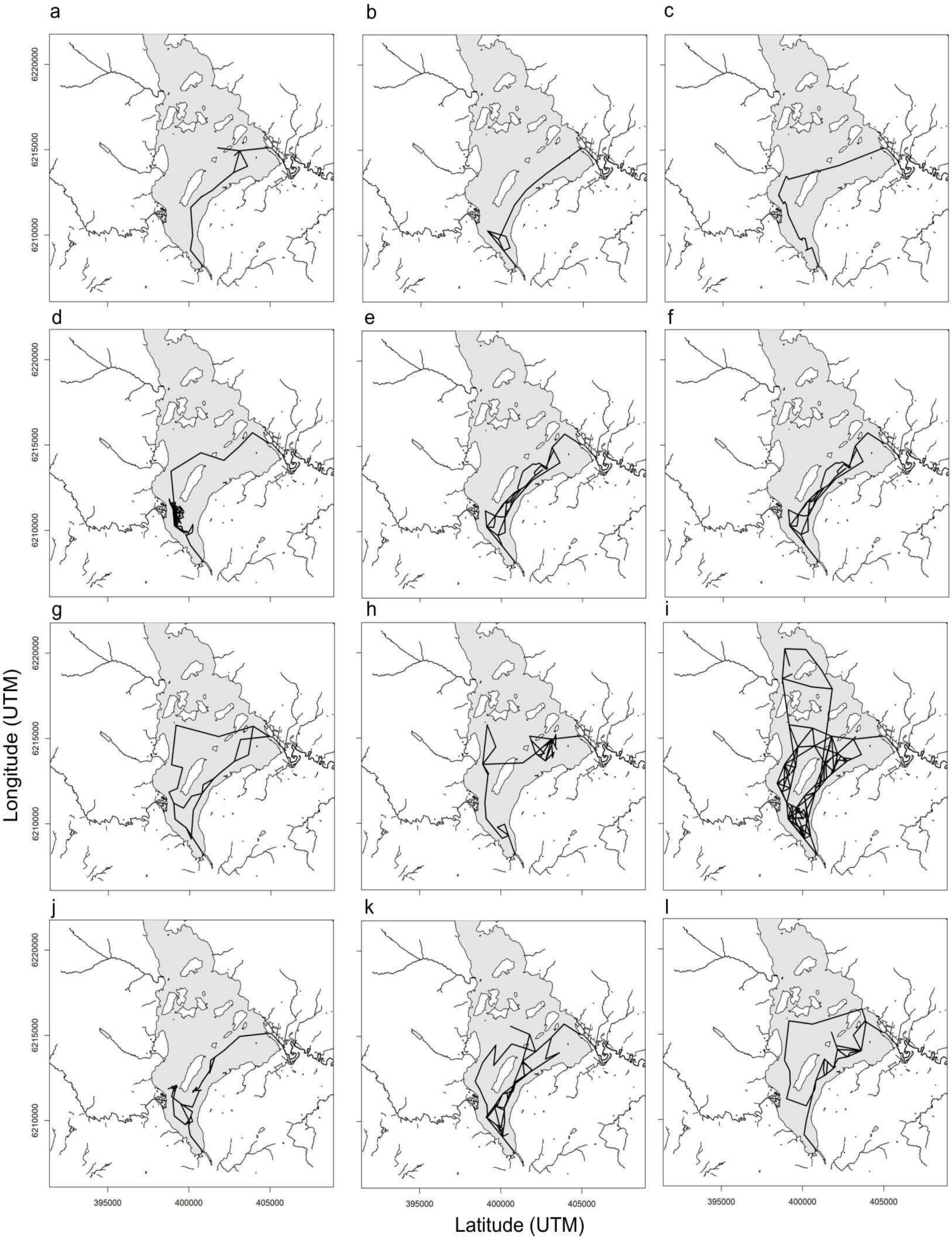


Figure A1.1. Plot of the various migratory trajectories of successful Atlantic salmon smolts (*n* = 28) in Loch Lomond during 2020.

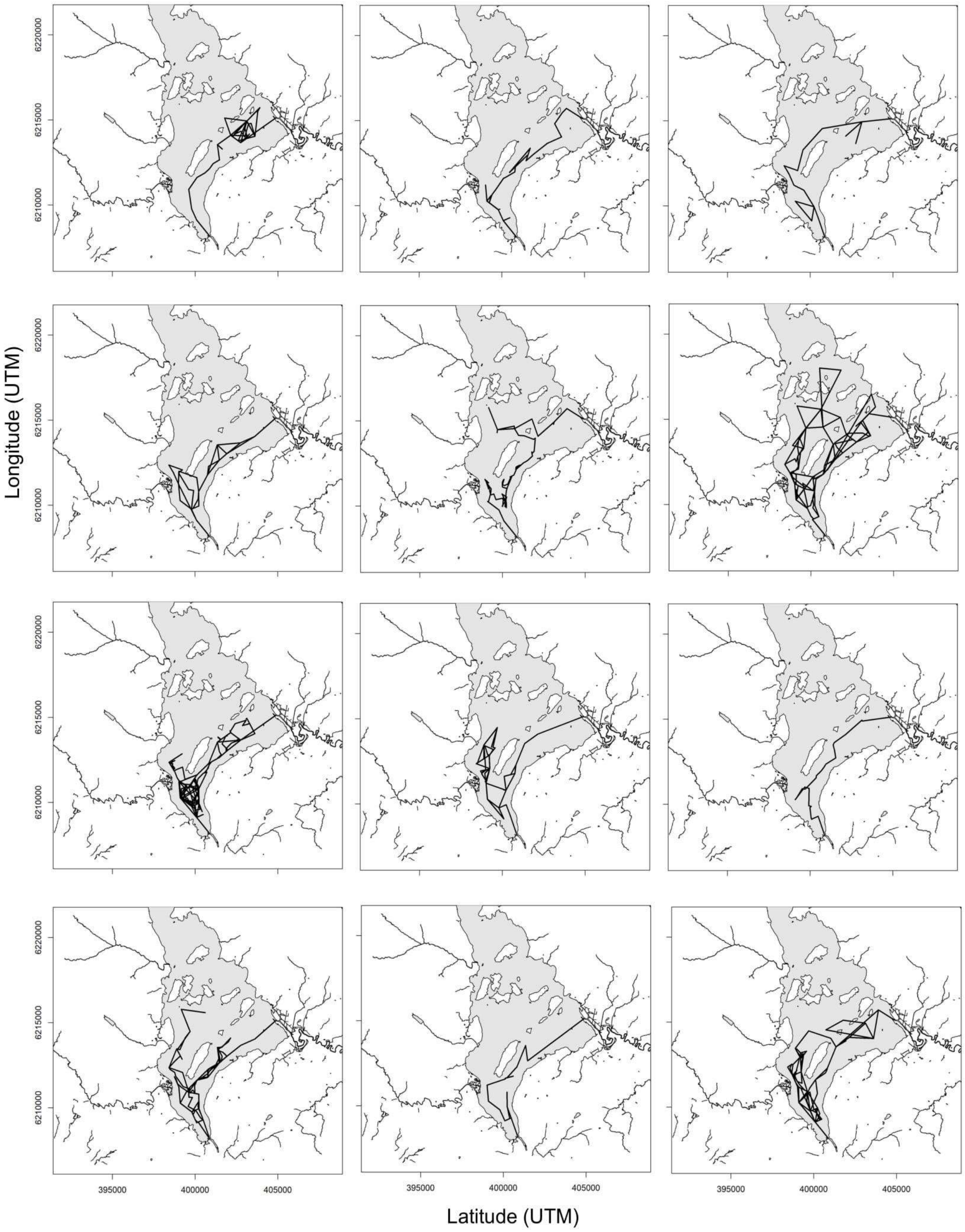


Figure A1.1. Plot of the various migratory trajectories of successful Atlantic salmon smolts (*n* = 28) in Loch Lomond during 2020.

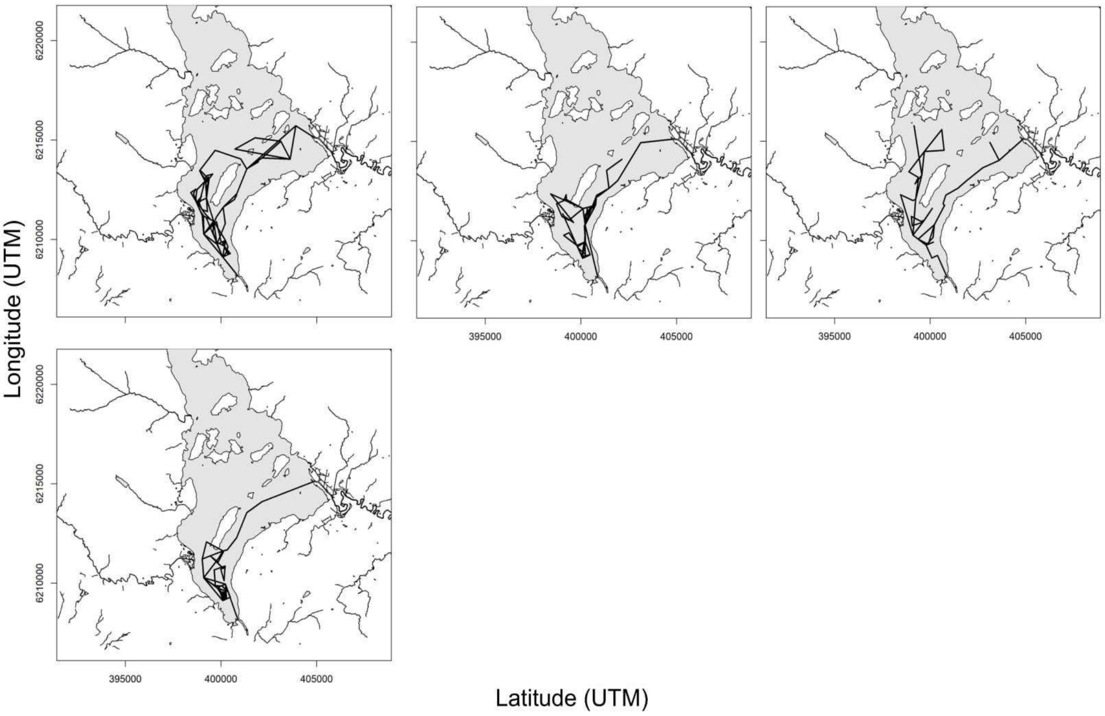


Figure A1.1. Plot of the various migratory trajectories of successful Atlantic salmon smolts (*n* = 28) in Loch Lomond during 2020.

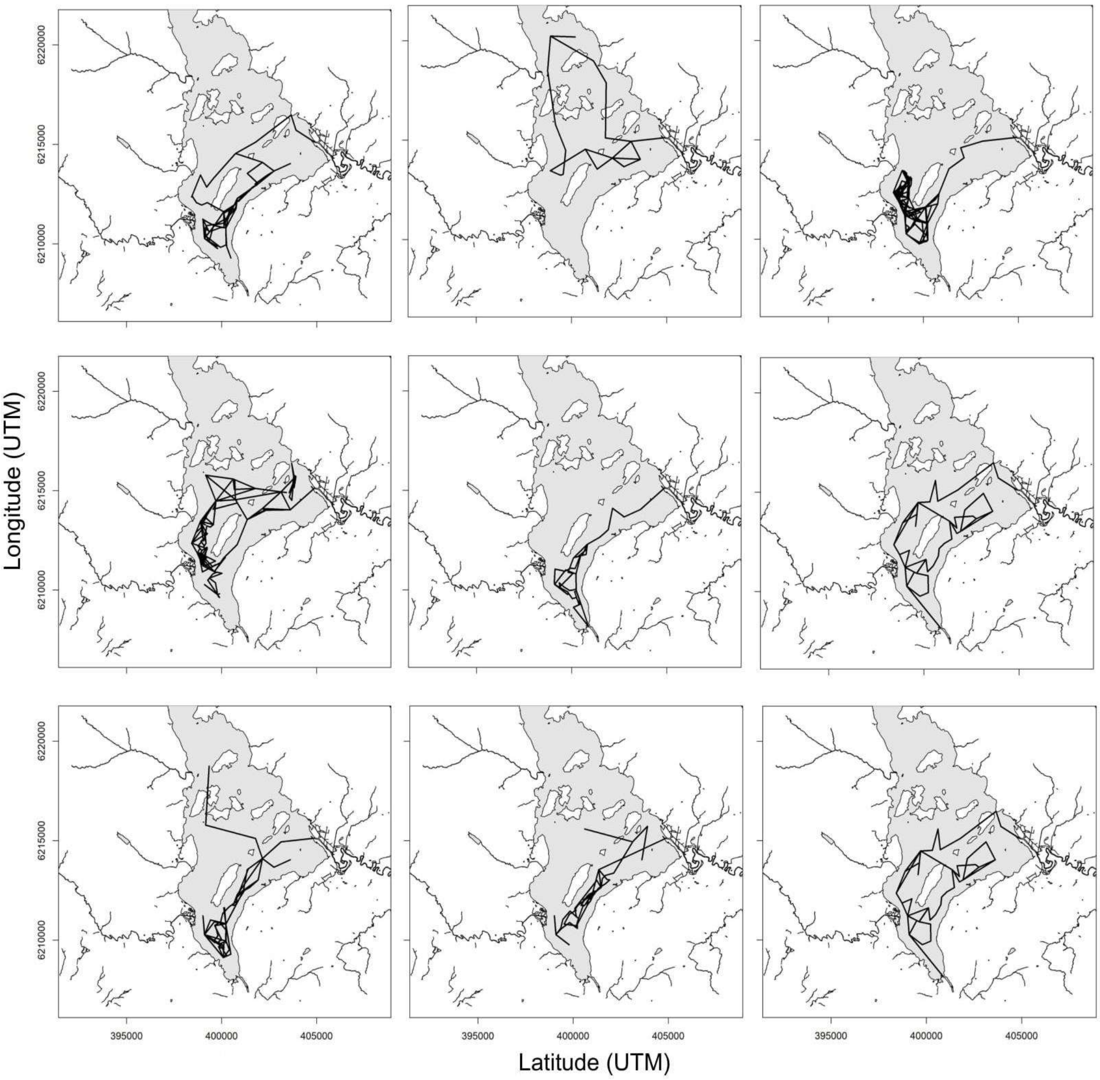


Figure A1.2. Plot of the various migratory trajectories of unsuccessful Atlantic salmon smolt migrants ($n = 9$) in Loch Lomond during 2020. The dataset of unsuccessful migrants was filtered to include detections that extended to the 95% Confidence Interval (CI) of the duration successful smolts occupied Loch Lomond. The duration successful smolts spent in Loch Lomond was calculated based upon their last detection on the final receiver in the River Endrick and initial receiver on the River Leven.

Appendix 2: Supplementary Information for Chapter 3

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

The following supplementary material provides further information about the receiver detection efficiency in the fresh water zone for this study.

Table A2.1 Total number of Atlantic salmon smolts (No.) tagged and released (Rel) in the River Endrick (End), Leven (Lev), and Gryffe (Gry) that were detected at the exit of the River Endrick (Fig. 3.1 R17), and within the River Leven (Fig. 3.1 R18-20) and Gryffe (Fig. 3.1 R1-R3), respectively. Receivers are labeled in sequential order towards the exit of the Clyde estuary. Receiver efficiency for the final River Leven and Gryffe receiver was estimated based upon the number of smolts detected on monitoring line E (Fig. 3.1). Receiver efficiency for River Leven release smolts was not estimated for the first River Leven receiver, as smolts were released a ~170m downstream of the receiver. The number of salmon smolts that were not detected at a receiver but were detected at the subsequent downstream receiver is indicated by brackets.

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

Appendix 3: Supplementary Information for Chapter 4

(Migration patterns and navigation cues of Atlantic salmon post-smolts migrating from 14 rivers through coastal zones around the Irish Sea)

The following supplementary material provides further information about the number of acoustic receivers deployed by each project involved in this chapter, and the behavioural metrics of Atlantic salmon post-smolts during their migration through the Irish Sea.

Table A3.1. Table displaying the total number and duration acoustic receivers were deployed during 2021 in the estuarine and marine environment (for ID's see Fig. 4.1). This table is replicated from Rodger *et al*. (2022) with permission.

Type	**Region**	**ID**	**Number of receivers deployed**	**Number of receivers recovered**	**Lat.**	**Long.**	**Deployment Duration**
River	Leven	-	1	1	55.939	-4.563	16-03 to 05-07
River	Gryfe	-	1	1	55.890	-4.406	09-04 to 20-07
River	Bladnoch	-	1	1	54.862	-4.434	24-03 to 19-07
River	Nith	-	1	1	55.046	-3.607	06-04 to 01-07
River	Bush	-	1	1	55.219	-6.532	01-04 to 13-09
River	Glendun	-	1	1	55.124	-6.044	06-04 to 06-10
River	Bann	-	2	2	55.171	-6.773	07-04 to 04-08
River	Carey	-	1	1	55.201	-6.233	06-04 to 27-08
River	Derwent	-	1	1	54.646	-3.542	24-03 to 22-07
River	Roe	-	1	1	55.109	-6.951	26-04 to 15-10
River	Faughan	-	1	1	55.035	-7.226	26-04 to 15-10
River	Burishoole	-	1	1	53.906	-9.578	04-05 to 14-06
Estuary	Burrishoole	-	1	1	53.887	-9.589	04-05 to 14-06
Estuary	Clyde Estuary	-	8	4	55.725	-5.000	02-04 to 06-08
Estuary	Lough Foyle	-	1	13	55.202	-6.948	24-03 to 26-08
Marine	Clew Bay	-	10	9	53.844	-9.963	28-04 to 22-06
Marine	Irish Sea	E	108	99	55.494	-6.886	27-02 to 14-09
Marine	Irish Sea	A	22	20	55.931	-5.477	19-03 to 03-08

Table A3.2 (continued) The total number of Atlantic salmon smolts detected at key monitoring lines in this study (Fig. 4.1: Monitoring line A,B). If Atlantic salmon post-smolts were not detected on an array but were detected on a subsequent array that should have intercepted their migratory path, than those additional smolts were added to the number at the start array (No.start array). The statistics calculated in this table were calculated for each section of the migratory journey, including the number of post-smolts detected at the start and end arrays and the date range post-smolts were detected on the end array for each section. The total duration (days) and Rate of Movement (RoM) between monitoring lines (kilometres per day (km.day^{-1})) were also calculated. There were some instances were not all smolts detected on the end array were also detected on the start array, therefore, in these cases ROM was calculated using a proportion of the smolts detected (No. used).

River	**Type**	**Start array**	**End array**	**Distance (km)**	**No.start array**	**No. end array (%)**	**Loss rate (%km^{-1})**	**Date range (dd-mm)**	**No. used**	**Mean RoM (km.day^{-})^{1}**	**Mean passage time (days) ± SD (range)**
Derwent	Mar	Derwent	A	139.00	41	15 (36.58)	-	11-05 to 06-06	3	11.56 ± 6.01 (6.86 - 18.33)	14.17 ± 6.35 (7.58 - 20.25)
	Mar	Derwent	B	256.00	41	11 (26.83)	-	13-05 to 20-06	7	14.03 ± 7.32 (5.52 - 25.28)	23.04 ± 12.14 (10.13 - 46.53)
	Mar	A	B	117.00	15	11 (73.33)	-	13-05 to 20-06	3	53.25 ± 4.25 (48.58 - 56.88)	2.21 ± 0.18 (2.06 - 2.41)
Nith & Crawick	Mar	Nith	A	170	89	20 (22.47)	-	11-05 to 01-06	17	15.84 ± 5.49 (6.17 – 25.34)	2.54 ± 5.94 (6.71 – 27.55)
	Mar	Nith	B	278.00	89	5 (5.62)	-	19-05 to 06-06	5	14.27 ± 7.03 (8.94 – 26.86)	22.81 ± 8.45 (10.35 – 31.10)
	Mar	A	B	108	20	6 (30.0)	-	19-05 to 06-06	3	36.70 ± 17.09 (18.89 – 51.29)	3.59 ± 2.13 (2.11 – 6.04)
Bladnoch	Mar	Bladnoch	A	123.00	54	12 (22.22)	-	13-05 to 06-06	9	12.85 ± 4.17 (9.71 - 20.69)	10.28 ± 2.50 (5.95 - 12.66)
	Mar	Bladnoch	B	238.00	54	5 (9.26)	-	16-05 to 07-06	5	14.87 ± 4.17 (9.96 - 18.75)	20.06 ± 6.14 (14.83 - 27.92)
	Mar	A	B	108.0	12	5 (41.67)	-	16-05 to 07-06	5	38.99 ± 2.77 (37.03 - 40.95)	2.78 ± 0.2 (2.64 - 2.92)

Table A3.2 (continued) The total number of Atlantic salmon smolts detected at key monitoring lines in this study (Fig. 4.1: Monitoring line A,B). If Atlantic salmon post-smolts were not detected on an array but were detected on a subsequent array that should have intercepted their migratory path, than those additional smolts were added to the number at the start array (No.start array). The statistics calculated in this table were calculated for each section of the migratory journey, including the number of post-smolts detected at the start and end arrays and the date range post-smolts were detected on the end array for each section. The total duration (days) and Rate of Movement (RoM) between monitoring lines (kilometres per day ($km.day^{-1}$)) were also calculated. There were some instances were not all smolts detected on the end array were also detected on the start array, therefore, in these cases ROM was calculated using a proportion of the smolts detected (No. used).

River	**Type**	**Start array**	**End array**	**Distance (km)**	**No.start array**	**No. end array (%)**	**Loss rate ($\%km^{-1}$)**	**Date range (dd-mm)**	**No. used**	**Mean RoM ($km.day^{-}$)^1**	**Mean passage time (days) ± SD (range)**
Endrick	Est	Leven	Clyde est.	46.70	50	38 (76.00)	0.51	28-04 to 31-05	38	10.14 ± 5.62 (2.12 - 27.61)	4.75 ± 1.25 (3.30 - 16.21)
	Mar	Clyde est.	A	86.80	38	4 (10.23)	-	13-05 to 25-05	3	7.18 ± 2.62 (4.3 - 9.45)	13.50 ± 9.19 (5.86 - 20.18)
	Mar	Clyde est.	B	168	38	9 (23.68)	0.45	21-05 to 18-06	9	9.69 ± 1.71 (7.11 - 11.95)	17.86 ± 14.05 (3.37 - 23.63)
Gryffe	Est	Gryffe	Clyde est.	58.40	93	80 (86.02)	0.24	22-04 to 22-05	80	13.65 ± 5.51 (3.64 - 27.56)	5.18 ± 2.12 (2.66 - 16.05)
	Mar	Clyde est.	A	86.80	80	6 (7.50)	-	06-05 to 04-06	6	6.05 ± 2.85 (2.38 - 10.33)	17.80 ± 8.40 (10.02 - 36.48)
		Clyde est.	B	168.00	80	27 (33.75)	0.39	04-05 to 06-06	25	14.87 ± 5.59 (4.41 - 28.84)	13.15 ± 5.83 (6.32 - 38.09)
		A	B	86.80	80	2 (33.33)	0.57	04-05 to 06-06	2	43.33 ± 41.32 (14.11 - 72.55)	4.95 ± 4.72 (1.61 - 8.29)
Bann and Agivey	Mar	Bann	B	45.60	34	21 (61.76)	0.84	05-05 to 26-05	17	38.56 ± 12.86 (20.29 - 61.64)	1.31 ± 0.44 (0.74 to 2.25)
Bush	Mar	Bush	B	47.10	73	39 (53.42)	0.99	21-04 to 07-05	39	26.65 ± 10.13 (7.76 - 53.32)	2.11 ± 1.06 (0.88 - 6.07)
Carey	Mar	Carey	B	60.40	6	3 (50)	0.95	05-05 to 07-05	2	14.18 ± 4.89 (10.73 - 17.64)	4.53 ± 1.56 (3.42 - 5.63)

Table A3.2 (continued) The total number of Atlantic salmon smolts detected at key monitoring lines in this study (Fig. 4.1: Monitoring line A,B). If Atlantic salmon post-smolts were not detected on an array but were detected on a subsequent array that should have intercepted their migratory path, than those additional smolts were added to the number at the start array (No.start array). The statistics calculated in this table were calculated for each section of the migratory journey, including the number of post-smolts detected at the start and end arrays and the date range post-smolts were detected on the end array for each section. The total duration (days) and Rate of Movement (RoM) between monitoring lines (kilometres per day (km.day^{-1})) were also calculated. There were some instances were not all smolts detected on the end array were also detected on the start array, therefore, in these cases ROM was calculated using a proportion of the smolts detected (No. used).

River	**Type**	**Start array**	**End array**	**Distance (km)**	**No.start array**	**No. end array (%)**	**Loss rate (%km^{-1})**	**Date range (dd-mm)**	**No. used**	**Mean RoM (km.day^{-})^{1}**	**Mean passage time (days) ± SD (range)**
Glendun	Mar	Glendun	B	83.40	21	5 (23.81)	0.91	02-05 to 15-05	5	16.39 ± 3.25 (12.09 - 21.04)	2.97 ± 0.61 (2.24 - 3.90)
Roe	Est	Roe	Lough Foyle	14.80	9	6 (66.67)	2.52	05-05 to 13-05	3	5.38 ± 3.3 (1.62 - 7.78)	4.41 ± 1.9 (4.1 -9.15)
	Mar	Lough Foyle	B	37.80	6	5 (83.33)	0.44	06-05 to 13-05	5	39.94 ± 12.04 (27.69 - 52.93)	1.02 ± 0.71 (0.3 - 1.37)
Faughan	Est	Faughan	Lough Foyle	27.00	38	19 (50.00)	1.85	12-05 to 02-06	11	13.75 ± 4.76 (8.68 - 23.11)	2.16 ± 1.17 (0.66 - 3.11)
	Mar	Lough Foyle	B	37.80	19	18 (94.73)	0.14	13-05 to 01-06	11	29.56 ±15.30 (3.87 - 55.78)	2.24 ± 0.68 (2.74 - 9.76)
Burrishoole (Wild)	Mar	Burrishoole estuary	Clew Bay 1	4.89	17	15 (88.24)	2.41	07-05 to 15-05	14	25.31 ± 16.90 (2.87 - 54.17)	0.37 ± 0.42 (0.09 - 1.71)
(Ranched)	Mar	Burrishoole estuary	Clew Bay 1	4.89	51	37 (72.55)	5.61	06-05 to 05-06	35	23.72 ± 26.48 (0.16 - 72.59)	3.47 ± 6.09 (0.07 - 30.27)
(Wild)	Mar	Burrishoole estuary	Clew Bay2	25.70	17	7 (41.18)	2.29	12-05 to 22-05	7	23.08 ± 16.81 (2.83 - 43.18)	2.72 ± 3.17 (0.60 - 9.07)
(Ranched)	Mar	Burrishoole estuary	Clew Bay 2	25.70	51	15 (29.41)	2.75	09-05 to 15-05	15	25.44 ± 17.39 (6.61 - 53.71)	1.64 ± 1.09 (0.48 - 3.89)

Table A3.3. Total number of Atlantic salmon post-smolts that exited their natal river/estuary in this study that completed a successful migration through the Irish Sea (past monitoring line B; Fig. 4.1) or entered the west coast of Ireland (Clew Bay; Fig. 4.1) as well as the quantiles for Irish Sea entry and exit dates (dd-mm; SD (Standard Deviation)). At the exit of some riverine/estuarine systems there were post-smolts that were not detected at the final riverine/estuarine receiver that were detected at monitoring line A/B. These post-smolts were added to the total number that migrated out of the river or estuary. The number used (no.used) reflects the number of post-smolts that were detected exiting their natal river/estuary.

						Quantiles of sea/west coast of Ireland entry								**Quantiles of Irish Sea exit**		
River	**No. entered Irish Sea/west coast of Ireland (no.used)**	**% entered Irish sea/west coast of Ireland**	**Initial entry**	**Final entry**	**SD**	**25%**	**50%**	**75%**	**No. exited Irish Sea**	**% exited Irish Sea**	**Initial exit**	**Final exit**	**SD**	**25%**	**50%**	**75%**
Endrick	38 (38)	76.00	29-04	31-05	6.72	08-05	12-05	17-05	9	23.68	21-05	18-06	8.06	27-05	29-05	31-05
Gryffe	80 (80)	86.02	22-04	22-05	7.02	29-04	04-05	07-05	27	33.75	04-05	06-06	8.65	15-05	17-05	26-05
Nith (Crawick)	89 (89)	31.90	29-04	29-05	7.76	05-04	05-05	-1105	5	5.56	19-05	06-06	6.31	28-05	30-05	03-06
Bladnoch	53 (53)	40.77	25-04	27-05	7.09	05-03	11-05	14-05	5	9.43	16-05	07-06	8.96	28-05	06-04	06-06
Derwent	41 (33)	27.33	01-05	24-05	6.56	04-05	10-05	17-05	11	26.83	14-05	20-06	8.64	31-05	02-06	05-06
Roe	6 (3)	66.67	05-05	13-05	3.06	05-05	06-05	08-05	5	83.33	06-05	13-05	2.88	07-05	07-05	10-05
Faughan	19 (11)	50	12-05	02-06	5.31	17-05	17-05	18-05	18	94.74	13-05	01-06	4.48	13-05	17-05	19-05
Bush	73 (73)	91.25	18-04	09-05	4.84	24-04	26-04	01-05	39	53.42	21-04	07-05	4.64	24-04	28-04	02-05
Glendun	21 (21)	87.50	29-04	20-05	5.21	03-05	08-05	12-05	5	23.81	02-05	15-05	3.0	07-05	13-05	15-05

Table A3.3. (continued) Total number of Atlantic salmon post-smolts that exited their natal river/estuary in this study that completed a successful migration through the Irish Sea (past monitoring line B; Fig. 4.1) or entered the west coast of Ireland (Clew Bay; Fig. 4.1) as well as the quantiles for Irish Sea entry and exit dates (dd-mm; SD (Standard Deviation)). At the exit of some riverine/estuarine systems there were post-smolts that were not detected at the final riverine/estuarine receiver that were detected at monitoring line A/B. These post-smolts were added to the total number that migrated out of the river or estuary. The number used (no.used) reflects the number of post-smolts that were detected exiting their natal river/estuary.

						Quantiles Irish sea/west coast of Ireland entry								Quantiles Irish sea exit		
River	**No. entered Irish Sea/west coast of Ireland (no.used)**	**% entered Irish sea/west coast of Ireland**	**Initial entry**	**Final entry**	**SD**	**25%**	**50%**	**75%**	**No. exited Irish Sea**	**% exited Irish Sea**	**Initial exit**	**Final exit**	**SD**	**25%**	**50%**	**75%**
Bann (Agivey)	34 (34)	34.00	05-05	26-05	5.99	11-05	13-05	15-05	21	61.76	07-05	28-05	7.0	09-05	14-05	17-05
Carey	7(6)	66.67	01-05	09-05	3.87	01-05	03-05	07-05	3	42.86	05-05	07-05	1	05-05	07-05	07-05
Burrishoole (wild)	7(7)	41.18	12-05	22-05	3.86	12-05	16-05	19-05	-	-	-	-		-	-	-
Burrishoole (ranched)	15(15)	29.41	09-05	15-05	2.04	09-05	11-05	12-05	-	-	-	-	-	-	-	-

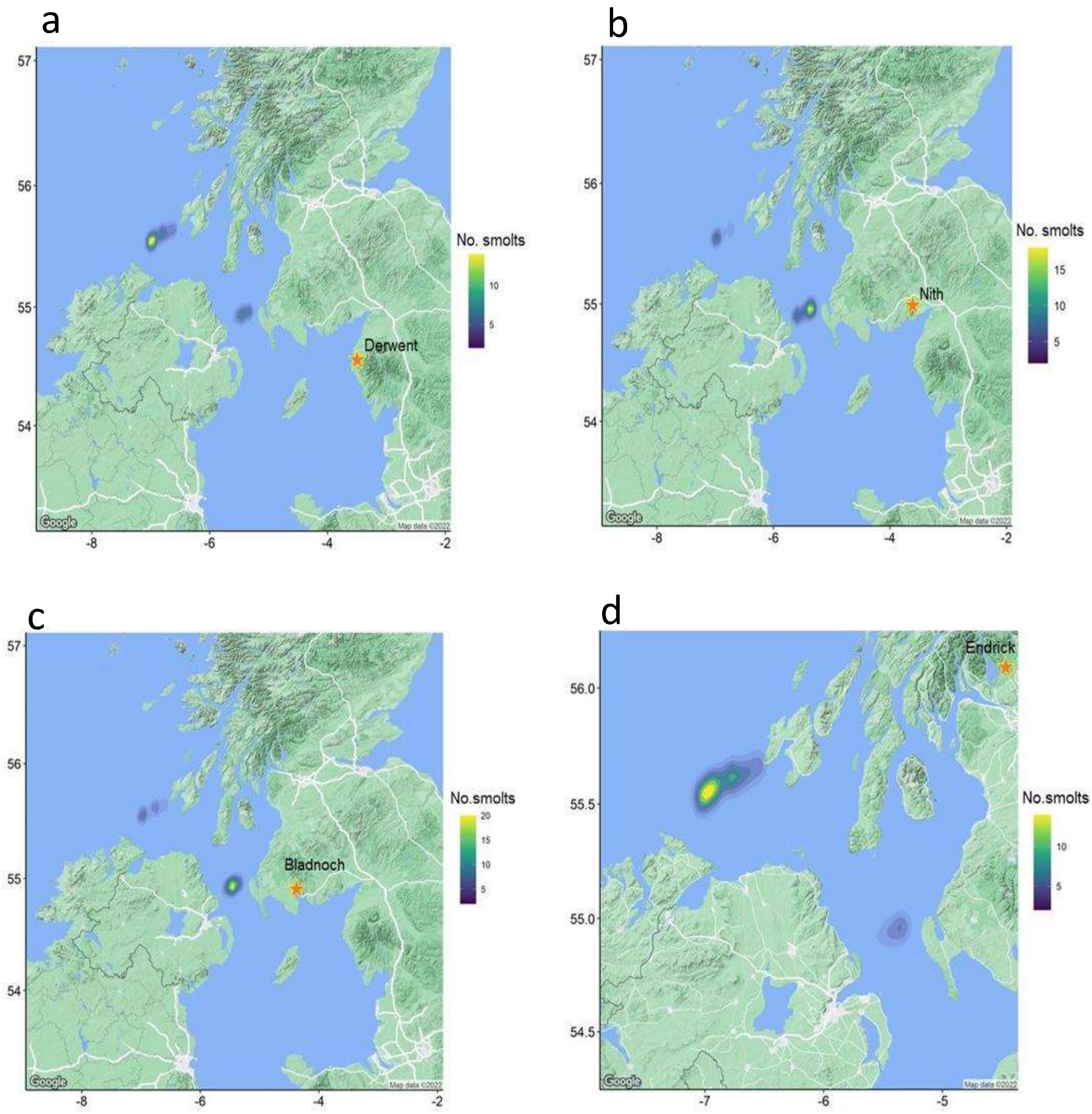


Figure A3.1. Heatmaps displaying the number of Atlantic post-smolts (no. smolts) detected at each acoustic receiver on monitoring line A and B (Fig. 4.1) during the period of this study. The orange stars represent the location of each river (*n* = 11) where Atlantic salmon smolts were acoustically tagged.

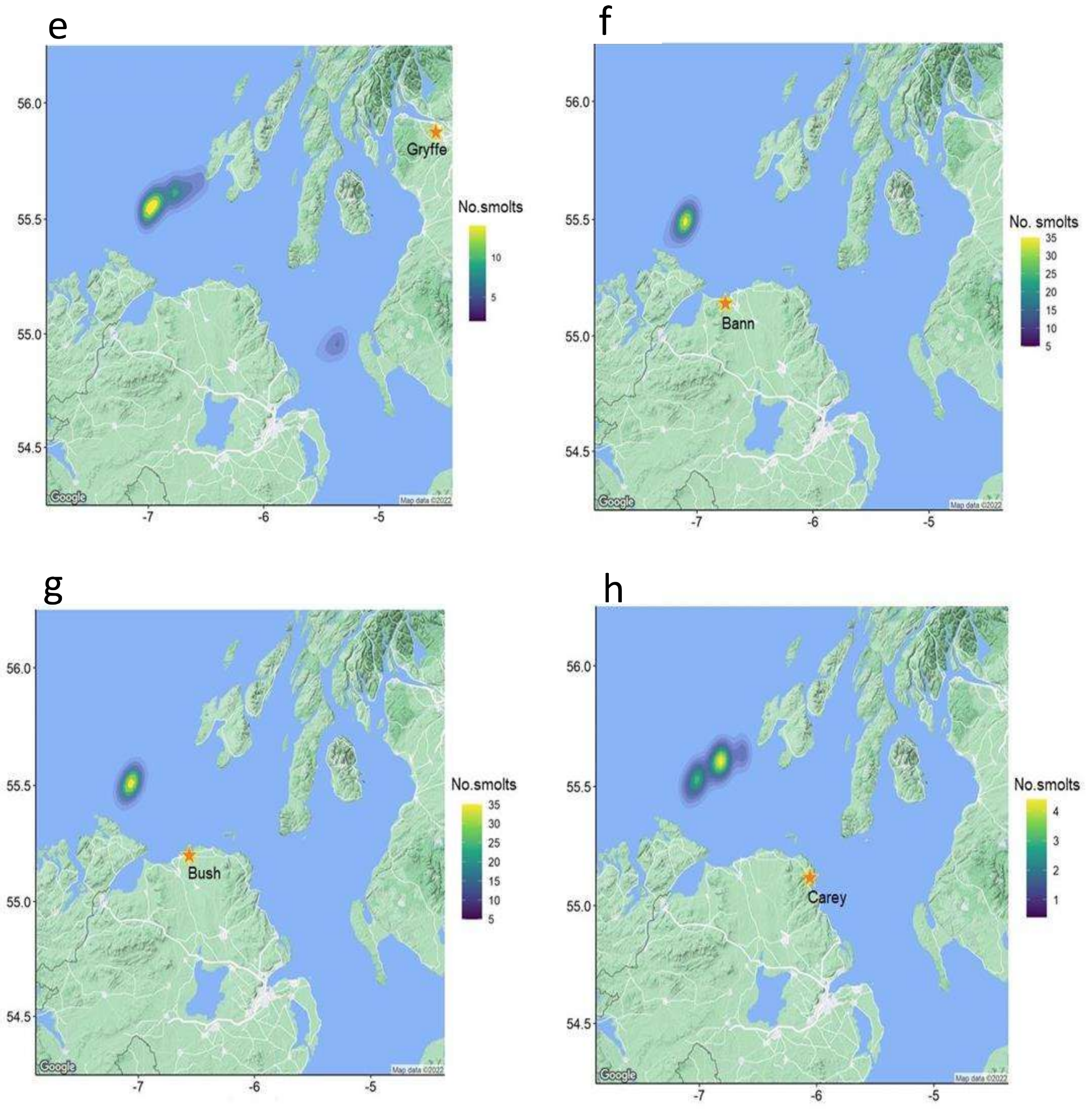


Figure A3.1. (continued) Heatmaps displaying the number of Atlantic post-smolts (no. smolts) detected at each acoustic receiver on monitoring line A and B (Fig. 4.1) during the period of this study. The orange stars represent the location of each river (*n* = 11) where Atlantic salmon smolts were acoustically tagged.

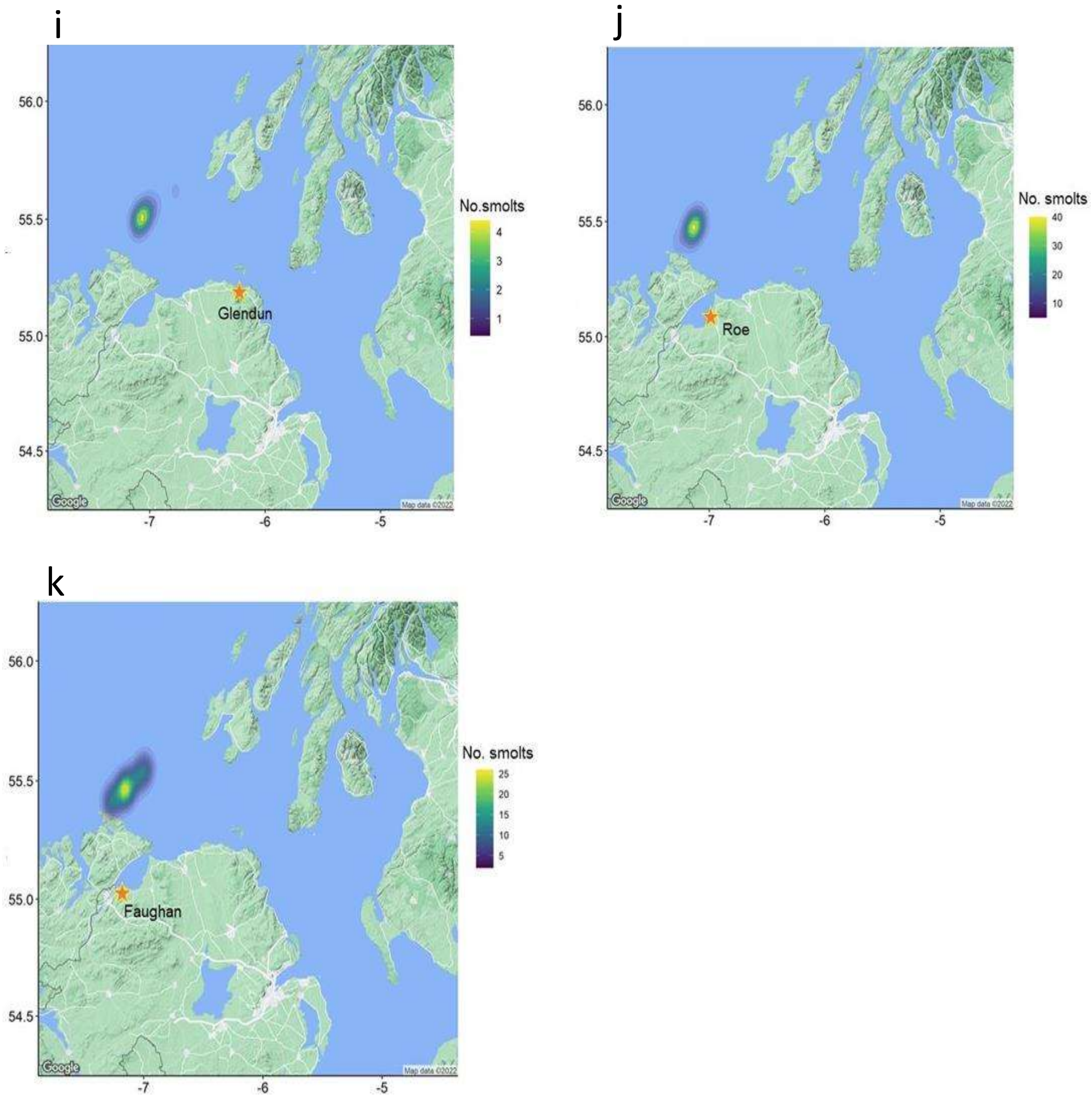


Figure A3.1. (continued) Heatmaps displaying the number of Atlantic post-smolts (no. smolts) detected at each acoustic receiver on monitoring line A and B (Fig. 4.1) during the period of this study. The orange stars represent the location of each river (*n* = 11) where Atlantic salmon smolts were acoustically tagged.

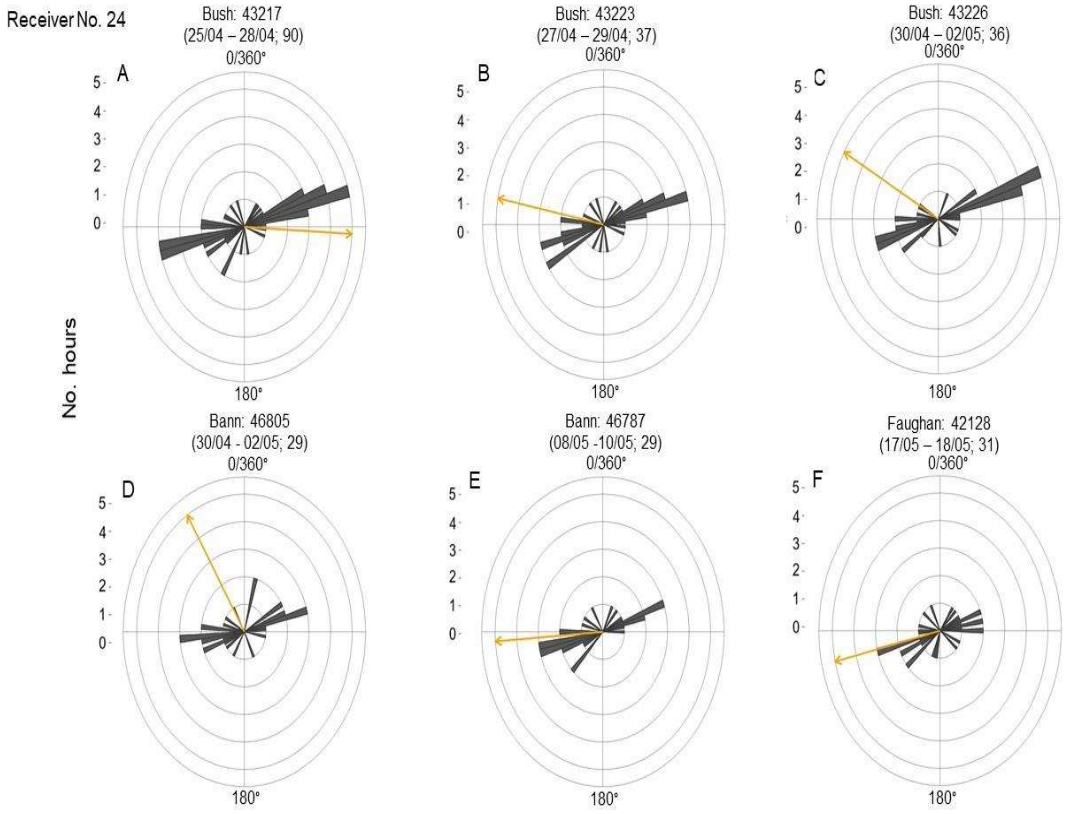


Figure A3.2. Rose diagrams depicting the direction of current (orange arrow) when a unique post-smolt (River location: identification number) was initially detected on monitoring line B, as well as the number of hours when currents were in a specific direction (grey bars) for the duration they were present in the Irish sea (Irish sea entry date – exit date, total number of hours). Modelled currents at each receiver location for the duration post-smolts were detected in the Irish sea was obtained from the Marine Institutes Northeast Atlantic hydrodynamic model (NEA-ROMS; Dabrowski et al., 2016). The graphs depict the top five receivers where the highest number of initial post-smolt detections occurred (Receiver 24: A-F; 40: G-L; 47: M-R; 47: S-X; 42: Y-A4).

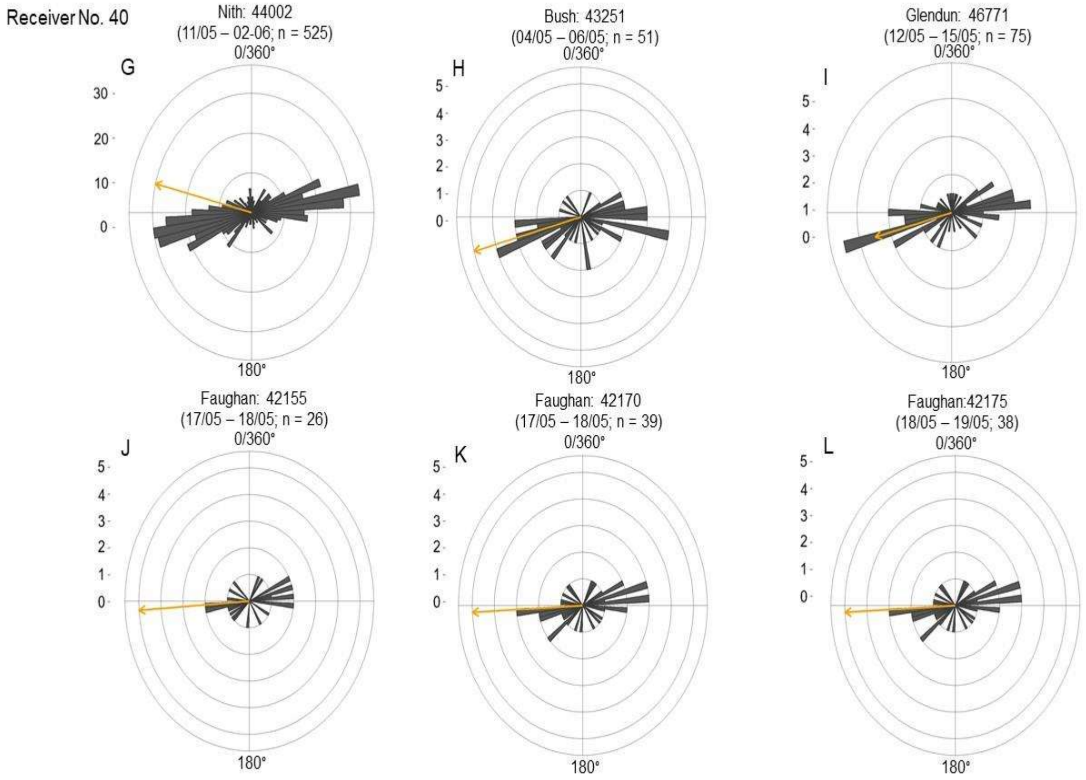


Figure A3.2. (continued) Rose diagrams depicting the direction of current (orange arrow) when a unique post-smolt (River location: identification number) was initially detected on monitoring line B, as well as the number of hours when currents were in a specific direction (grey bars) for the duration they were present in the Irish sea (Irish sea entry date – exit date, total number of hours). Modelled currents at each receiver location for the duration post-smolts were detected in the Irish sea was obtained from the Marine Institutes Northeast Atlantic hydrodynamic model (NEA-ROMS; Dabrowski et al., 2016). The graphs depict the top five receivers where the highest number of initial post-smolt detections occurred (Receiver 24: A-F; 40: G-L; 47: M-R; 47: S-X; 42: Y-A4).

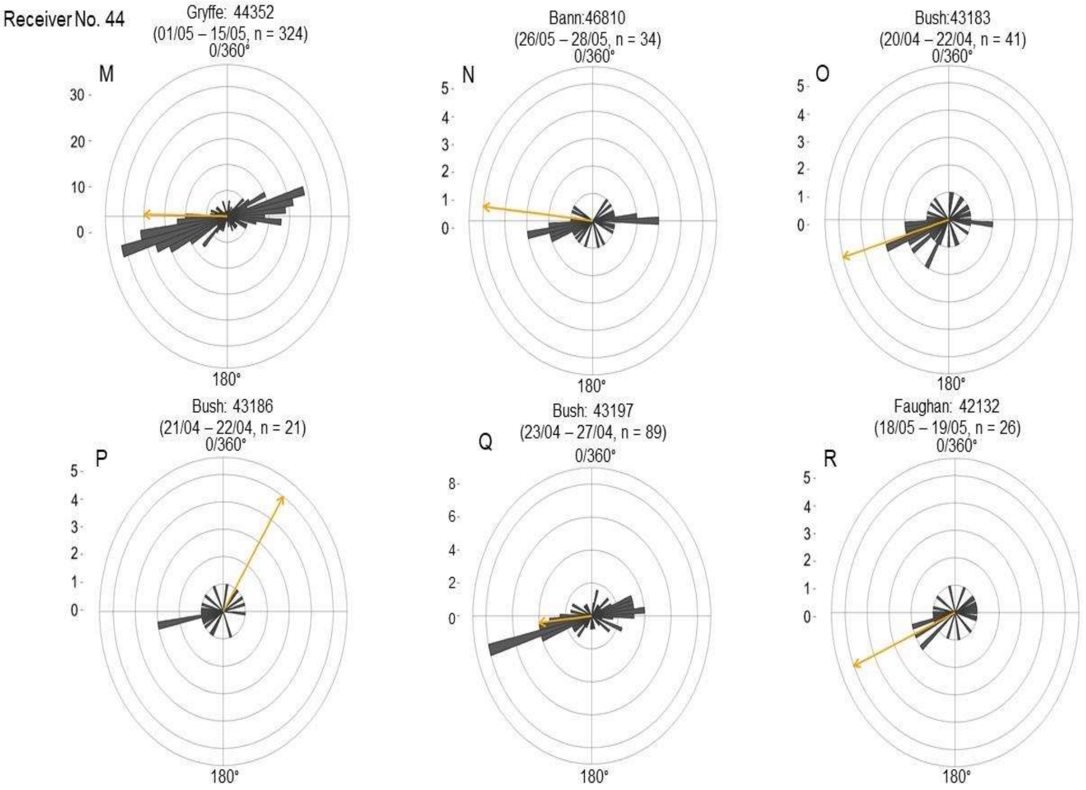


Figure A3.2. (continued) Rose diagrams depicting the direction of current (orange arrow) when a unique post-smolt (River location: identification number) was initially detected on monitoring line B, as well as the number of hours when currents were in a specific direction (grey bars) for the duration they were present in the Irish sea (Irish sea entry date – exit date, total number of hours). Modelled currents at each receiver location for the duration post-smolts were detected in the Irish sea was obtained from the Marine Institutes Northeast Atlantic hydrodynamic model (NEA-ROMS; Dabrowski et al., 2016). The graphs depict the top five receivers where the highest number of initial post-smolt detections occurred (Receiver 24: A-F; 40: G-L; 47: M-R; 47: S-X; 42: Y-A4).

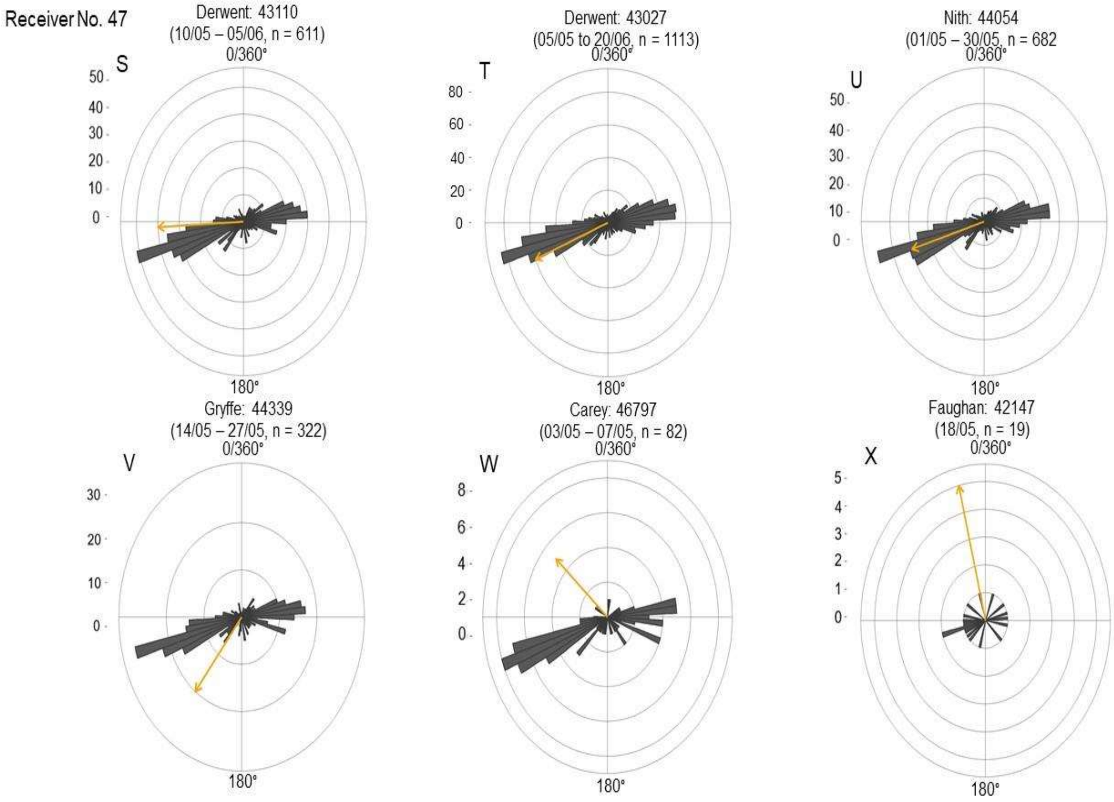


Figure A3.2. (continued) Rose diagrams depicting the direction of current (orange arrow) when a unique post-smolt (River location: identification number) was initially detected on monitoring line B, as well as the number of hours when currents were in a specific direction (grey bars) for the duration they were present in the Irish sea (Irish sea entry date – exit date, total number of hours). Modelled currents at each receiver location for the duration post-smolts were detected in the Irish sea was obtained from the Marine Institutes Northeast Atlantic hydrodynamic model (NEA-ROMS; Dabrowski et al., 2016). The graphs depict the top five receivers where the highest number of initial post-smolt detections occurred (Receiver 24: A-F; 40: G-L; 47: M-R; 47: S-X; 42: Y-A4).

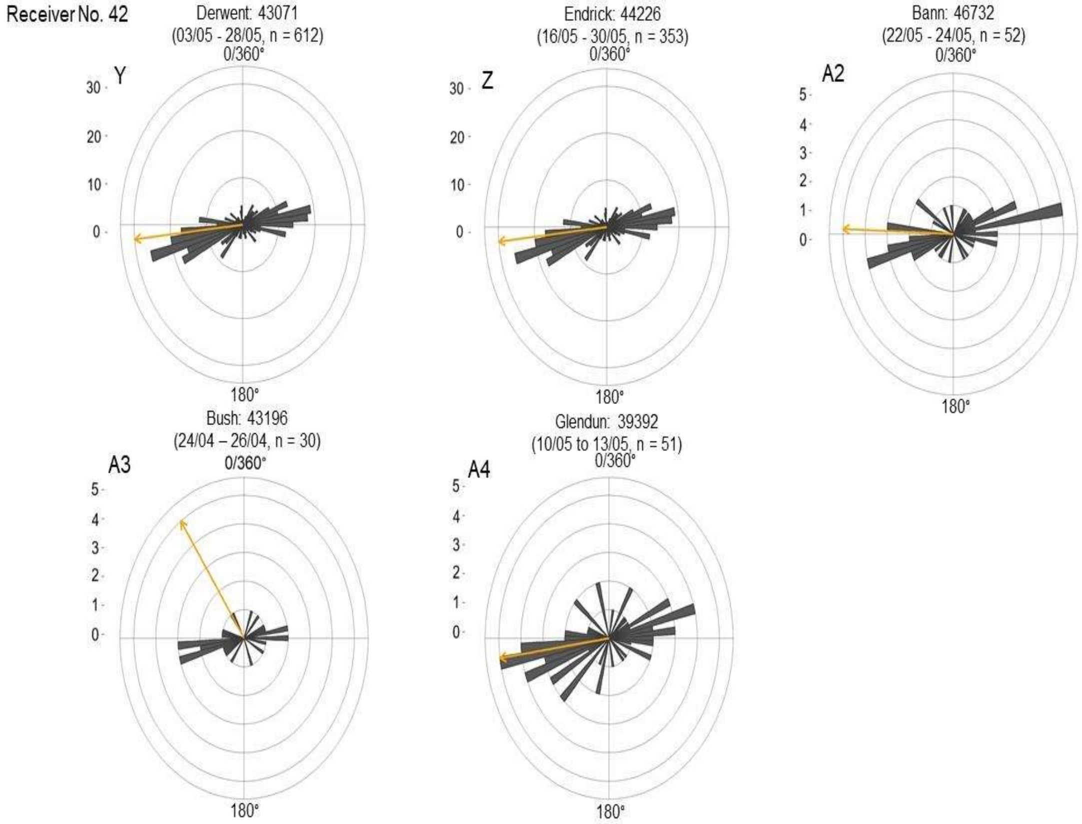


Figure A3.2. (continued) Rose diagrams depicting the direction of current (orange arrow) when a unique post-smolt (River location: identification number) was initially detected on monitoring line B, as well as the number of hours when currents were in a specific direction (grey bars) for the duration they were present in the Irish sea (Irish sea entry date – exit date, total number of hours). Modelled currents at each receiver location for the duration post-smolts were detected in the Irish sea was obtained from the Marine Institutes Northeast Atlantic hydrodynamic model (NEA-ROMS; Dabrowski et al., 2016). The graphs depict the top five receivers where the highest number of initial post-smolt detections occurred (Receiver 24: A-F; 40: G-L; 47: M-R; 47: S-X; 42: Y-A4).

Appendix 4: Supplementary Information for Chapter 5

(The early phase of the marine migration pathways of Atlantic salmon post- smolts from multiple rivers in Scotland, England, Northern Ireland and Ireland)

The following supplementary information provides further information about the projects involved in this chapter, the number of acoustic receivers deployed by each project, and the behavioural metrics of post-smolts during their coastal marine migration.

Table A4.1. Table describing the objectives of each project involved in the project as well as the rivers included in that project.

Project	Project dates	Objectives	Rivers included
SeaMonitor Project	2019 – 2022	Understand aspects of the early marine migratory behaviour of Atlantic salmon migrating from rivers in the British Isles	Endrick, Gryffe, Burrishoole, Carey, Glendun, Bush, Bann, Roe and Faughan
West Coast Tracking Project	2020 – 2023	Determine migration pathways of salmon post-smolts from a number of river catchments on the West of Scotland, through sea lochs and embayments towards the slope current at the continental shelf.	Nith, Bladnoch, Etive, Orchy, Loy, Lundy, Laxford, Badnabay and Laxay
Nith Smolt Tracking Project	2021	Examining the fresh water migration of salmon smolts throuth the River Nith	Nith, Crawick
Derwent Tracking Project	2020 – 2022	Understanding the behaviour of Atlantic salmon smolts migrating through the River Derwent and Irish Sea	Derwent
Torridon Tracking Project	2018 - present	Understand habitat usage and escapement timings of salmon and sea trout within Loch Torridon, Wester Ross, Scotland	Balgy and Torridon

Table A4.2. Table displaying the total number of acoustic receivers deployed and retrieved, as well as the duration they were deployed during 2021. Four types of acoustic receivers were deployed in this study, including VR2W, VR2Tx, and VR2AW, a basic description of each receiver type can be found in Lilly et al. (2021). Where there is a – under deployment duration this information was not provided by a partner.

Type	**Region**	**ID**	**Number of receivers recovered (Number of receivers deployed)**	**Latitude**	**Longitude**	**Deployment Duration**
River	Leven	-	1 (1)	55.939	-4.563	16-03 to 05-07
River	Gryfe	-	1 (1)	55.890	-4.406	09-04 to 20-07
River	Bladnoch	-	1 (1)	54.862	-4.434	24-03 to 19-07
River	Nith	-	1 (1)	55.046	-3.607	06-04 to 01-07
River	Lochy	-	1 (1)	56.832	-5.085	25-03 to 01-07
River	Etive	-	1 (1)	56.566	-5.064	11-04 to 22-07
River	Orchy	-	1 (1)	56.440	-5.227	12-04 to 21-07
River	Laxford	-	1 (1)	58.375	-5.017	16-04 to 01-07
River	Badnabay	-	1 (1)	58.372	-5.045	23-04 to 01-07
River	Laxay	-	1 (1)	58.099	-6.535	30-03 to 01-07
River	Bush	-	1 (1)	55.219	-6.532	01-04 to 13-09
River	Glendun	-	1 (1)	55.124	-6.044	06-04 to 06-10
River	Bann	-	2 (2)	55.171	-6.773	07-04 to 04-08
River	Carey	-	1 (1)	55.201	-6.233	06-04 to 27-08
River	Derwent	-	1 (1)	54.646	-3.542	24-03 to 22-07
River	Roe	-	1 (1)	55.109	-6.951	26-04 to 15-10
River	Faughan	-	1 (1)	55.035	-7.226	26-04 to 15-10
River	Derwent	-	1 (1)	54.646	-3.542	24-03 to 22-07
River	Burrishoole	-	1 (1)	53.906	-9.580	04-05 to 14-06
River	Balgy	-	1 (1)	57.531	-5.596	-
River	Torridon	-	1 (1)	57.540	-5.515	-
Estuary	Burrishoole	-	1 (1)	53.887	-9.588	04-05 to 14-06
Estuary	Clyde Estuary	C	6 (6)	55.725	-5.000	02-04 to 06-08
Fjord	Firth of Clyde	D	6 (6)	55.694	-5.437	02-04 to 06-08
Sea Loch	Laxford	-	5 (5)	58.424	-5.141	12-04 to 30-08
Sea Loch	Laxay	-	6 (6)	58.123	-6.358	13-04 to 17-12
Sea Loch	Etive	-	2 (2)	56.455	-5.411	01-04 to 26-08

Table A4.2. (continued) Table displaying the total number of acoustic receivers deployed and retrieved, as well as the duration they were deployed during 2021. Four types of acoustic receivers were deployed in this study, including VR2W, VR2Tx, and VR2AW, a basic description of each receiver type can be found in Lilly et al. (2021). Where there is a – under deployment duration this information was not provided by a partner.

Type	**Region**	**ID**	**Number of receivers recovered (Number of receivers deployed)**	**Latitude**	**Longitude**	**Deployment Duration**
Sea Loch	Linnhe	-	2 (2)	56.801	-5.150	01-04 to 26-08
Coastal Embayment	Runkerry Bay	-	7 (7)	55.226	-6.557	03-04 to?
Fjord	Lough Foyle	-	10 (10)	55.202	-6.948	24-03 to 26-08
Coastal Embayment	Waterfoot Bay	B	1 (1)	55.064	-6.041	-
Coastal Embayment	Clew Bay 1	-	5(5)	53.871	-9.656	28-04 to 22-06
Coastal Embayment	Clew Bay 2	-	9 (10)	53.843	-9.964	28-04 to 22-06
Sea Loch	Loch Torridon	-	1(1)	57.560	-5.704	-
Marine	Mull (Sound of Mull)	H	7 (8)	56.512	-5.767	01-04 to 26-08
Marine	Mull (Sound of Lorne)	G	10 (12)	56.383	-5.620	31-03 to 26-08
Marine	Harris to North Uist	K	15 (15)	57.791	-7.201	02-04 to 22-08
Marine	North Uist to Benbecula	K	1 (1)	57.466	-7.208	02-04 to 22-08
Marine	Benbecula to South Uist	K	2 (2)	57.391	-7.269	02-04 to 22-08
Marine	South Uist to Eriskay	I	1 (2)	57.092	-7.270	02-04 to 22-08
Marine	Eriskay to Barra	I	9 (11)	57.030	-7.324	02-04 to 22-08
Marine	Vatersay to Sandray	I	2 (2)	56.907	-7.533	03-04 to 22-08
Marine	Sandray to Pabbay	I	2 (6)	56.871	-7.557	03-04 to 22-08
Marine	Pabbay to Mingulay	I	3 (4)	56.840	-7.601	03-04 to 22-08
Marine	Mingulay to Bernasay	I	1 (1)	56.796	-7.643	03-04 to 22-08
Marine	Lewis	L	8 (12)	58.249	-6.047	12-04 to 17-12
Marine	Sutherland	M	17 (18)	58.506	-5.248	13-04 to 30-08
Marine	Skye to Uist	J	58 (69)	57.269	-6.863	01-04 to 26-08

Table A4.2. (continued) Table displaying the total number of acoustic receivers deployed and retrieved, as well as the duration they were deployed during 2021. Four types of acoustic receivers were deployed in this study, including VR2W, VR2Tx, and VR2AW, a basic description of each receiver type can be found in Lilly et al. (2021). Where there is a – under deployment duration this information was not provided by a partner.

Type	**Region**	**ID**	**Number of receivers recovered (Number of receivers deployed)**	**Latitude**	**Longitude**	**Deployment Duration**
Marine	Islay to Jura	G	1 (1)	56.141	-5.629	31-03 to 29-08
Marine	Jura to mainland Scotland	G	6 (10)	55.883	-6.108	31-03 to 29-08
Marine	Skye to mainland Scotland	J	1 (2)	57.224	-5.654	31-03 to 29-08
Marine	Irish Sea	E	103 (112)	55.494	-6.886	27-02 to 14-09
Marine	Irish Sea	A	20 (22)	55.931	-5.477	19-03 to 3-08
Marine	North Atlantic Ocean (south of Hebridean Islands)	N	1 (1)	56.604	-7.855	-
Marine	North Atlantic Ocean (west of Hebridean Islands)	O	1 (1)	58.092	-8.913	-
Marine	North Atlantic (west of Hebridean Islands)	P	1 (1)	58.0918	-8.913	
Marine	North Atlantic (Continental Shelf – submersible glider)	Q	1 (1)	58.584	-8.614	-

Table A4.3. The total number of Atlantic salmon post-smolts (TCI) and marine (Mar) waters. The statistics calculated in this table were calculated for each section of the migratory journey, which included the number of post-smolts detected at the start and end arrays and the date range post-smolts were detected on the end array for each section. The loss rate was only calculated through tidal coastal inlets and for monitoring lines C, D and E. The total duration (days) and Rate of Movement (RoM) between monitoring lines (body length per second (LF s-1) / kilometres per day (km.day-1)) were also calculated. There were some instances where not all smolts detected on the end array were also detected on the start array, therefore, in these cases ROM was calculated using a proportion of the smolts detected. Note, Est – Estuary and CE – Coastal Embayment.

River	**Type**	**Start array**	**End array**	**Distance (km)**	**No. start array**	**No. end array (%)**	**Loss rate (%.km^{-1})**	**Date range for detections at end array**	**No. used to calculate ROM**	**Mean RoM (L_F s^{-1}) ± SD (range)**	**Mean RoM (km.day^{-1}) ± SD (range)**	**Mean passage time (days) ± SD (range)**
Endrick	Est	Leven	C	46.70	50	38 (76.00)	0.51	28-04 to 31-05	38	0.81 ± 0.44 (0.17 - 2.14)	10.14 ± 5.62 (2.12 - 27.61)	4.75 ± 1.25 (3.30 - 16.21)
	Mar	C	A	86.80	38	4 (10.23)	-	13-05 to 25-05	3	0.59 ± 0.24 (0.33 - 0.82)	7.18 ± 2.62 (4.3 - 9.45)	13.50 ± 9.19 (5.86 - 20.18)
	Mar	C	E	168.00	38	9 (23.68)	0.45	12-05 to 18-06	9	0.77 ± 0.14 (0.55 - 0.96)	9.69 ± 1.71 (7.11 - 11.95)	17.86 ± 14.05 (3.37 - 23.63)
Gryffe	Est	Gryffe	C	58.40	93	80 (86.02)	0.24	22-04 to 22-05	80	1.06 ± 0.43 (0.3 - 2.22)	13.65 ± 5.51 (3.64 - 27.56)	5.18 ± 2.12 (2.66 - 16.05)
	Mar	C	D	27.90	80	4 (5.00)	-	28-04 to 30-05	4	0.34 ± 0.17 (0.16 - 0.57)	4.32 ± 2.37 (2.05 - 7.64)	8 ± 3.65 (4.14 - 13.63)
	Mar	C	A	86.80	80	6 (7.50)	-	06-05 to 04-06	6	0.46 ± 0.23 (0.18 - 0.82)	6.05 ± 2.85 (2.38 - 10.33)	17.80 ± 8.40 (10.02 - 36.48)
	Mar	C	E	168.00	80	27 (33.75)	0.39	04-05 to 06-06	25	1.18 ± 0.47 (0.33 - 2.38)	14.87 ± 5.59 (4.41 - 28.84)	13.15 ± 5.83 (6.32 - 38.09)
	Mar	A	E	86.80	80	6 (7.5)	1.07	06-05 to 04-06	6	0.46 ± 0.23 (0.18 - 0.82)	6.05 ± 2.85 (2.38 - 10.33)	17.80 ± 8.40 (10.02 - 36.48)
	Mar	C	B	111.00	80	1 (1.25)	-	15-05	1	0.4	6.77	16.39
	Mar	C	Q	548	80	1	-	23-05	1	1.5	22.52	24.33
Nith and Crawick	Mar	Nith	A	170.00	90	20 (22.22)	0.46	11-05 to 01-06	17	1.25 ± 0.44 (0.44 – 2.01)	15.84 ± 5.49 (6.17 – 25.34)	12.54 ± 5.94 (6.71 – 27.55)
		A	E	108.00	20	6 (30.00)	0.65	19-05 to 06-06	3	2.69 ± 1.19 (1.34 – 3.62)	36.70 ± 17.09 (18.89 – 51.29)	3.59 ± 2.13 (2.11 – 6.04)
		Nith	E	278.00	90	6 (6.67)	0.36	19-05 to 06-06	6	1.05 ± 0.49 (0.66 – 1.90)	14.27 ± 7.03 (8.94 – 26.86)	22.81 ± 8.45 (10.35 31.10)

Table A4.3. (continued) The total number of Atlantic salmon post-smolts detected at key monitoring points/ lines in this study in both tidal coastal inlets (TCI) and marine (Mar) waters. The statistics calculated in this table were calculated for each section of the migratory journey, which included the number of post-smolts detected at the start and end arrays and the date range post-smolts were detected on the end array for each section. The loss rate was only calculated through tidal coastal inlets and for monitoring lines C, D and E. The total duration (days) and Rate of Movement (RoM) between monitoring lines (body length per second (LF s-1) / kilometres per day (km.day-1)) were also calculated. There were some instances where not all smolts detected on the end array were also detected on the start array, therefore, in these cases ROM was calculated using a proportion of the smolts detected. Note, Est – Estuary and CE – Coastal Embayment.

River	Type	Start array	End array	Distance (km)	No. start array	No. end array (%)	Loss rate (%.km^{-1})	Date range for detections at end array	No. used to calculate ROM	Mean RoM (L_F s^{-1}) ± SD (range)	Mean RoM (km.day^{-1}) ± SD (range)	Mean passage time (days) ± SD (range)
Bladnoch	Mar	Bladnoch	A	123.00	53	12 (22.22)	0.63	13-05 to 06-06	9	1.05 ± 0.33 (0.77 - 1.66)	12.85 ± 4.17 (9.71 - 20.69)	10.28 ± 2.50 (5.95 - 12.66)
		A	E	108.00	12	5 (41.67)	0.54	16-05 to 07-06	2	3.17 ± 0.6 (2.75 - 3.59)	38.99 ± 2.77 (37.03 - 40.95)	2.78 ± 0.2 (2.64 - 2.92)
		Bladnoch	E	238.00	53	5 (9.43)	0.38	16-05 to 07-06	5	1.18 ± 0.38 (0.73 - 1.63)	14.87 ± 4.17 (9.96 - 18.75)	20.06 ± 6.14 (14.83 - 27.92)
Etive	Mar	Loch Etive	G	15.30	62	22 (35.48)	-	29-04 to 22-05	21	1.22 ± 0.70 (0.42 – 3.07)	14.56 ± 8.25 (4.83 – 34.98)	1.46 ± 0.87 (0.44 – 3.17)
	Mar	Loch Etive	H	24.20	62	6 (9.70)	-	30-04 to 23-05	5	0.99 ± 0.31 (0.56 – 1.43)	11.93 ± 4.66 (6.43 – 19.29)	2.29 ± 0.92 (1.25 – 3.76)
	Mar	Loch Etive	J	172.00	62	1 (1.61)	-	27-05	0	-	-	14.16
	Mar	Loch Etive	N	159.00	62	1 (1.61)	-	25-05	0	-	-	11.53
Orchy	Mar	Loch Etive	G	15.30	90	24 (26.67)	-	23-04 to 24-05	23	1.39 ± 0.63 (0.38 – 2.57)	16.38 ± 7.47 (4.29 – 30.43)	1.27 ± 0.87 (0.50 – 3.56)
	Mar	Loch Etive	H	24.20	90	17 (18.89)	-	28-04 to 23-05	15	1.32 ± 0.53 (0.56 – 0.23)	16.72 ± 7.15 (6.99 – 32.60)	1.75 ± 0.83 (0.74 – 3.46)
	Mar	Loch Etive	E	139.00	90	1 (1.11)	-	15-05	1	1.30	16.26	8.55
	Mar	Loch Etive	I	142.00	90	2 (2.22)		11-05 to 13-05	2	1	11.62	11.40
	Mar	Loch Etive	J	137.00	90	1 (1.11)	-	07-05	1	0.73	9.61	14.16
	Mar	Loch Etive	Q	362	90	1	-	29-05	1	1.48	17.87	20.25
Loy and Lundy	Mar	Loch Linnhe	G	53.00	107	33 (30.84)	-	02-05 to 21-07	27	1.75 ± 0.63 (0.87 – 3.36)	20.70 ± 7.20 (10.12 – 38.05)	2.87 ± 1.0 (1.39 – 5.23)
		Loch Linnhe	H	52.00	107	48 (44.86)	-	21-04 to 20-07	42	2.14 ± 0.79 (0.85 – 4.18)	25.16 ± 9.26 (9.92 – 46.96)	2.41 ± 1.04 (1.11 – 5.24)
		G	J	234.00	107	1 (0.93)	-	14-05	1	1.19	14.02	16.69

Table A4.3. (continued) The total number of Atlantic salmon post-smolts detected at key monitoring points/ lines in this study in both tidal coastal inlets (TCI) and marine (Mar) waters. The statistics calculated in this table were calculated for each section of the migratory journey, which included the number of post-smolts detected at the start and end arrays and the date range post-smolts were detected on the end array for each section. The loss rate was only calculated through tidal coastal inlets and for monitoring lines C, D and E. The total duration (days) and Rate of Movement (RoM) between monitoring lines (body length per second (LF s-1) / kilometres per day (km.day-1)) were also calculated. There were some instances where not all smolts detected on the end array were also detected on the start array, therefore, in these cases ROM was calculated using a proportion of the smolts detected. Note, Est – Estuary and CE – Coastal Embayment.

River	Type	Start array	End array	Distance (km)	No. start array	No. end array (%)	Loss rate (%.km^{-1})	Date range for detections at end array	No. used to calculate ROM	Mean RoM (L_F s^{-1}) ± SD (range)	Mean RoM (km.day^{-1}) ± SD (range)	Mean passage time (days) ± SD (range)
		H	J	172.00	107	1 (0.93)	-	02-05 to 08-05	1	1.68	19.56	8.79
Badnabay	Mar	Loch Laxford	M	11.70	4	2 (50.00)	-	02-05 to 11-05	1	1.88	22.78	0.51
Laxford	Mar	Loch Laxford	M	11.70	62	27 (43.55)	-	01-05 to 17-05	22	2.52 ± 0.94 (1.12 – 4.44)	31.07 ± 12.08 (13.16 – 53.38)	0.44 ± 0.19 (0.22 – 0.89)
Laxay	Mar	Loch Eireasort	L	22.80	64	12 (18.75)	-	22-04 to 17-05	6	1.40 ± 0.41 (0.63 – 1.73)	16.93 ± 5.32 (7.20 – 21.19)	1.55 ± 0.81 (1.08 – 3.16)
	Mar	Loch Eireasort	M	74.30	64	13 (20.31)	-	02-05 to 17-05	13	1.07 ± 0.42 (0.50 – 2.09)	13.45 ± 5.1 (6.75 – 24.93)	6.30 ± 2.41 (2.98 – 11.01)
Roe	xxx	Roe	Lough Foyle	14.80	9	6 (66.67)	2.52	05-05 to 13-05	3	0.4 ± 0.25 (0.12 - 0.6)	5.38 ± 3.3 (1.62 - 7.78)	4.41 ± 1.9 (4.1 -9.15)
	Mar	Lough Foyle	E	37.80	6	5 (83.33)	0.44	06-05 to 13-05	5	3.08 ± 0.9 (2.21 - 4.05)	39.94 ± 12.04 (27.69 - 52.93)	1.02 ± 0.71 (0.3 - 1.37)
Faughan	xxx	Faughan	Lough Foyle	27.00	38	19 (50.00)	1.85	12-05 to 02-06	19	1.13 ± 0.4 (0.69 - 1.88)	13.75 ± 4.76 (8.68 - 23.11)	2.16 ± 1.17 (0.66 - 3.11)
	Mar	Lough Foyle	E	37.8	19	18 (94.73)	0.14	13-05 to 01-06	10	2.39 ± 1.19 (0.33 - 4.45)	29.56 ±15.30 (3.87 - 55.78)	2.24 ± 0.68 (2.74 - 9.76)
Bush	CE	Bush	Runkerry Bay	1.81	73	64 (87.67)	6.81	18-04 to 09-05	64	2.43 ± 2.14 (0.05-8.35)	35.22 ± 30.75 (0.7 - 119.1)	0.19 ± 0.36 (0.02 - 2.58)
	Mar	Runkerry Bay	E	45.3	64	39 (60.94)	0.86	07-05 to 29-04	37	2.02 ± 0.82 (0.45 - 4.17)	29.44 ± 12.23 (7.51 - 59.81)	1.9 ± 1.07 (0.76 - 6.04)
	Mar	Runkerry Bay	G	124	64	1 (1.56)	-	28-04	1	1.03	16.23	7.64

Table A4.3. (continued) The total number of Atlantic salmon post-smolts detected at key monitoring points/ lines in this study in both tidal coastal inlets (TCI) and marine (Mar) waters. The statistics calculated in this table were calculated for each section of the migratory journey, which included the number of post-smolts detected at the start and end arrays and the date range post-smolts were detected on the end array for each section. The loss rate was only calculated through tidal coastal inlets and for monitoring lines C, D and E. The total duration (days) and Rate of Movement (RoM) between monitoring lines (body length per second (LF s-1) / kilometres per day (km.day-1)) were also calculated. There were some instances where not all smolts detected on the end array were also detected on the start array, therefore, in these cases ROM was calculated using a proportion of the smolts detected. Note, Est – Estuary and CE – Coastal Embayment.

River	Type	Start array	End array	Distance (km)	No. start array	No. end array (%)	Loss rate (%.km^{-1})	Date range for detections at end array	No. used to calculate ROM	Mean RoM (L_F s^{-1}) ± SD (range)	Mean RoM (km.day^{-1}) ± SD (range)	Mean passage time (days) ± SD (range)
Glendun	Mar	Glendun	E	83.40	21	5 (23.81)	0.91	02-05 to 15-05	5	1.34 ± 0.24 (1.08 - 1.74)	16.39 ± 3.25 (12.09 - 21.04)	2.97 ± 0.61 (2.24 - 3.90)
	Mar	Glendun	I	233.00	21	1 (4.76)	-	05-06	0	-	-	-
	Mar	Glendun	P	391.0	21	1	-	19-05	1	1.93	25.87	15.11
	Mar	Glendun	G	150.0	21	1	-	26-05	1	0.51	6.57	22.84
Bann and Agivey	Mar	Bann	E	45.60	34	21 (61.76)	0.84	05-05 to 26-05	17	2.79 ± 0.93 (1.47 - 4.67)	38.56 ± 12.86 (20.29 - 61.64)	1.31 ± 0.44 (0.74 to 2.25)
	Mar	Bann	Q	402.0	34	1	-	31-05	1	1.7	22.10	18.19
Carey	Mar	Carey	E	60.40	7	3 (60.00)	0.95	05-05 to 07-05	2	0.99 ± 0.28 (0.8 - 1.19)	14.18 ± 4.89 (10.73 - 17.64)	4.53 ± 1.56 (3.42 - 5.63)
Derwent	Mar	Derwent	A	139.00	41	15 (36.58)	0.46	11-05 to 06-06	3	0.98 ± 0.53 (0.6 - 1.58)	11.56 ± 6.01 (6.86 - 18.33)	14.17 ± 6.35 (7.58 - 20.25)
	Mar	Derwent	C	235.00	41	1 (2.44)	-	25-06	1	0.72	9.1	25.83
	Mar	Derwent	D	218.00	41	3 (7.32)	-	06-06 to 13-07	2	0.63 ± 0.11 (0.55 - 0.7)	7.76 ± 1.6 (6.63 - 8.89)	28.71 ± 5.91 (24.53 - 32.89)
	Mar	Derwent	E	256.00	41	11 (26.83)	0.29	13-05 to 20-06	7	1.18 ± 0.61 (0.46 - 2.18)	14.03 ± 7.32 (5.52 - 25.28)	23.04 ± 12.14 (10.13 - 46.53)
	Mar	Derwent	P	564.00	41	1 (2.44)	-	08-06	0	-	-	-

Table A4.3. (continued) The total number of Atlantic salmon post-smolts detected at key monitoring points/ lines in this study in both tidal coastal inlets (TCI) and marine (Mar) waters. The statistics calculated in this table were calculated for each section of the migratory journey, which included the number of post-smolts detected at the start and end arrays and the date range post-smolts were detected on the end array for each section. The loss rate was only calculated through tidal coastal inlets and for monitoring lines C, D and E. The total duration (days) and Rate of Movement (RoM) between monitoring lines (body length per second (LF s-1) / kilometres per day (km.day-1)) were also calculated. There were some instances where not all smolts detected on the end array were also detected on the start array, therefore, in these cases ROM was calculated using a proportion of the smolts detected. Note, Est – Estuary and CE – Coastal Embayment.

River	Type	Start array	End array	Distance (km)	No. start array	No. end array (%)	Loss rate (%.km^{-1})	Date range for detections at end array	No. used to calculate ROM	Mean RoM (L_F s^{-1}) ± SD (range)	Mean RoM (km.day^{-1}) ± SD (range)	Mean passage time (days) ± SD (range)
	Mar	Derwent	E	256.00	41	11 (26.83)	0.29	13-05 to 20-06	7	1.18 ± 0.61 (0.46 - 2.18)	14.03 ± 7.32 (5.52 - 25.28)	23.04 ± 12.14 (10.13 - 46.53)
	Mar	Derwent	P	564.00	41	1 (2.44)	-	08-06	0	-	-	-
Burrishoole (Wild)	CE	Burrishoole estuary	Clew Bay 1	4.89	17	15 (88.24)	2.41	07-05 to 15-05	14	1.94 ± 1.25 (0.23 - 3.95)	25.31 ± 16.90 (2.87 - 54.17)	0.37 ± 0.42 (0.09 - 1.71)
(Ranched)	CE	Burrishoole estuary	Clew Bay 1	4.89	51	37 (72.55)	5.61	06-05 to 05-06	35	1.40 ± 1.57 (0.01 - 4.22)	23.72 ± 26.48 (0.16 - 72.59)	3.47 ± 6.09 (0.07 - 30.27)
(Wild)	CE	Burrishoole estuary	Clew Bay2	25.70	17	7 (41.18)	2.29	12-05 to 22-05	7	1.77 ± 1.30 (0.23 - 3.29)	23.08 ± 16.81 (2.83 - 43.18)	2.72 ± 3.17 (0.60 - 9.07)
(Ranched)	CE	Burrishoole estuary	Clew Bay 2	25.70	51	15 (29.41)	2.75	09-05 to 15-05	15	1.50 ± 1.01 (0.37 - 2.91)	25.44 ± 17.39 (6.61 - 53.71)	1.64 ± 1.09 (0.48 - 3.89)
(Ranched)	Mar	Clew Bay 2	N	364	15	2 (13.33)	-	24-05	0	-	-	-
(Ranched)	Mar	Clew Bay 2	O	386	15	1 (6.67)	-	06-05	1	0.75	65	5.92
(Ranched)	Mar	Clew Bay 2	Q	541	15	1 (6.67)	0.17	04-06	1	0.24	20.74	26.09

Table A4.3. (continued) The total number of Atlantic salmon post-smolts detected at key monitoring points/ lines in this study in both tidal coastal inlets (TCI) and marine (Mar) waters. The statistics calculated in this table were calculated for each section of the migratory journey, which included the number of post-smolts detected at the start and end arrays and the date range post-smolts were detected on the end array for each section. The loss rate was only calculated through tidal coastal inlets and for monitoring lines C, D and E. The total duration (days) and Rate of Movement (RoM) between monitoring lines (body length per second (LF s-1) / kilometres per day (km.day-1)) were also calculated. There were some instances where not all smolts detected on the end array were also detected on the start array, therefore, in these cases ROM was calculated using a proportion of the smolts detected. Note, Est – Estuary and CE – Coastal Embayment.

River	**Type**	**Start array**	**End array**	**Distance (km)**	**No. start array**	**No. end array (%)**	**Loss rate (%.km^{-1})**	**Date range for detections at end array**	**No. used to calculate ROM**	**Mean RoM (L_F s^{-1}) ± SD (range)**	**Mean RoM (km.day^{-1}) ± SD (range)**	**Mean passage time (days) ± SD (range)**
Torridon	Mar	Loch Torridon	M	118	3	2 (66.67)	-	06-05 to 11-05	1	1.50 ± 0.80 (0.94 - 2.06)	18.13 ± 10.41 (10.77 - 25.49)	7.79 ± 4.48 (4.63 - 10.96)
Balgy	Mar	Loch Torridon	L	81.50	5	1 (20)	-	01-05	1	1.46	19.39	4.20
	Mar	Loch Torridon	M	118	5	4 (80)	-	10-05 to 13-05	4	11.64 ± 3.23 (0.09 - 15.98)	0.12 ± 0.03 (0.09 - 0.15)	10.69 ± 2.68 (7.39 - 12.99)

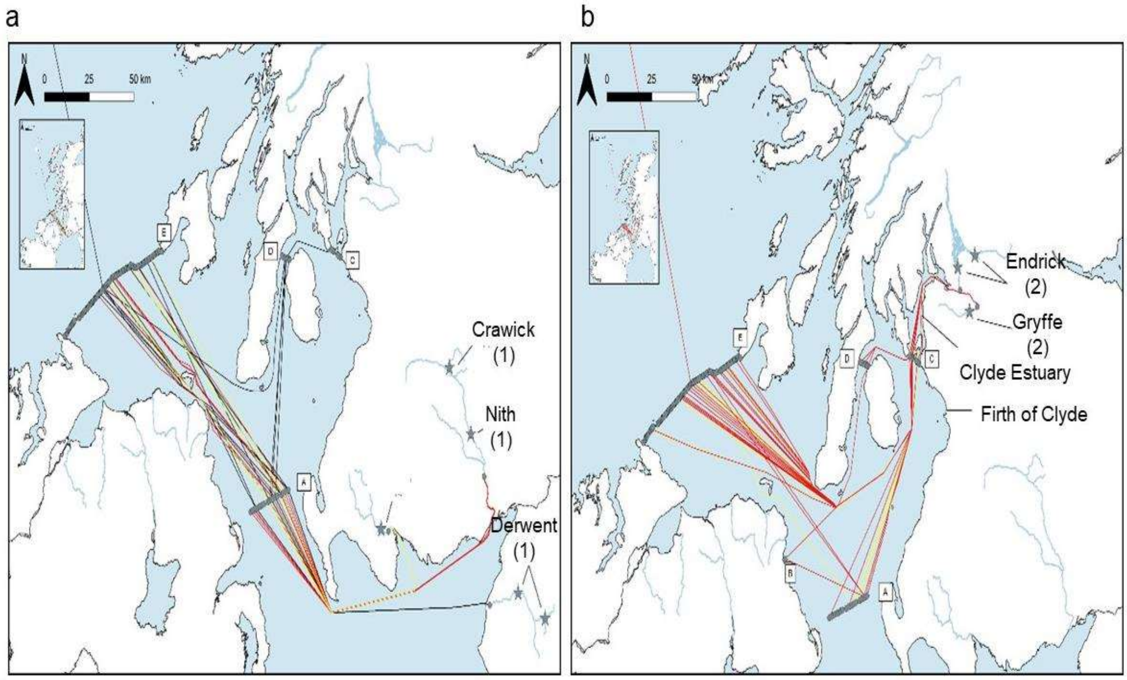
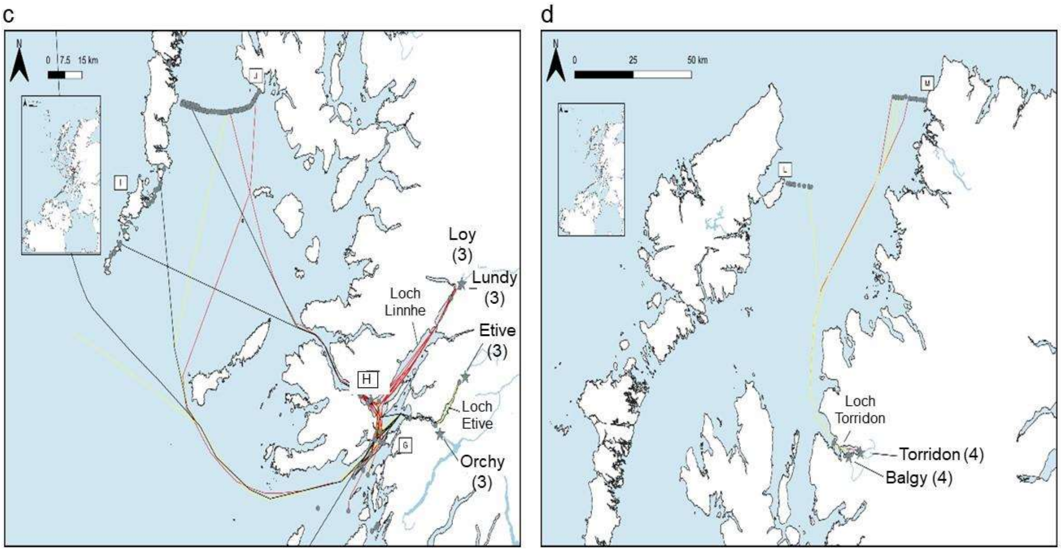


Figure A4.1. Maps illustrating the migratory pathways of Atlantic salmon post-smolts as they migrate from their natal rivers to sea. The pathways illustrated are simplified representations and do not represent the true migratory pathways post-smolts undertook. Migratory pathways were grouped into eight monitoring regions, based on rivers that drain into the same coastal environment this includes a - Region 1: Solway Firth (rivers Derwent, Nith, Crawick, Bladnoch); b - Region 2: Clyde marine region (rivers Endrick, Gryffe); c - Region 3: Loch Linnhe (rivers Loy, Lundy, Etive, Orchy); d - Region 4: Loch Torridon (Rivers Balgy and Torridon), e -Region 5:Loch Eireasort (River Laxay); f - Region 6: Loch Laxford (rivers Laxford, Badnabay); g - Region 7: Bush marine region (rivers Bann, Agivey, Bush, Carey, Glendun); h - Region 8: Foyle marine region (rivers Roe, Faughan); and i - Region 9 (River Burrishole). The pathways of post-smolts from each river system is given a unique colour and each line represents an individual post-smolts pathway.



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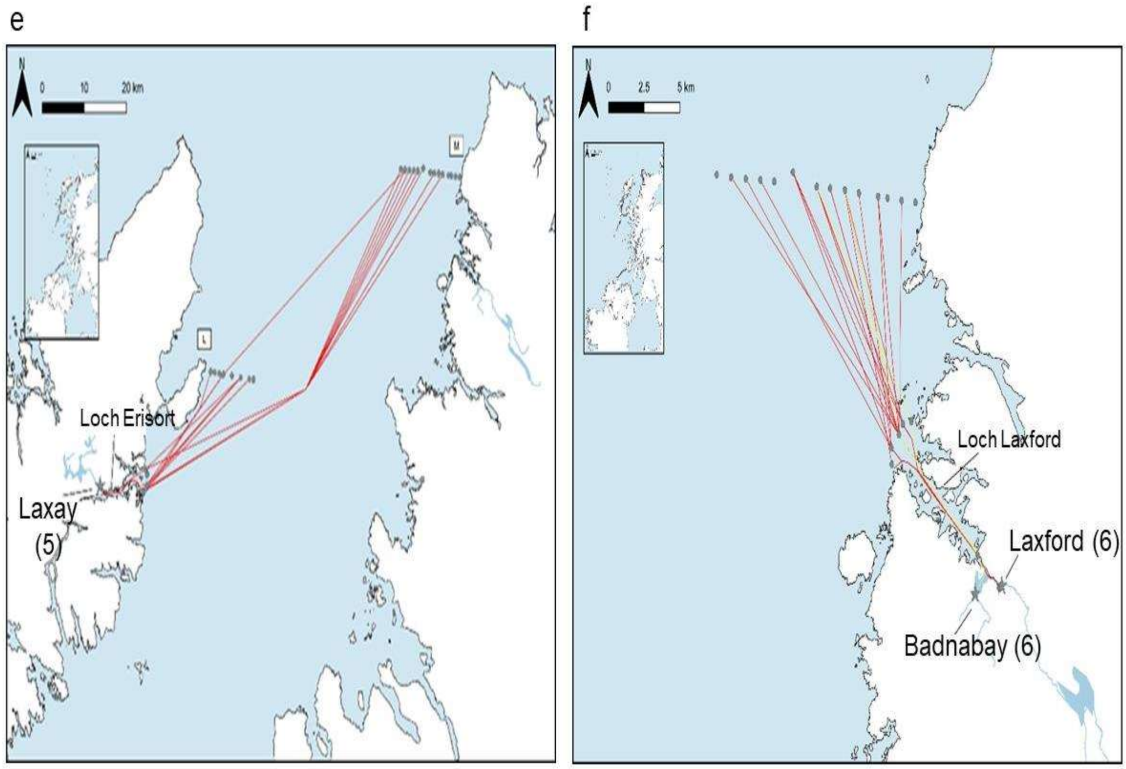

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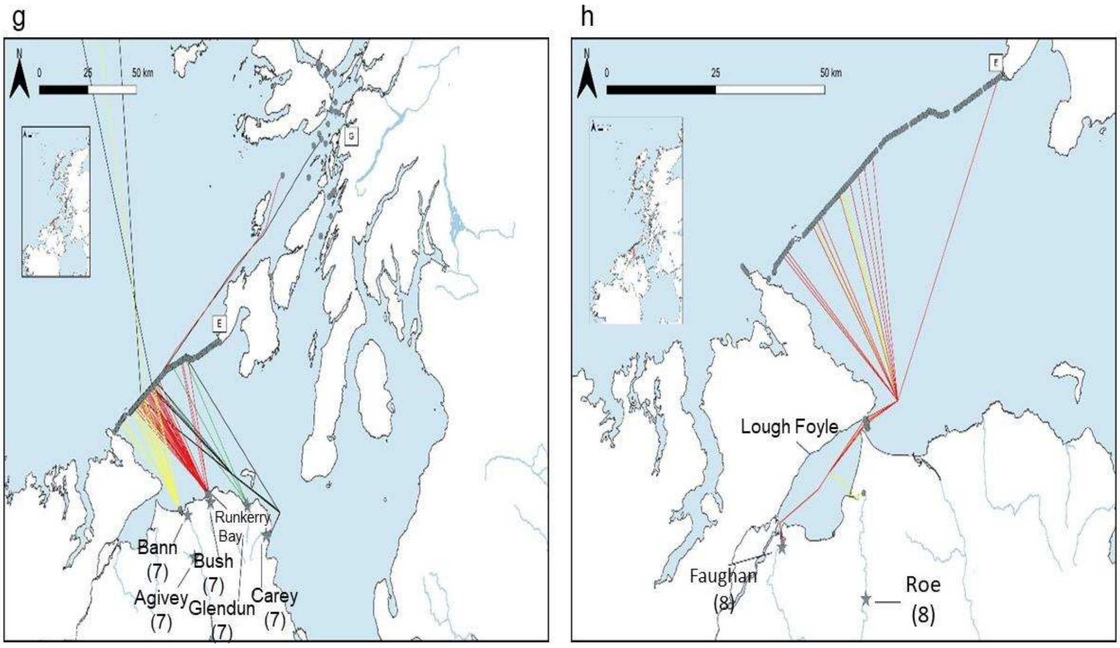

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i

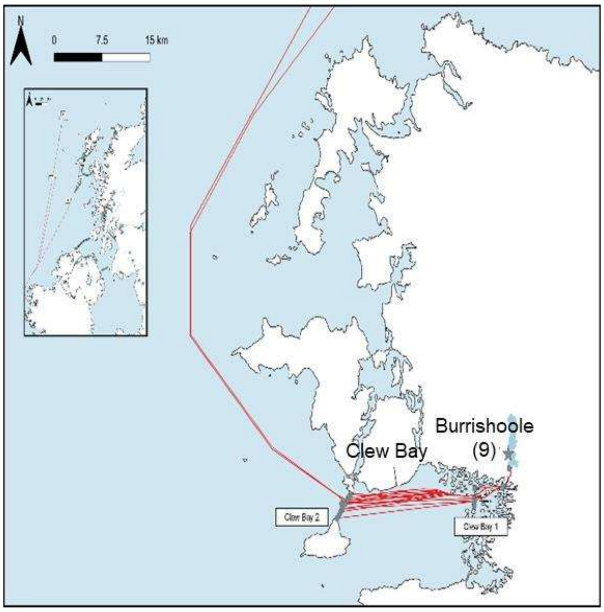

Figure A4.1. (continued) Maps illustrating the migratory pathways of Atlantic salmon post-smolts as they migrate from their natal rivers to sea. The pathways illustrated are simplified representations and do not represent the true migratory pathways post-smolts undertook. Migratory pathways were grouped into eight monitoring regions, based on rivers that drain into the same coastal environment this includes a - Region 1: Solway Firth (rivers Derwent, Nith, Crawick, Bladnoch); b - Region 2: Clyde marine region (rivers Endrick, Gryffe); c - Region 3: Loch Linnhe (rivers Loy, Lundy, Etive, Orchy); d - Region 4: Loch Torridon (Rivers Balgy and Torridon), e -Region 5:Loch Eireasort (River Laxay); f - Region 6: Loch Laxford (rivers Laxford, Badnabay); g - Region 7: Bush marine region (rivers Bann, Agivey, Bush, Carey, Glendun); h - Region 8: Foyle marine region (rivers Roe, Faughan); and i - Region 9 (River Burrishole). The pathways of post-smolts from each river system is given a unique colour and each line represents an individual post-smolts pathway.

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