# Assessing the impact of river barriers on successful seaward migration of Atlantic salmon, *Salmo salar* L. along the River Derwent, Cumbria

by


**Amy Green**
BSc (Hons), University of Hull, 2018
MRes, Newcastle University, 2019



**Scottish Centre for Ecology and the Natural Environment**
**Institute of Biodiversity, One Health and Veterinary Medicine**
**College of Medical, Veterinary and Life Sciences**
**University of Glasgow**


This thesis is submitted in fulfilment of the requirements of the degree of Doctor of Philosophy

**May 2024**

**Abstract**

The Atlantic salmon, *Salmo salar,* Linnaeus 1785, is well studied due to its economical, ecological, and cultural importance across Europe, Scandinavia, and North America. Nonetheless significant gaps in our understanding persists when it comes to their life history, particularly during the smolt phase which has been considered as one of the most vulnerable phases in the Atlantic salmon life cycle. In recent decades, management and research incentives have concentrated primarily on enhancing and understanding migration behaviour of Atlantic salmon within freshwater environments. Despite management efforts, Atlantic salmon populations continue to decline with some European populations becoming extinct. Previous research has suggested that the decline is at least in part, related to increased habitat fragmentation resulting from artificial river-spanning infrastructure within the riverine environment which partially or completely impedes migration. This thesis describes a series of studies using acoustic telemetry that have provided evidence to fill the knowledge gaps in literature regarding downstream migratory behaviour of Atlantic salmon smolts from a UK tributary (River Derwent, Cumbria) draining into the Solway Firth.

Although Atlantic salmon migration through riverine environments have been extensively researched, there are gaps in literature regarding the inter-annual spatial variation in migration success through the river system. Previous studies have mostly focussed on overall river migration success rates. In this study I focus with greater precision on potential bottleneck zones within a river system which contribute to reduced migration success rates of Atlantic salmon. By combining acoustic telemetry and statistical modelling, smolts were tracked through the entire River Derwent. A

number of potential factors that might influence migration success were assessed to understand specific geographic areas in which success is reduced and identify the factors which change the likelihood of smolts completing a successful riverine migration. Upstream areas of the River Derwent had a greater impact on migrating smolts, although variation in migration success across the three years of the study were observed. Consistent with previous literature, smolts experiences high overall loss rates during river migration (2020: 8% (*n=8*), 2021: 27.3% (*n=41*), 2022: 41.7% (*n=48*)). Migration speed (Rate of Movement ($m.s^{-1}$) and ground speed ($km.day^{-1}$) varied across river section and year but was consistently slow. There was also variation between years. Speed of migration in 2021 was found to be significantly higher when predicting rate of movement compared to 2020 and 2022, which is consistent with high water levels observed during tagging and release in 2021. Further investigations into the spatial variation of riverine systems across longer time scales are required to fully identify and understand how individual river reach characteristics may impact on migration success rates and speed; to determine if these are site specific or if these reach effects can be applied more widely.

The natural standing water present in the River Derwent (Bassenthwaite Lake) was identified as a bottleneck zone for migration and was found to decrease the likelihood of migration success. The understanding of the effect of natural standing waters remains limited and speculation still remains as to the cues associated with successful smolt navigation though these systems. Previous studies have highlighted natural standing waters associated with reduced migration rates, where some studies suggest non-directional pathways are one of the direct causes of migration mortality. Using acoustic telemetry and statistical modelling, I investigated potential factors which may increase successful migration likelihood through the most northernly un-impounded lake in the Derwent catchment. The evidence from this study is consistent with previous research and showed that migrating Derwent smolts experience high loss rates within Bassenthwaite Lake (33%), slow migration (0.16 $m.s^{-1}$) and non-directional movements. There was no evidence of phenotypic, behavioural or environmental effects that distinguished successful from unsuccessful lake migrant smolts. This suggests that migration success in Bassenthwaite Lake was random. I determined that the concept of a "Goldilocks Zone" is applicable to Bassenthwaite Lake and estimated the average minimum distance of this zone to be 0.72 ± 0.6 km (mean ± SD; range: 0.13 – 1.24) from the lake exit, though it remains unclear if the "Goldilocks Zone" is more generally applicable to all standing waters or if its specific to only natural lake systems.

The effect of small river-spanning infrastructure (low-head weirs, >5m height) on downstream migrating smolts remains poorly understood. In Chapter 4, the success rates, behaviours associated with success and the ability to choose alternative passage around weir structures was investigated using a combination of acoustic telemetry and statistical modelling. Smolt migration failure rates differed across both weirs, with Coops Weir having a failure rate of 1.49-2.24%.$km^{-1}$ and between 0–32.2%.$km^{-1}$ for Yearl Weir. Both of these figures are considerable higher when compared to other studies and overall riverine failure rates elsewhere within the River Derwent, although there was evidence to suggest that smolts may choose to migrate by an alternative route around and not over the low head weirs studied in this work. Although it remains unclear as to whether migration failure rate across weirs was due to lack of preparedness to high salinity environments, injury or disorientation/stress as a result of passage or predation.

Once smolts successful migrate through the riverine environment across both natural and anthropogenic barriers, transitioning from freshwater to saltwater environments smolts must navigate through the early marine environment to reach key feeding grounds. However, despite the rapidly developing understanding of migration in freshwater systems, the knowledge gaps around marine environment migration trajectories remain. By combining data from five acoustic telemetry studies we are able to document the migration of post-smolts from the west coast of northern England. Migration success differed significantly across the three years of the study, although migration success rate (%.$km^{-1}$) was found to be higher in freshwater systems compared with the early marine environment. It was found that in 2021 smolts, used a northward migration pathway through the Irish Sea, although this study provided evidence to suggest that the Derwent populations may be impacted by aquaculture sites around the coast of Arran through which smolts were found to migrate around.

The five data chapters presented in this thesis employed acoustic telemetry to model and assess Atlantic salmon smolt migration behaviour across a three-year study period through the riverine and early marine environment. The results obtained from this thesis will be developed by future research and used by government bodies to aid in identifying potential stressors on migration within the riverine environment which could impact Atlantic salmon populations.

# Table of Contents

## List of Figures

.

## List of Tables

.

# Appendices

# Abbreviations

| | |
|---|---|
| CEFAS | Centre for Environment, Fisheries and Aquaculture Science |
| COA | Centre of Activity |
| COMPASS | Collaborative Oceanography and Monitoring for Protected Areas and Species |
| BBKUD | Brownian Bridge Kernel Utilisation Distribution |
| $BL.s^{-1}$ | Body lengths per second |
| BST | British summer time |
| EA | Environment Agency |
| ESU | Evolutionary significant units |
| $L_F$ | Fork length |
| GLM | General linear model |
| GLMM | General linear mixed model |
| GMT+1 | Greenwich mean time |
| hrs | Hours |
| IQR | Interquartile range |
| $km.day^{-1}$ | Kilometres per day |
| MDT | Minimum distance travelled |
| MSW | Multi sea-winter |
| $m.s^{-1}$ | Meters per second |
| NE | Natural England |
| NASCO | North Atlantic Salmon Conservation Organization |
| ROM | Rate of movement |
| SD | Standard deviation |
| SJB | St Johns Beck |
| TT | Trap and Transport |
| UTC | Coordinated universal time |
| WCRT | West Cumbria's River Trust |
| 1SW | One sea-winter |
| $\%.km^{-1}$ | Migration success/failure per kilometre |

## Acknowledgements

Firstly, I would like to thank my supervisors Professor Colin Adams and Dr Hannele Honkanen who provided me with this amazing opportunity. Thank you for always being there to support during the long field study days particularly when deploying at Coops Weir and during the unpredictable pandemic and thank you both for always having patience and believing in me especially during statistical work which I know we all dreaded. There have been countless ups and downs across these 4 years, but I have been incredibly lucky to have such dedicated scientists and teachers as my supervisors. You have both provided me with skill which have allowed be to develop into an Ecologist and I am excited to go forward using these skills throughout my career.

I would like to thank everybody at the governing bodies such as the Environment Agency (EA), Natural England (NE) and West Cumbria Rivers Trust (WCRT) which included the following people: Phil Ramsden, Mike Farrell, Brian Shields (EA), Melanie Fletcher (NE) and Ruth Mackay and all the additional volunteers from WCRT. Without all of your support, financial aid and continuous efforts this project would not have been possible, particularly during the 2021 downpour where we held the record for 900 smolts captured in 1 day. Additionally, I would like to thank Bassenthwaite Sailing Club and Derwent Anglers Association for their continuous support throughout.

To all of the people who kept me sane or somewhat sane at SCENE, thank you so much! Even if we from time to time all butted heads with each other you were such a big support to me during both the pandemic and during the days/nights when internet was down, or the power had shut off! I would like to say a massive thank you to Jen

Page for being my partner in crime and cooking buddy and the person who introduced me to my biggest fear…CATERPILLARS! I will never be able to go in the woods surrounding SCENE without the constant flashbacks. Additionally, thank you to the interns (Adam and Marc) and technicians (Rowan, Phoebe and Jemma) who helped me during my field seasons, providing endless entertainment whilst hanging out the back of the ranger for tagging and helping me with my statistical analysis.

To Mum, Dad and Katie, thank you so much for all your support throughout the 4 years, during mental breakdowns every so often, and for your support throughout everything I have done. Thank you for always being at the other end of a phone line when I needed you all the most and coming to visit me whenever you could.

Lastly, and certainly by no means least, David. We may have met during Covid, but you have been there for me throughout for all my highs and lows and even have come to the rescue and helped tag during your weekends off. Thank you for encouraging me through all my statistical analysis and motivating me to get writing! You have patiently listened to countless hours of me droning on about salmon and my love for them and you have been my biggest rock during this Ph.D. Love you so much for all the support you have given me.

## Authors Declarations

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 November 2019 until November 2023 under the supervision of Professor Colin Adams and Dr Hannele Honkanen. This included deploying acoustic receivers across the River Derwent catchment in Cumbria, as well as acoustically tagging Atlantic salmon smolts at St Johns Beck, Cumbria. I also declare to writing this thesis and conducted all analysis that are not listed below. No part of these thesis has been submitted for another degree. The acoustic telemetry data used in Chapter 5 and Chapter 6 was compiled by projects COMPASS, Marine Scotland and SeaMonitor oceanographic data. All permission was granted prior to data use.

Amy Green

May 2024

# *Chapter 1:* Introduction of the Atlantic Salmon

## 1.1 General introduction

The *Salmonidae* is a teleost family which belongs to the order *Salmoniformes* (Bleeker 1859). The *Salmonidae* diverged from other teleost fish species approximately 88 million years ago during the late Cretaceous period (Cuvier, 1816). They are a group of ray-finned fish endemic throughout the northern hemisphere. The *Salmonidae* family contains a variety of species such as trout, chars, freshwater whitefishes, graylings though only a specific few species belong to the genus *Salmo* (Linnaeus 1758). *Salmo* species such as Atlantic salmon (*Salmo salar,* Linnaeus 1785) are well studied due to their economical, ecological, and cultural importance across Europe, Scandinavia, and North America (Hansen *et al*., 1993; Thorstad *et al*., 2012b; Havn *et al*., 2020). Due to rapid declines seen across the northern hemisphere within the last few decades, further attention has been focused on understanding their migration strategies, the costs and benefits of migration behaviours and implications of habitat fragmentation on this already vulnerable species.

## 1.2 Life cycle of Atlantic salmon

The Atlantic salmon has a complex life cycle (Figure 1.1). It is typically anadromous with a life span extending up to ten years (Hendry & Cragg-Hine, 2003). The species is well known for its long-distance migrations through an array of habitats from their natal freshwater systems to reach important habitats in the marine environment for feeding and growth (Klemetsen *et al*., 2003).

Atlantic salmon is an iteroparous species, meaning it is capable of multiple spawning throughout its lifetime (Bordeleau *et al*., 2020; Thorstad *et al*., 2012b), with some populations spawning six or more times (Ducharme, 1969; Moore *et al*., 1995; Atkinson & Moore, 1999; Klemetsen *et al*., 2003; O'Connell *et al*., 2006; Reid & Chaput, 2012). However, not all adults exhibit multiple spawning, with only on average 11% individuals spawning more than once in their lifetime (Bordeleau *et al*., 2020; Fleming, 1998). Studies have found increased multiple reproduction increases with decreasing latitude through the northern hemisphere (Bordeleau *et al*., 2020; Fleming, 1998).

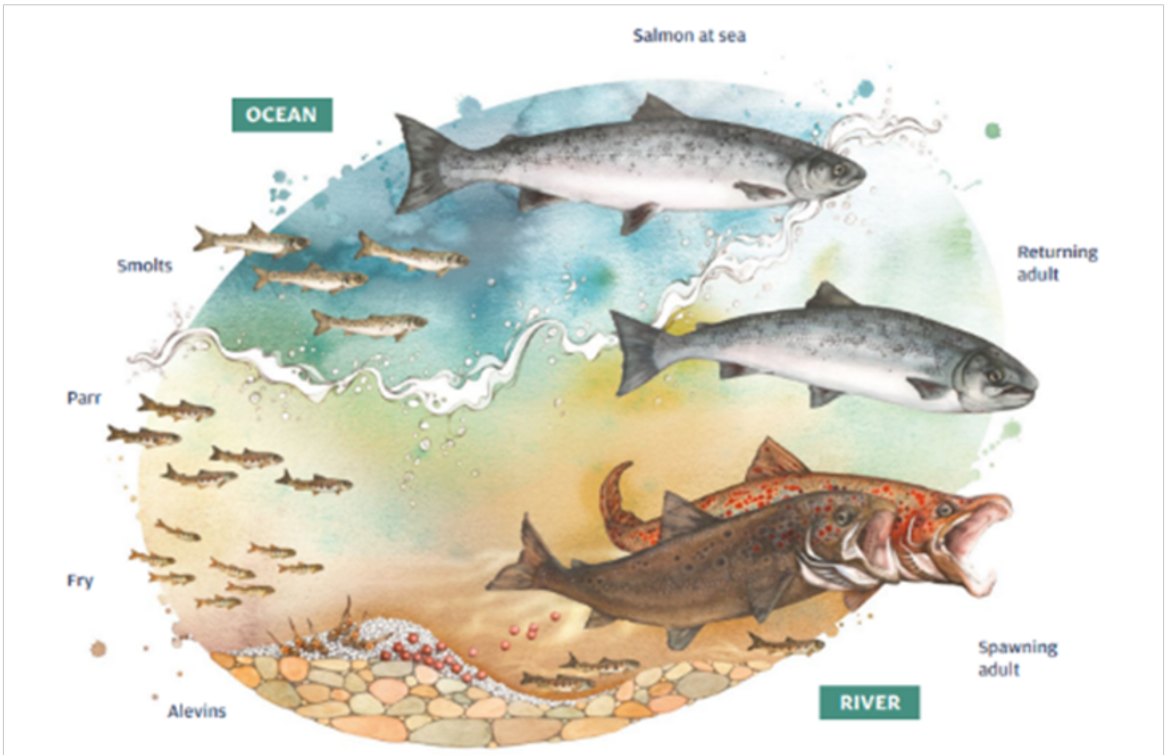



***Figure 1.1*** *The life cycle of Salmo salar (Atlantic salmon) in river and ocean environments (©The State of Wild North Atlantic Salmon, 2019).*

On their migration from sea usually during spring and summer, adult Atlantic salmon return to their natal river systems (Hansen *et al*., 1993; McCormick *et al*., 1998; Fjeldstad *et al*., 2012), travelling up to approximately 50 – 100km.day$^{-1}$ at Sea (Hansen & Quinn, 1998) to spawn several months later in autumn/winter months

(Fleming & Einum, 2011; Frechette *et al*., 2018; Jonsson & Jonsson, 2003). Adult salmon return to their natal tributaries which provide important habitats such as suitable gravel substrates (Hendry & Cragg-Hine, 2003). Between November and February female (hen) Atlantic salmon locate appropriate gravel substrate with moderate current velocity and depth (Fleming, 1996, 1998; Bardonnet & Bagliniere, 2000; Fleming & Einum, 2011; Hendry & Cragg-Hine, 2003) in order to lay their eggs (1.5k – 1.8k per kg (Verspoor *et al*., 2007) in nests called "redds" (McCormick *et al*., 1998), dispersing their eggs in a low depth (~30cm), high velocity, rich oxygenated environments, over clean gravel and cobbled substrates (Bardonnet & Bagliniere, 2000; Fleming & Einum, 2011; Hendry & Cragg-Hine, 2003). Males (cocks) expend a vast amount of energy during this period, actively competing and engage in fighting to gain access to females to facilitate fertilization. Post-fertilization eggs are buried to ensure protection from predation (Bardonnet & Bagliniere, 2000; Fleming & Einum, 2011). After mature spawning, a proportion of Atlantic salmon (female and male) leave the nursery area, directly residing downstream for a couple of months before returning to the marine environment (Bardonnet & Bagliniere, 2000), though not all adults survive post-spawning due to a large proportion of their total energy reserves (60%) being depleted during the upstream migration event (Jonsson *et al*., 1997).

The Atlantic salmon is a rheophilic species when In the riverine environment and during the winter months. The riverine environment provides cold water temperatures, rich in oxygen which is essential in the reproduction and successful spawning of Atlantic salmon. Over the course of three/four months (385–545 degree days) (Crisp, 1988; Jonsson & Jonsson, 2011) the eggs hatch into alevins, though, this time frame is highly dependent on environmental factors such as temperature (Klemetsen *et al*., 2003).

Post hatching, Atlantic salmon are referred to as "alevins", and at this stage access nutrients from the yolk sac (Gustafson-Marjanen & Dowse, 1983; Crisp & Hurley, 1991). Alevins remain in the redd for a few weeks, emerging from gravels in April/May, having absorbed the yolk sac to feed on macro-invertebrates (Bardonnet & Bagliniere, 2000; Johansen *et al*., 2011), they are then referred to as "Fry", where they passively drift downstream or remain in the vicinity of the redd.

Usually by the second year in streams, fry develop into "parr", becoming much larger over time after utilizing feeding opportunities in the stream. Parr develop camouflage to suit their ambient river environments and become more territorial (Kallberg, 1958; Keenleyside & Yamamoto, 1962; Arnold *et al*., 1991). When access during the transitional phase to key habitats is limited and/or competition within a population is increased both the fry and parr phase may incur density dependent mortality (Bujold *et al*., 2004; Hedger *et al*., 2013).

Environmental factors such as water temperature and food availability determine the temporal variability in which individuals remain in the parr phase (Kallberg, 1958; Grant *et al*., 1998; McCormick *et al*., 1998). It has been suggested that parr need to reach an approximate "threshold size" (~>/=10cm) which has been found to take up between one to eight years to develop (Thorstad *et al*., 2008; Klemetsen *et al*., 2003), before transitioning into the next phase "smolt" (smolting). During smoltification, individuals undergo physiological, behavioural, and morphological changes to enable future survival in high salinity environments (Thorstad *et al*., 2012a; Handeland *et al*., 1996), allowing smolts to begin the downstream migration to sea.

Once smolts have entered an estuarine/ marine environment, they are referred to as "post-smolts". Behavioural changes observed in post-smolts within estuarine environments such as increased swimming speeds, is hypothesized to be a predator avoidance strategy (Plantalech Manel-la *et al*., 2011). In estuaries, post-smolts are reported to engage in active swimming behaviour in addition to passive swimming with surface currents (Hedger *et al*., 2011; Mork *et al*., 2012; Økland *et al*., 2006).

Knowledge of the marine migration trajectories of post-smolts remains limited, though a number of authors have shown that Atlantic post-smolts from European tributaries, migrate to the Norwegian Sea at least in part utilising currents as directional cues (Barry *et al*., 2020, 2024; Mork *et al*., 2012; Ounsley *et al*., 2020; Thorstad *et al*., 2012b; Green *et al*., 2022). Previous research using particle tracking off the northwest coast of the UK, has alluded to post-smolts utilising the continental shelf edge currents off Scotland (Ounsley *et al*., 2020) to aid migration towards marine feeding zones in the Norwegian Sea. However, some fish migrate to the northwest Atlantic, to the seas off west Greenland (Klemetsen *et al*., 2003; Thorstad *et al*., 2012a; Dunbar & Thomson, 1979). However, for salmon from northeast coast rivers in the UK, it has been hypothesised that active swimming must take place in order to reach the Norwegian Sea, due to lack of northern directional currents in the North Sea, where prevailing currents are in a south-easterly direction (Ounsley *et al*., 2020). Post-smolts have been recorded, using acoustic telemetry research, travelling up to ca.7–-30km.day$^{-1}$ (Barry *et al*., 2020; Mork *et al*., 2012; Ounsley *et al*., 2020; Thorstad *et al*., 2012b) during their migration to the Norwegian Sea.

Once post-smolts have reached their feeding grounds they remain at sea for one to four years although occasionally more (ICES, 2018), utilising available marine food resources which ensures rapid growth (Klemetsen *et al*., 2003) until they mature. Atlantic salmon post-smolts can remain at sea feeding for approximately one year, prior to migrating back to their natal tributaries as one sea-winter (1SW) salmon. Such fish are referred to as “grilse”. Alternatively, individuals can choose to spend multiple years in the marine environment, these are referred to as “Multi Sea Winter (MSW) Atlantic salmon” (Jacobsen & Hansen, 2001; Rikardsen *et al*., 2008). Around 73% of MSW Atlantic salmon that migrate further to the feeding grounds on the West coast of Greenland have been reported to be 2SW fish (Sheehan *et al*., 2017).

The preferred feeding grounds in the Norwegian Sea change with season. Atlantic salmon diet includes hyperiid amphipods, euphausiids, and mesopelagic shrimp are commonly found during autumn period. In the winter, Atlantic salmon diets shift to forage on lantern fish (e.g., *Benthosema glaciale*), pearlsides (e.g., *Maurolicus muelleri*) and barracudinas (e.g., *Paralepis coregonoides*) (Jacobsen & Hansen, 2001). Although, studies have found correlations between the number of sea-winters spent in the marine environment and the diet shifts. For example, Jacobsen & Hansen (2001) observed 1SW Atlantic salmon diet consisted of a high abundance of amphipods compared to MSW Atlantic salmon which had a higher fish component in their diet.

## 1.3 Smolting as a process

Development from the parr into the smolt phase is dependent on individual growth rate, which is positively correlated with water temperatures (Metcalfe & Thorpe, 1990). During smolting, the fish go through morphological, physiological, and behavioural changes that prepare them for migration to the marine environment (Milner *et al*., 2003; Thorstad *et al*., 2012b; Zydlewski *et al*., 2014). Once development from parr to smolt has occurred, individuals develop essential behaviours to initiate migration behaviour. Researchers hypotheses the key changes found to occur in an individual's morphology, only occurs when parr have accumulated satisfactory lipid resources (Thorpe, 1986). Metcalfe *et al*. (1989), Thorstad *et al*. (2012b) and Barry *et al*. (2017) show that behavioural, morphological and physiological changes help pre-adapt individuals for marine life. Smolting reduces territorial behaviour in individuals, allowing schooling behaviour to be displayed. Fish become slimmer and skin pigmentation changes where parr marks disappear, the fins darken, the body of salmon begins to turn silver, which allows for extensive counter shading camouflage. This change is required for the migration in pelagic zones (Alexander *et al*., 1994; McCormick *et al*., 1998) and changes in plasma ion concentrations have been observed which aids in survival within marine environments (McCormick, 2013; McCormick *et al*., 1985; Stefansson *et al*., 2007; Zydlewski *et al*., 2014).

To initiate migration, smolts require specific environmental cues and once prepared physiologically, environmental cues such as temperature and water discharge initiate down-stream migration behaviour (Riley *et al*., 2012). Thorstad *et al*., (2012b) stated the importance of these factors may change across populations, where some populations migrations are found to be solely initiated by temperature migration, whereas other rivers require the specific water discharge during the spring spate (Jonsson & Ruud-Hansen, 1985; Hvidsten *et al.*, 1995). Additionally, Hvidsten et al., (1998, 2009) hypotheses the use of such cues aid in predicting foreseeable ocean conditions which has been found in Norwegian smolts where different populations entered the sea at different periods using varied environmental cues for migration though all appeared to be adapted to enter the sea when temperatures reach ~8°C. Hvidsten *et al.*, (1998, 2009) study implied a longitudinal gradient influence on migration timings, where southern populations migrate earlier than northern counterparts where sea conditions are warmer later in the migration season.

## 1.4 Status, range and distribution

Historically, Atlantic salmon had a distribution range of more than approximately 2600 river systems across the North Atlantic zone (Fjeldstad *et al*., 2012; Windsor *et al*., 2012; WWF, 2001). The species is widely distributed across Europe, from the Kola Peninsula in Russia down to Portugal (Mills, 1991; Parrish *et al*., 1998; Fjeldstad *et al*., 2012; Koed *et al.,* 2020). In North America, its range extends from the North-East coast of Canada southwards to Maine, USA (Figure 1.2). In order to assist in management decisions, Atlantic salmon populations have been subdivided into geographic groups: 1) West Atlantic, 2) East Atlantic, 3) Baltic Sea (Jonsson & Jonsson, 2011*)*.

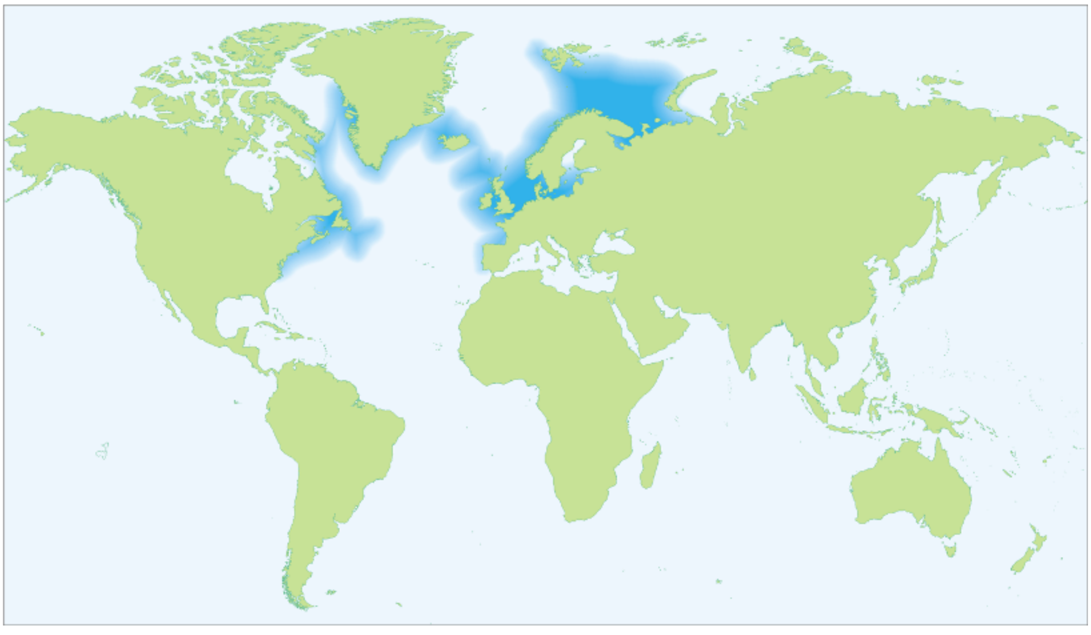


***Figure 1.2*** *Global distribution of wild Atlantic salmon (Salmo salar L.) (©Cherry, 2016).*

Currently, wild Atlantic salmon are considered to be in a serious decline across the large proportion of river systems in which they are found. According to the North Atlantic Salmon Conservation Organizatio''s (NASCO) database (2016) detailed global stocks in the majority of river systems are likely to be under considerable pressure and population declines are impacting spawning population sizes and reproductive success (Jutila *et al.,* 2003). The species has all but disappeared in Germany, Switzerland, the Netherlands, Belgium, the Czech Republic, and Slovakia. In Estonia, Portugal, Poland, and in parts of the United States of America, the species is on the brink of extinction (ICES, 2018). Waples (1991, 1995) detailed the evolutionary significant units (ESU) framework which proposed that it is not enough to consider actual numbers of wild Atlantic salmon when considering conservation and management of the species, but that instead we should focus on ESU, which is a population/group of populations that i) is substantially reproductively isolated from other conspecific population units; and ii) represents an important component in the evolutionary legacy of the species". Thus, with prior knowledge that Atlantic salmon individuals always return to the same natal river systems, each river system should therefore be accounted for separately as they essentially provide for unique salmon populations, or even several, within one river.

Due to the declines seen in Atlantic salmon populations, the species has been listed in Annexes II and V of the European Union's Habitats Directive (92/43/EEC) as a species of European importance (Hendry & Cragg-Hine, 2003). Nevertheless, Hendry & Cragg-Hine (2003, Mills (1991) and McLeod *et al*., (2005) have highlighted that distribution of populations is heavily restricted by various anthropogenic stressors including deteriorated water quality, increased urbanisation, changes in agricultural practices and over-exploitation.

The UK holds a large proportion of Atlantic salmon populations from the total European stock (Figure 1.3), with a total of 547 of rivers within the NASCO database (NASCO, 2018) where a total of 2,395 rivers are assessed across the northern hemisphere. There are 79 rivers in England and Wales which regularly support Atlantic salmon (ICES, 2018) (Figure 1.4) 64 of which are designated as principle salmon rivers (PSR). Most recent estimates of returning adults in England and Wales have declined significantly between 2000 and 2022 for 1SW individuals from 91,910 to 36,311 (ICES, 2023). Interestingly though, it was found a higher number of MSW salmon returned during the same period: the numbers changed from 48,513 in 2000 to 104,705 in 2022 (ICES, 2023). This could potentially be an example of salmon changing their marine migration patterns so that a higher proportion of fish are now returning as MSW rather than 1SW salmon.

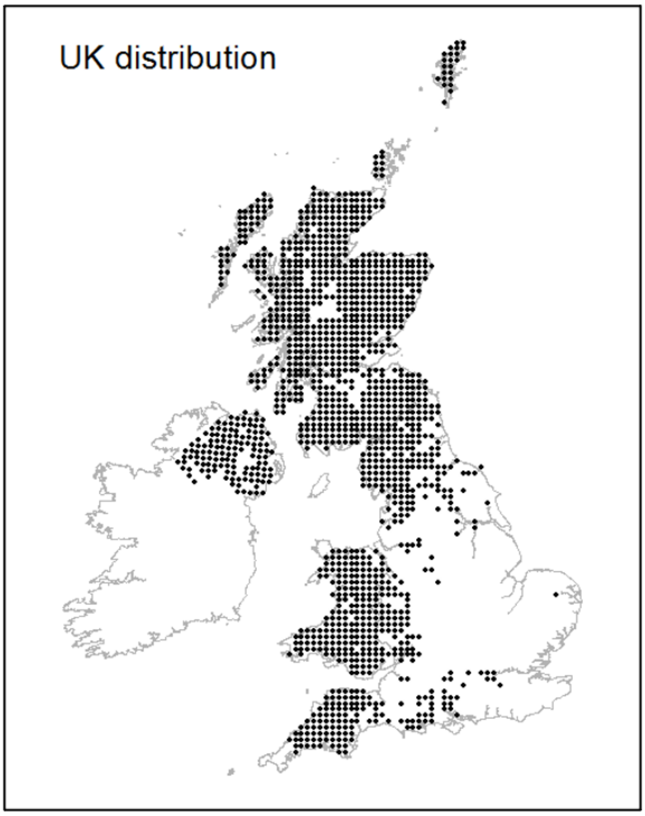



***Figure 1.3*** *UK stock distribution of Atlantic salmon (Salmo salar) (©Hendry & Cragg-Hine 2003).*

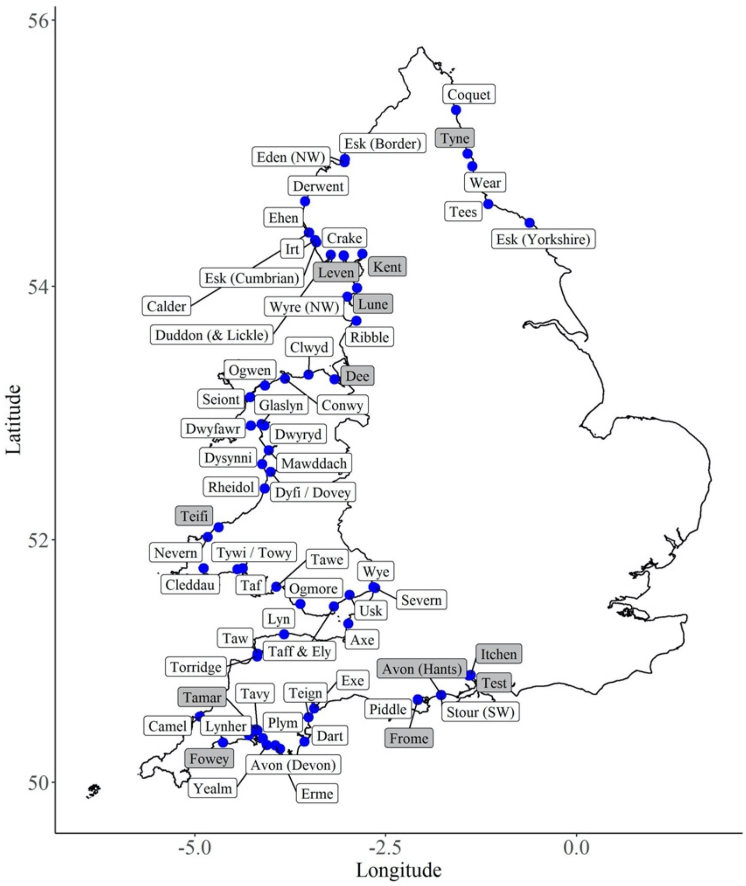



***Figure 1.4*** *64 English and Welsh rivers which regularly support Atlantic salmon (©Gregory et al., 2023).*

Throughout England, Scotland, Ireland and Wales there has been a steady decline in population abundances throughout the past three decades (ICES, 2023). Poor salmonid recruitment was found to be a significant concern back in 2016 and has since been an area of interest for England and Wales river systems (ICES, 2018). ICES (2018) discussed the main cause of decline was a result of increased temperatures due to unusual seasonal fluctuations, providing a warmer winter in 2016 than previously recorded. Furthermore, extreme river flows were also recorded which in turn adversely affected spawning success in 2016 and thus resulted in a poor smolt migration across the following years.

## 1.5 <u>Pressures on Atlantic salmon</u>

The migration of Atlantic salmon between riverine and marine environments is seen as a strategy of adaptive value (Thorstad *et al*., 2008), where the costs of migration are less than the fitness benefits obtained by a population (Lucas & Baras, 2001). For Atlantic salmon, the benefits are assumed to be the ability to exploit new feeding grounds and resources leading to increased growth, resulting in higher fitness and reproductive success (Dingle & Drake, 2007; Lucas & Baras, 2001; Kärgenberg *et al.*, 2020).

Studies have found a correlation between female size and a higher volume of eggs produced; therefore, migration is predominantly important for females (Reid & Chaput, 2012; Thorpe *et al*., 1984; Randall, 1989; Fleming, 1996; Heinimaa & Heinimaa, 2004; Moffett *et al*., 2006). However, not all males undergo migration as a life strategy, where a proportion remain within the river system maturing as “precocious parr” and are able to fertilize a high proportion of eggs from sea migrating females as a key reproductive strategy (Martínez *et al*., 2000; García-Vázquez *et al*., 2001; Jones & Hutchings, 2001, 2002; Taggart *et al*., 2001; Saura *et al*., 2008) Evropeizeva, 1958). The costs experienced by individuals that migrate include increased energy expenditure, exposure to novel environmental stressors, increased mortality and exposure to new predators (Halfyard *et al*., 2012), although the severity of each cost likely varies between populations and individuals. An assortment of external pressures contributes to the costs and benefits of migration, such as: i) environmental conditions; ii) man made or natural physical infrastructure of the landscape; and iii) biotic and abiotic components (Storebakken, 2009).

### 1.5.1 Natural pressures

#### 1.5.1.1 Predation

Not only is the transitional stress from riverine environments to marine environments costly due to increased osmotic stress and the physiological, behavioural and morphological changes required, but additionally predation poses a considerable risk to smolts during their seaward and early marine migration. Primarily within riverine systems, avian and piscivore predation has been reported to contribute to mortality experienced by smolts within these systems (Dieperink *et al*., 2002; Thorstad *et al*., 2011). Avian predators are often found within riverine and estuarine systems (Dieperink *et al*., 2002), and often located at bottleneck zones where migration is partly or fully halted due to in river obstructions or environmental factor fluctuations (i.e., river levels). Common avian predators found in UK waters are Cormorants (*Phalacrocorax carbo carbo,* Linnaeus 1785) and Goosanders (*Mergus merganser,* Linnaeus 1785). A variety of avian species within estuaries are often found in high abundance during migration periods, suggesting avian species heavily rely on them as a seasonal prey source (Allegue *et al*., 2020; Arso Civil *et al*., 2019; Carter *et al*., 2001; Kennedy & Crozier, 2010; Thorstad *et al*., 2012a, b; Wilson *et al*., 1997).

Riverine systems with in-river channel spanning infrastructure can delay migration and lead to an increase in predation and smolt stress (Koed *et al*., 2002; Thorstad *et al*., 2008). Chavarie *et al*. (2022) measured smolt predation during migration along the Endrick Water, Scotland using an active tracking approach and found avian predators to be the main cause of mortality (42%), though a considerable level of piscivore predation was also recorded (14%). Not only are Atlantic salmon smolts susceptible to avian and piscivore predation, but mammals, such as the European otter (*Lutra lutra,* Linnaeus 1785) have also been found to prey on both juvenile and adult Atlantic salmon (Carss *et al*., 1990; Berry, 1934; Mills, 1967, 1971; Ade, 1989).

Thorstad *et al*. (2012b) highlighted  that the highest rates of mortality during salmon migration occur within the marine environment, during the smolt to post-smolt phase. Predators such as harbour seals (*Phoca vitulinai,* Linnaeus 1785), grey seals (*Halichoerus gyprus,* Linnaeus 1785) and bottlenose dolphins (*Delphinus truncates,* Linnaeus 1785) are highly abundant throughout the northern hemisphere, particularly surrounding Great Britain (Carter *et al*., 2001). Carter *et al*. (2001) analysed the foraging behaviour of both harbour and grey seals, and found that both species utilized estuaries in greater abundances during the important migrating seasons (winter/spring), therefore, both species experience temporal overlap with migrating Atlantic salmon smolts, and retuning adults post spawning. Although, studies have been conducted on seal diets, observational data is limited to surface foraging and further studies are required to investigate full foraging behaviour to understand foraging strategies and the implications on Atlantic salmon populations.

Furthermore, various piscivorous species such as Atlantic cod (*Gadus morhua,* Linnaeus 1785) and European Seabass (*Dicentrachus labrax,* Linnaeus 1785) are reported to predate on Atlantic salmon (Hedger *et al*., 2011). Hedger *et al*. (2011) noted potential evidence of smolt predation strategies emerging in European cod populations, finding European cod in Norwegian fjords were engaging in similar seasonal migratory patterns to that of Atlantic salmon and utilising the water surface. European cod are predominately bottom dwelling species, and changes in their migratory behaviour is potential evidence of deviations in foraging strategy in order to benefit as a population.

#### 1.5.1.2 Natural standing waters

Not only do smolts have the difficulty of riverine passage alone to reach estuarine environments, but passage to and from natal tributaries may also increase costs associated with natural geographical pressures for some populations. Longer journeys can further increase the risk of predation and increase energetic costs associated with migration. Hanssen *et al*. (2022), Honkanen *et al*. (2018, 2021) and Kennedy *et al*. (2018) investigated natural geographical pressures on migrating smolts, such as natural standing water passage through lakes/ lochs, reporting substantial migration loss within these system. Riverine catchments which support Atlantic salmon populations often flow through large natural standing-waters through which smolts must successfully navigate before proceeding seaward (Honkanen *et al*., 2018). Natural standing-waters lack directional surface currents on which smolts likely rely on for successful navigation cues, thus high mortality rates have been recorded within what are natural geographical landscape barriers. It has been reported smolts have a in higher energy expenditure and experience an increased overall migration duration within lakes, further increasing the risk of predation (Hanssen *et al*., 2022; Honkanen *et al*., 2018, 2021; Jepsen *et al*., 1998; Thorstad *et al*., 2012b).

Riverine migration has been well studied, it has been reported that smolts utilize riverine discharge not only to initiate migratory behaviour but as a navigation cue to migrate towards marine environments (Thorstad *et al*., 2012b; Davidsen *et al*., 2009; Lacroix *et al*., 2004a,b; Svendsen *et al*., 2007). In contrast, the cues smolts require to successfully migrate through lakes remains poorly understood.

### 1.5.2 Anthropogenic pressures

#### 1.5.2.1 Climate change

Increased greenhouse gas emissions over the last century have been found to correlate with increase surface water temperatures both in the riverine and marine environments (Beaugrand *et al*., 2002). Warmer surface temperatures across natal rivers have been shown to correlate with smolting occurring earlier in the season, further correlating to increased growth rate parameters, which is thought to aid in predator avoidance strategies (Friedland *et al*., 2000, 2003; Pepin, 1991).

The optimal sea surface temperature for early marine entry is approximately 8 – 10ºC (Friedland *et al*., 2000), however, smolts emigrating early in the season are likely to be exposed to lower temperatures during their migration into marine waters. Friedland *et al*. (2000) reported smolts emigrating out of the River Figgjo in Northern Norway had a higher rate of survival when marine surface temperatures were higher during their first month of migrating throughout the marine environment (Friedland *et al*., 2003; Kennedy & Crozier, 2010).

Not only is the smolt phase impacted, but researchers have reported climatic impacts due to surface temperatures being highly correlated with declining abundances of MSW Atlantic salmon returning to natal tributaries (Friedland *et al*., 2003; Scarnecchia, 1984; Thorstad *et al*., 2021). Surface temperatures have also been postulated to impact adult Atlantic salmon maturity in the marine environment (Friedland *et al*., 2003). Studies found a reduction of MSW salmon of 51%, 81% and 88%, in populations in the N-NEAC (Northern North-East Atlantic Commission), S-NEAC (Southern North-East Atlantic Commission) and NAC (North American Commission) areas respectively (Martin & Mitchill, 1985; Saunders *et al*., 1983; Scarnecchia, 1984), though increases in in 1SW Atlantic salmon have also been reported (Chaput, 2012).

Researchers propose that the decline recorded in MSW Atlantic salmon is partially a consequence of a shift in prey availability in the feeding grounds off the West coast of Greenland (Todd *et al*., 2008). Climate shifts have been recorded to heavily impact the distribution and production of zooplankton with the northward shift of cooler waters recorded in 1990 linked with a reduction in Capelin (*Mallotus villosus,* Müller 1776), a main food source of Atlantic salmon (Buren *et al*., 2014). The shift in prey availability to post-smolts has likely resulted in the increase of Atlantic salmon maturing after one year at sea (1SW) (Utne *et al*., 2022).

#### 1.5.2.2 Artificial infrastructure

Habitat fragmentation has been found to be one of the leading causes of Atlantic salmon population declines (Richter *et al*., 1997; Lucas & Baras, 2001; Deinet *et al*., 2020). Across riverine environments, anthropogenic riverine fragmentation is caused by construction of in-stream river-spanning infrastructure such as hydropower dams, low head weirs and culverts (Birnie-Gauvin *et al*., 2017a,b; Rosenberg *et al*., 2000; Lucas & Baras, 2001; Ceballos & Ehrlich, 2002; Limburg & Waldman, 2009; Baguette *et al*., 2013; Hill *et al*., 2019). Due to river habitat connectivity being primarily longitudinal confined to the river corridor (Newton *et al*., 2019), species which have complex life cycles are most likely to be affected due to single impoundments potentially isolating adjacent habitats required for particular life stage requirements to be facilitated (Hill *et al*., 2019).

Hydropower dams are the largest global renewable electricity source (International Energy Agency 2012; Havn *et al*., 2017; Pringle, 2001) with over 59,000 dams higher than 15m having been built (ICOLD 2018). Hindar *et al.* (2004) and Riddell & Tautz (2003) speculate hydropower dams are one of the leading causes of increased mortality of Atlantic salmon (Hindar *et al.*, 2004; Riddell & Tautz , 2003) via both direct impacts such as turbine blade strikes and indirect impacts such as delayed migration and predation. As a result of increased delays found to occur at hydropower structures,  correlated energy expenditure of migration through the riverine system is found to increase (Thorstad *et al*., 2012b), thus increasing the costs associated with migration.

Weirs are used for a variety of reasons such as flood prevention, hydropower production, water discharge measures, boat navigation and fish farming (Havn *et al*., 2020). Weirs not only restrict fish populations' essential life stage connectivity but may also impact habitat by altering downstream flux of water, temperature, sediment and nutrient movements within river ecosystems (Antonio *et al*., 2007; Branco *et al*., 2012; Gauld *et al*., 2013). A national walkover survey, estimated there are approximately 66,381 barriers to migration across Great Britain river systems, indicating >97% of UK river networks are fragmented, with 1% of catchments within Great Britain being free form artificial infrastructure (Jones *et al*., 2019). Although the size and scale of in-river barriers is highly variable (Tetzlaff *et al*., 2007), all in-river spanning infrastructure have the potential to partially and/or fully impede migration.

The38igrlogical consequences of38igrationon delays to Atlantic salmon are still unclear and require investigation, although Newton *et al*. (2018) hypothesised smolts will increase movement and searching behaviours when faced with an impassable or temporarily impassable in-river structure, looking for the most direct passage route are most likely to incur energy expenditure costs. There are various examples of increased energy expenditure negatively impacting migration success of anadromous species (Gowans *et al*., 2003; Caudill *et al*., 2007; Frank *et al*., 2009; Dodd *et al*., 2018). Studies on Atlantic salmon in Danish river systems showed negative effects resulting from increased delays and mortality seen at low-head weirs (Aarestrup & Koed, 2003). O'Connor *et al*. (2006) highlighted other anadromous species such as murray cod (*Maccullochella peels*, Mitchell 1838) and golden perch (*Macquaria ambigua,* Richardson 1845) have been shown to be impacted by river obstructions. Studies conducted by O'Connor et al. (2006) in Australia, found that these river species exhibited behavioural reluctance to move past low-head weirs when migrating downstream. However, research conducted by Hansen & Jonsson (1985) and Davidsen *et al*. (2005) found that when Atlantic salmon smolts enter accelerated flow fields close to river obstructions, such as weirs, smolts have adapted their behaviour to turn against the current to establish control of movement and reduce injury.

Passage across weir structures relies on variations in environmental conditions, in combination with fish characteristics (e.g., body size (fork length, $F_L$) and species) which create discrete periods during which fish passage is successful (Kemp & O'Hanley, 2010). River flow is essential for successful passage: if water levels are too low, movement of fish is impeded, conversely, elevated levels can have negative effects, as when water velocity is too high it can exceed the swimming capability of fish (Fraser *et al*., 2015; KLTAP, 2015; Dodd *et al*., 2018), incurring potential injury and increased stress responses in Atlantic salmon. Havn *et al*. (2020) assessed the impact of river-spanning infrastructure (weir and power station) presence on mortality rates along the River Sieg, finding the potential causes of induced mortality was not due to the presence or physical properties of the Buisdorf weir (i.e., height or length) but due to the physical damage suffered by individuals when passing over the weir. This in turn caused an increased delay in migration which led to increased predation vulnerability. It has also been suggested that obstacles can result in negative behavioural consequences after passage when smolts accumulate in a location if they have been stunned, stressed, or disorientated (Stich *et al*., 2015; Havn *et al*., 2020).

Barriers can also negatively impact upstream migration behaviours and female Atlantic salmon have been found to reproduce downstream in the nearest habitat which resembles their natal spawning grounds where clean gravel substrates and high velocity flows are present (Bardonnet & Bagliniere, 2000; Fleming & Einum, 2011; Hendry & Cragg-Hine, 2003).  In some cases they have be found to abandon spawning all together (Thorstad *et al*., 2008) indicating a potential reduction in spawning population size may occur. When females are forced to spawn downstream of the artificial in-river infrastructure, redds were significantly closer to each other, compared with what was found upstream in their natal spawning grounds in areas with unrestricted access across a 15-year study period (Tentelier & Piou, 2011). As a result of impassable structures resulting in downstream spawning adult amalgamations, there is increased disease prevalence probability within a population (Fujihara & Hungate, 1971; Thorstad *et al*., 2008). This also has further implications for potential population size and the future status of regional stocks.

Considerable efforts have been made to develop ways in which fish can pass obstacals through the installation of fish passages (Larinier, 1998; Guiny *et al*., 2005; Bunt *et al*., 2012). In Europe, policy and legislation exists such as the Water Framework Directive (WFD; 2000/60/EC) and EU Eel Regulation (EC No. 1100/2007) which requires the provision of free passage for all migratory fish species that require access to specific upstream/downstream habitat in order to complete essential life stages (Gauld *et al*., 2013; Newton *et al*., 2018, 2019; Dodds *et al*., 2018). Failure to comply with the WFD regulations can result in the waterbody being deemed to be of less than "Good Ecological Status". There are various types of fish passages that have been explored in the scientific literature, these include bypasses, spill gates/spillways and low sloping turbine intake racks. Nygvist *et al*. (2018) suggest that the efficiency of fish passage installations is questionable, as most migrating fish still experience migratory failure, potentially suffering direct or delayed mortality as an effect of spill, bypass, or turbine passage (Muir *et al*., 2001; Ferguson, 2005; Ferguson *et al*., 2006; Nyqvist *et al*., 2017). Kärgenberg *et al*. (2020) found that Atlantic salmon smolt mortality (acute or delayed) was lowest when using the bypass which best mimics the river channel regardless of the low water flow throughout. They found fewer smolts migrated over dam spillways indicating spillways are not an efficient alternative passage route.

Gaps within literature regarding Atlantic salmon smolt passage across artificial structures, with or without fish passes remain high regarding UK river systems. Further research is required to understand the delay implications for various life stages (smolt/returning spawner) across artificial structures to aid in management , mitigation and construction of in-river infrastructure (Newton *et al*., 2018).

## 1.6 Where are the current declines during migration occurring?

The transition between freshwater and saltwater environments is a critical life phase for Atlantic salmon (Gross, 1987; Kennedy & Crozier, 2010; Hoar, 1976), and it is heavily associated with high mortality rates (Halfyard *et al*., 2012) particularly during the outward smolt migration. Reports of high mortality rates throughout juvenile life stages are not uncommon throughout the published literature (Thorstad *et al*., 2012b, 2011; Dieperink *et al*., 2002), although spatial data relating to migration mortality rates in riverine systems is limited. Atlantic salmon smolts from the River Bush, Ireland, studied by Flávio *et al*., (2020) found significant temporal variation in survival rates of smolts throughout the study site, where across three years (2014, 2017 – 2018) survival rates were 70%, 39%, 26% respectively. Moreover, Flávio *et al*. (2020) found there was spatial variation in mortality rates, whereby smolts released downstream, closer to saltwater habitat had a greater loss rate compared to smolts released upstream which suffered an average mortality rate of 0.4%.$km^{-1}$ in 2015, 4%.$km^{-1}$ in 2017, and 10.3%.$km^{-1}$ in 2018. This analysis showed decreasing temporal survival probability of smolts throughout the riverine system. In 2014 it was proposed that environmental factors such as high-water flow was a contributing factor to the high survival probability recorded. Fluctuating flow regimes throughout the riverine environment may impact smolt survival chances, directly by the following: i) a current assisted increase in speed reducing overall duration spent in a river environment; ii) reducing visibility in the water column; and iii) increasing the number of smolts simultaneously migrating downstream (Hvidsten *et al*., 1995; Jonsson & Jonsson, 2009).

Additionally, Flávio *et al*. (2020) alluded to the requirement of environmental cues for smolts when approaching the marine environment. The lack of salinity or temperature gradients River Bush smolts endure provide little or no environmental cues to signal that they are approaching the marine environment, inducing stress responses and reducing circadian patterns when entering the sea (Kennedy & Crozier, 2010) which increase predation pressure when entering the sea during daylight hours (Kennedy & Greer, 1988).

The published scientific literature still remains limited as to the exact points within the riverine/estuarine environment at which migration mortality is at its highest and further investigation is required to differentiate spatial mortality rates. Additionally, the potential for differential impacts of the riverine and estuarine environments on smolts requires further investigation, potentially unearthing bottleneck zones within the transitional phase. It is this smolt and post-smolt migration phase that this study will focus on.

## 1.7 <u>Smolt migration</u>

McCormick (2013) and Zydlewski *et al*. (2014) have categorised the smolt migration into four categories: 1) initiation; 2) downstream migration,; 3) estuary migration; and 4) ocean migration, with the full smolt migration taking approximately 3–6 weeks. The timing of the initiation of migration is vital for migration success and marine survival (Hoar, 1976; McCormick *et al*., 1998), and it is hypothesised to be heavily influenced by photoperiod, water temperature and river discharge (McCormick, 2013; Zydlewski *et al*., 2005). Once smolts have undergone the required physiological, behavioural, and morphological changes to adapt them to high salinity environments (Thorstad *et al*., 2012a; Handeland *et al*., 1998), they begin their downstream migration. Havn *et al*. (2017) suggested that smolt migration was via passive displacement by river currents, but several studies have now documented that active migration occurs, with smolts swimming faster than river currents (Davidsen *et al*., 2005; Svendsen *et al*., 2007). Thorstad *et al*. (2012b) and Vollset *et al*. (2021) also linked latitudinal variation to the timing of downstream migration, where southern populations were found to migrate earlier compared to northern populations of Atlantic salmon smolts.

During the downstream migration further physiological changes allow smolts to adapt to the early marine environment, with researchers finding smolts increased their shoaling behaviour upon exit of their natal tributary which has been hypothesised as a predator avoidance strategy (Olsén *et al*., 1998; Riley, 2007).

## 1.8 Post-smolt migration

Upon initial entry to the estuary, smolts have been found to rapidly increase speed throughout the system, moving at ca.0.4–1.2 body length per second ($BL.s^{-1}$) to migrate into the early marine environment, utilising ebb tide and dark hours to emigrate (Hedger *et al*., 2008; Martin *et al*., 2009; Moore *et al*., 1998; Thorstad *et al*., 2012b). Once smolts leave their natal rivers they are referred to as “post-smolts”. Behavioural changes observed in post-smolts within estuarine environments such as increase swimming speeds is hypothesized to be a predator avoidance strategy (Plantalech Manel-la *et al*., 2011), where post-smolts are reported to engage in active swimming behaviour whilst also gaining advantage by swimming with surface currents (Hedger *et al*., 2011; Mork *et al*., 2012; Økland *et al*., 2006).

## 1.9 Studying migration

In order to study species migration and assess migration success (Welch *et al*., 2008; Klimley *et al*., 2013) various studies have incorporated biotelemetry as a primary method based on three technologies; i) acoustic; ii) radio; and iii) satellite (Hussey *et al*. 2015). Biotelemetry has been used in marine and freshwater ecology research for over 50 years (Gray & Haynes, 1977; Westerberg, 1982; Voegeli *et al*., 1998; Arnold & Dewar, 2001; Sibert & Nielsen, 2001; Clements *et al*., 2005). It has revolutionised the way in which migration can be observed (Klinard *et al.*, 2019) across various habitats where visibility is poor, in cases where individuals are in constant motion and it can be used to identify key areas in which mortality is high. Prior to recent advancements, ecologists relied heavily on mark-recapture techniques which provides only minimal data (capture data and location) and which was also exceedingly labour intensive.

Advances in electronic telemetry technologies has permitted tracking of a wide variety of species ranging in size from 10cm (e.g., salmon smolts) to 29m (e.g., blue whales genus *sp*.) in freshwater, brackish and marine environments (Bailey *et al.,* 2009; Rechisky *et al.,* 2013; Abecasis *et al.*, 2018). Acoustic telemetry, which involves the use of an acoustic transmitter to transmit a signal detected on acoustic receivers distributed throughout the species range (Hussey *et al*., 2015). This method has become popular to investigate fish migration patterns, site fidelity, diel movement patterns and predation events (Heupel *et al*., 2010; Hitt *et al*., 2011; Rowell *et al.,* 2015; Hussey *et al*., 2015). Tags have also been developed to also collect a wide array of various environmental and physiological data such as temperature, heart rate, salinity, and individual acceleration in the wild (Figure 1.5). Both passive and active tracking can occur (Crossin *et al*., 2017). Passive tracking requires continuously monitoring acoustic receivers with data logging capabilities to be located in fixed positions along a suspected species range whereby a migrating fish can be logged with individual unique ID codes for future analysis (Hussey *et al*., 2015). Additionally, active tracking can be conducted using a hydrophone to actively locate an individual, providing the individuals unique ID code (Crossin *et al*., 2017; Chavarie *et al*., 2022).


***Figure 1.5*** *Examples of acoustic tags that can be used for tracking an individual Atlantic salmon smolt (©Greene et al., 2009).*

Acoustic telemetry is the most commonly used method of tracking salmonids, in particular Atlantic salmon (Thorstad *et al*., 2011) due to the small tag size possible (12mm/0.65g), thus, allowing for various life stages to be tracked (Cooke *et al*., 2013; Honkanen *et al*., 2018). However, environmental property fluctuations can often limit the appropriateness of acoustic telemetry, such as increased water currents during transmitter deployment, increase noise audio of the water and potential unknown barriers below the surface water which can all adversely affect the tag signal, reducing detection efficiency (Sanderson *et al*., 2017; Halfyard *et al*., 2013) further limiting the amount of data the collected.

In order for acoustic telemetry to track Atlantic salmon successfully, ecologists using these methods must work under the assumption that all tagged fish are representative of the general population and that tagged fish do not display abnormal behaviour due to the insertion and burden of the tag itself (Zale *et al*., 2005; Moore *et al*., 1990). Behavioural defects (reduction in swimming speed) as a direct impact associated with acoustic tagging has been described in previous literature, though deficits are greatly reduced when the weight of the smolts tagged are considered (Lacroix *et al*., 2004a).

In telemetry studies the tag weight which is deemed appropriate for each individual is much debated. Winter (1996) proposed the '2% rule' which states that the tag weight should not exceed "2%" of a fish's bodyweight in air. The '2% rule' aims to minimise the risk of altered behaviour or increased chance of mortality caused by tagging. This issue is also known as the 'tag burden effect'(McCleave & Stred, 1975; Ross & McCormick, 1981; Adams *et al*., 1998; Honkanen *et al*., 2018; Lothian *et al*., 2018). The '2% rule' has however been challenged, with suggestions that the ratio of tag mass to body mass could be extended to approximately 6% - 12% (Brown *et al*., 1999; Rechisky & Welch, 2010; Newton *et al*., 2016; Chaput *et al*., 2019).

Furthermore, the circumstances around the capture and tagging of wild Atlantic salmon affects the probability of return as adults is also of concern (Riley *et al*., 2018). Riley *et al*. (2018) reviewed the effects of tags on the survival of Atlantic salmon and their return rates to freshwater, they found that particular environmental factors such as temperature and lunar events impacted the return rates. Those individuals that migrated in mild winters and during the night had a lower return rate, compared to years where weather conditions and temperature were normal, concluding capture handling and tagging did not affect future return rates. However, it should be noted that the effects brought on by acoustic tagging differ between species, their life history characteristics and on a population level, therefore, it is important to consider these before choosing a tagging procedure (Thorstad *et al*., 2000).

## 1.10 Study site

Despite the large volume of research on salmon within freshwater systems, there remain considerable gaps in our knowledge of natural and anthropogenic factors which could impact salmon in rivers.

The River Derwent in the northwest England supports Atlantic salmon and is a designated PSR. River Derwent catchment is ca.50km in length, where the River Greta confluxes with water draining from the Derwentwater Lake resulting in the River Derwent which further runs through Bassenthwaite Lake, and travelling through urbanised areas (Cockermouth and Workington) before discharging to the Port of Workington where it drains west into the Solway Firth and then into the Irish Sea (Figure 1.6). The River Derwent has been designated as a Special Area of Conservation (SAC) legally underpinned by multiple Sites of Special Scientific Interest (SSS"s) (Figure 1.7) where Annex II species river lamprey (*Lampetra fluviatilis,* Linnaeus 1785), Brooke lamprey (*Lampetra planeri,* Bloch 1784), Sea lamprey (*Petromyzon marinus,* Linnaeus 1785) and Atlantic salmon are detailed as a qualifying features. To ensure the integrity of The River Derwent is maintained and/or restored to ensure contribution to achieving "Favourable Conservation Status" for all qualifying features, the conservation objectives state maintaining or restoring; i) The extent and distribution of qualifying natural habitats and habitats of qualifying species; ii) The structure and function (including typical species) of qualifying natural habitats; iii) The structure and function of the habitats of qualifying species; iv) The supporting processes on which qualifying natural habitats and the habitats of qualifying species rely; v) The populations of qualifying species; and vi) The distribution of qualifying species within the site.

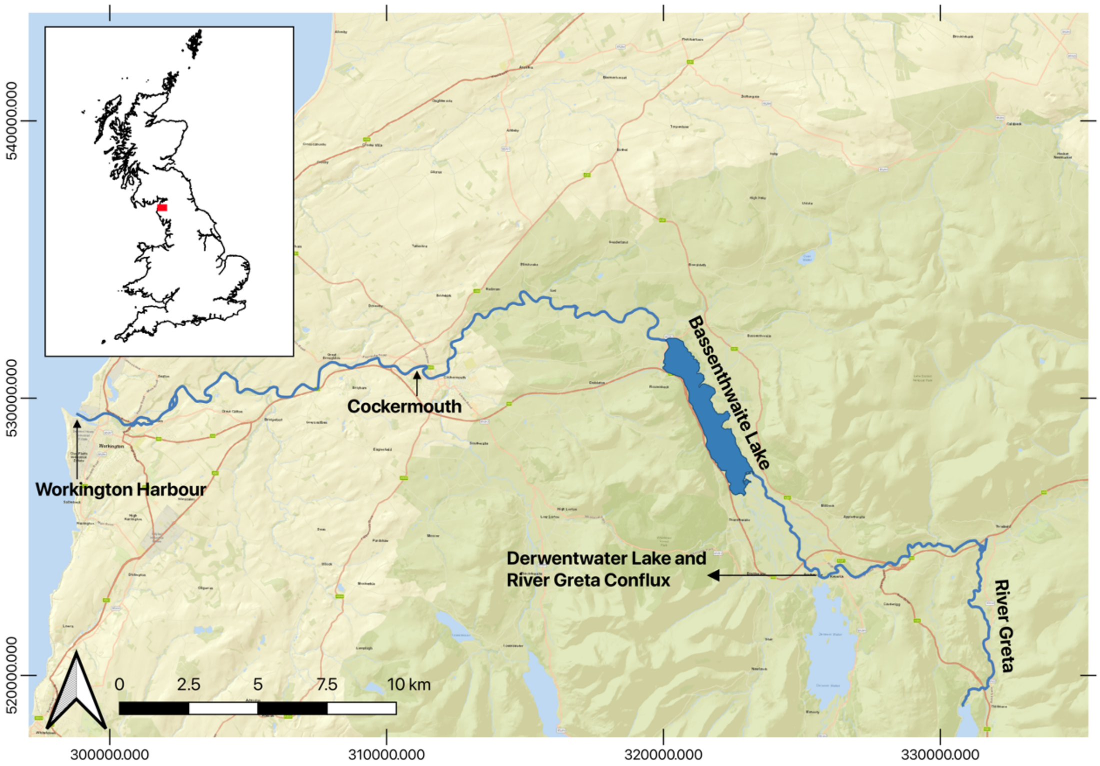



***Figure 1.6*** *River Derwent Catchment*

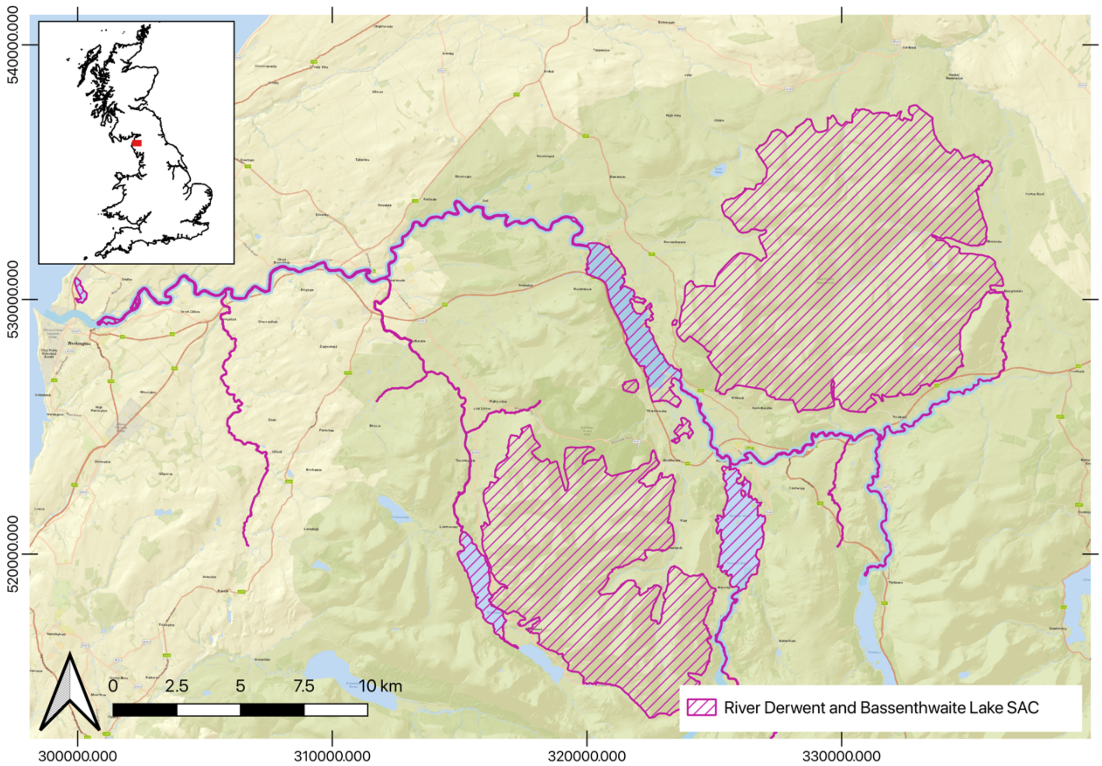



***Figure 1.7*** *River Derwent and Bassenthwaite Lake Special Area of Conservation statutory designation.*

Atlantic salmon smolt numbers on the River Derwent have been recorded for several years by the West Cumbrian Rivers Trust (Figure 1.8) and the Environment Agency has recorded a 77% reduction in rod catch across a 10-year period (Figure 1.9). Though, there is little information on smolt migration behaviour, the rate of success and the migration costs associated within this system. No previous research has been conducted on the River Derwent to examine zones where migration mortality may be high and to understand if mortality is equal across the whole catchment or whether specific stressors are a contributing factor to migration success.

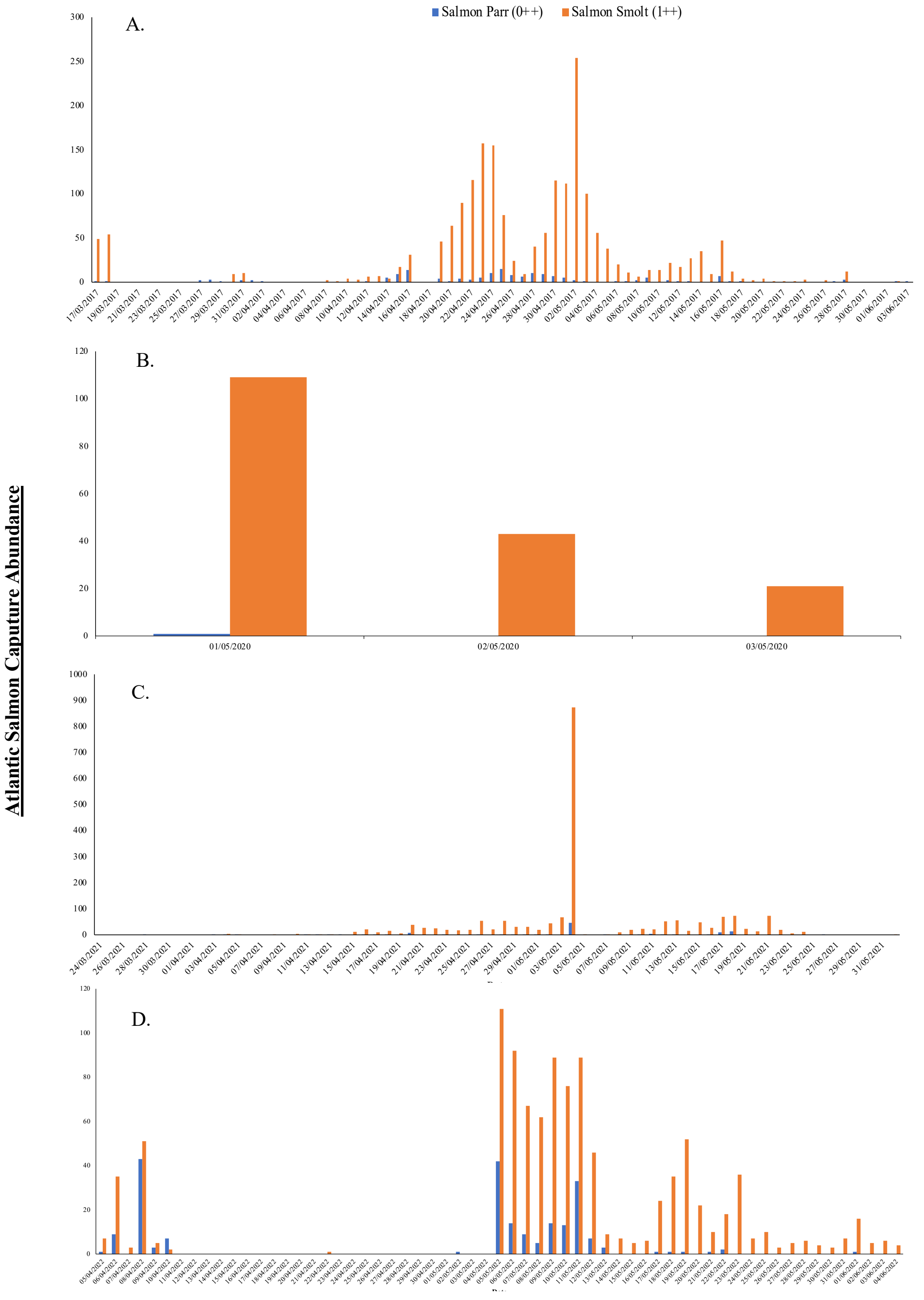



***Figure 1.8*** *Atlantic salmon rotary screw trap data from: A-2017; B-2020; C-2021; and D-2022 captured by West Cumbria Rivers Trust, displaying salmon smolts (1++) and salmon parr (0++).*

The River Derwent has many features that may have negative impacts on Atlantic salmon smolts during their seaward migration, including natural pressures such as a large natural standing water (Bassenthwaite Lake), and two anthropogenic pressures; Coops Weir and Yearl Weir located at the lower extent of the River Derwent catchment in Workington. Though, there is little information on smolt migration behaviour, the rate of success and the migration costs associated with in the system. No previous research has been conducted on the River Derwent to examine zones where migration mortality may be high and to understand if mortality is equal across the whole catchment or whether specific stressors are a contributing factor to migration success.

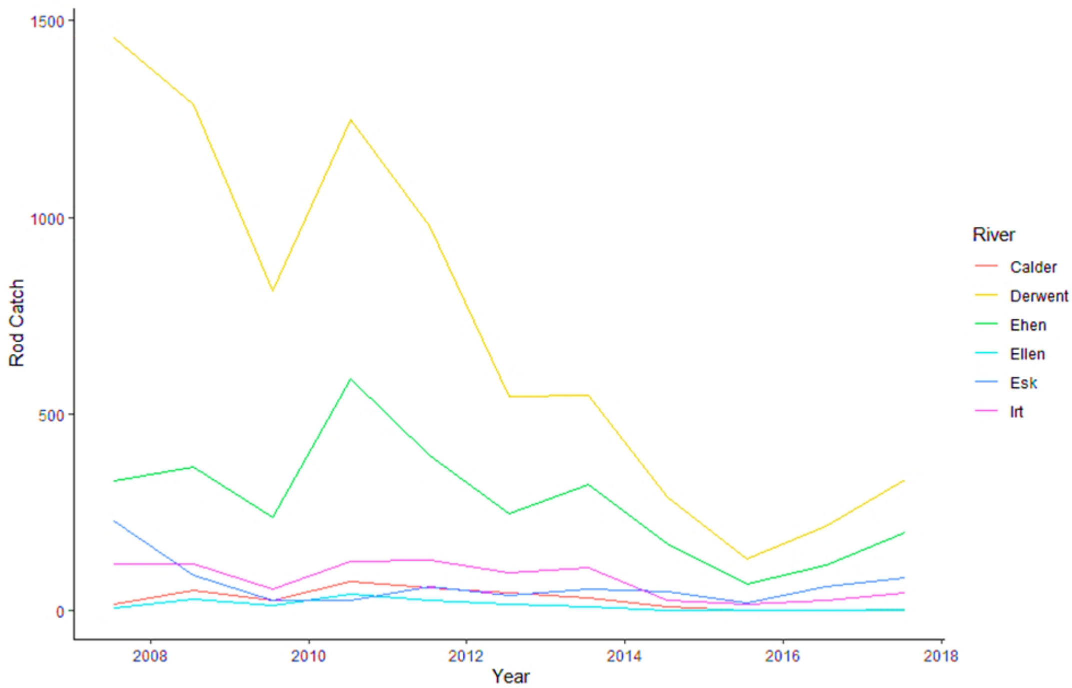



***Figure 1.9** Rod catch data from Atlantic salmon across the Cumbria catchment between 2007 and 2017. River Derwent declined significantly (77%) over the period.*

## 1.11 Study aims

The general aim of the work presented in this thesis is to add to our understanding of ecology and the status of Atlantic salmon migration along the River Derwent. This thesis comprises five separate studies each provides novel information concerning the riverine and early marine migration of Atlantic salmon smolts/post-smolts migrating from the River Derwent, Cumbria. These studies are:

Chapter 2: There is limited understanding of potential temporal and spatial variation riverine migration behaviours. Using acoustic telemetry combined with modelling, this study examines the temporal and spatial differences on smolt survival rate and rate of movement in River Derwent.

Chapter 3: Cues which aid in successful migration through natural standing waters are still poorly understood. This study aims to investigate potential behavioural factors that differentiate successful from unsuccessful lake migrants and identify influences of environment factors on migration.

Chapter 4: Knowledge of fish behaviour around engineered structures within riverine environments is still poorly understood, particularly during the smolt phase. This study investigates and describes the impact of weirs on passage choice and the potential costs associated with passage to the marine environment.

Chapter 5: This study details successful smolt passage through the early marine environment in 2020, describing the longest detected smolt migration in Europe to date.

Chapter 6: Early-marine migration is poorly understood. Current understanding is that smolts from west-coast UK tributaries migrate towards the continental slope edge. However, there is limited information of early marine phase survival rates and marine trajectory choice. This study will investigate the marine trajectory choices and the temporal differences in both pathways and survival rates from 2020 to 2022, utilizing data collected from five marine projects throughout the Irish Sea and off the west-coast of Scotland.

Lastly, Chapter 7 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:* Temporal patterns of spatial variation in migration success of Atlantic salmon in a riverine environment.


## Abstract

The Atlantic salmon, *Salmo salar* (Linnaeus 1758), is an anadromous species that has faced dramatic declines throughout its range across both riverine and marine environments. There is currently a lack of information on the spatial and temporal variation in migration success within river systems to help determine potential bottleneck zones for out-migrating smolts. This study provides baseline data on migration success rates of Atlantic salmon smolts within the River Derwent, Cumbria, across a three-year study period (2020-2022). It shows river sections which may be contributing to reduced migration success, potential mechanisms of tag loss across the riverine environment and inter-annual variation of smolt migration success through the riverine system. Consistent with some recent research, migration success rates from two release groups ("St Johns Beck" and "Trap and Transport") were low (2020: 8% ($n=8$), 2021: 27.1% ($n=40$), 2022: 41.7% ($n=48$)). Migration speed (Rate of Movement ($m.s^{-1}$) and ground speed ($km.day^{-1}$) varied across river section and year. Survival and rate of movement was low in upstream sections (1 and 2). The year 2021 was found to be a significantly different year when predicting rate of movement compared to 2020 and 2022, which is consistent with high water discharge during tagging and release in 2021. Future work needs to identify river section characteristics which may impact on migration to assess whether riverine migration success and speeds found in the River Derwent are site specific or more widely applicable.


*Key words: Smolt, Riverine, Migration, Mortality, Duration*

## 2.1 Introduction

In the UK, Atlantic salmon (*Salmo salar,* Linnaeus 1758) populations are declining (Condron *et al*., 2005; Adams *et al*., 2022b). In England and Wales, rod catche data showed an 88% decline rate of wild Atlantic salmon between 1988 and 2019, with 86% of the principal salmon rivers being predicted to be at risk by 2025 (CEFAS, 2019). There is growing concern that at least some of the underlying causes of this decline are within riverine systems.

Migration is a fundamental life history strategy for diadromous species (Limburg & Waldman, 2009; Lothian *et al*., 2018; Alerstam *et al*., 2003; Roff, 1988). Atlantic salmon leave their natal nursery habitats during the smolt phase, migrating downstream toward feeding areas in the sea. Between one and eight years in freshwater (Thorstad *et al*., 2012a), juvenile Atlantic salmon undergo morphological, behavioural, and physiological changes which pre-adapts individuals to estuarine and marine high salinity environments (McCormick *et al*., 1985; Thorstad *et al*., 2012a; Zydlewski *et al*., 2014; Hoar, 1976; Klemetsen *et al*., 2003; Metcalfe *et al*., 1989; Lothian *et al*., 2018; Stich *et al*., 2015); this transformation is known as smolting. The smolt phase is thought to be a particularly challenging period for Atlantic salmon partly because of the rapid and fundamental ontogenetic changes that occur (Nyqvist *et al*., 2017).

Smolt migration can be described as being either passive or active, requiring environmental cues such as water temperature, river discharge and photoperiod to initiate migratory behaviour (Riley *et al*., 2012). Passive movements can be defined as the displacement of an individual that is driven solely by water flow (Hedger *et al*., 2008; Lilly *et al*., 2022). In contrast, active movement is the influence of directional swimming in the direction and rate of displacement (Finstad *et al*., 2005; Hedger *et al*., 2008; Lilly *et al*., 2022; Davidsen *et al*., 2008; Fängstam, 1993). Lothian *et al*. (2018), Martin *et al*. (2009) and Thorstad *et al*. (2012b), detail riverine migration of Atlantic salmon smolts as being mostly passive, with fish migrating at a similar speed and direction as the river water discharge. Though this hypothesis has been contradicted, and additional research found that active migration is occurring, with smolts swimming faster than the currents (Davidsen *et al*., 2005; Svendsen *et al*., 2007; Havn *et al*., 2017). Costs associated with both passive and active migration differ between populations, potentially resulting in increased mortality rates (Bonte *et al*., 2012; Adams *et al*., 2022b). Thorstad *et al*. (2012b) highlighted there being potential mechanisms that may result in differential mortality rates between river systems. Mortality rates during migration within riverine environments has been shown to vary between 0.3% to 7.0% per km (%.km$^{-1}$) (Thorstad *et al*., 2012b). High avian predation is one of the mechanisms that has been implicated in mortality in river systems, though predation has been found to differ based on predator species presence (Thorstad *et al*., 2012b; Koed *et al*., 2006; Jepsen *et al*., 2010; Chavarie *et al*., 2022) with the some of the most common avian predators in the UK found throughout literature being Cormorants (*Phalacrocorax carbo carbo,* Linnaeus 1785) and Goosanders (*Mergus merganser,* Linnaeus 1785).

Increased anthropogenic pressures such as artificial infrastructure (hydropower dams, weirs and culverts) on specific river systems has also gained attention as a potential mechanism for increasing mortality (Rand *et al*., 2006; Welch *et al*., 2008). Newton *et al*. (2018) and Lothian *et al*. (2018) found evidence to suggest that artificial infrastructure induces migration delays or in some cases, completely halts migration due to their partial or fully impassable structures under specific environmental flow regimes. Such effects have been found to impact across all life stages, and in some circumstances may significantly impact spawning due to reduced habitat connectivity (Hill *et al*., 2019; Tetzlaff *et al*., 2007; Thorstad *et al*., 2008).

In addition to potential barriers to the migration of wild Atlantic salmon smolts, some elements of the condition of the migrating fish have been shown to affect migration success. Research has shown that smolts with higher condition factor, and of greater length, are more likely to successfully migrate. This is probably due to their enhanced ability to endure long distance migrations and larger fish having greater ability to evade predation within riverine environments (Tucker *et al*., 2016). For example, a study conducted by Antonsson *et al*. (2010) found that longer smolts had a significant advantage, showing higher survival rates compared to small or middle-aged sized smolts (i.e., in the middle part of the freshwater age distribution) within riverine environments.

Despite acoustic telemetry providing some understanding of the potential mechanisms contributing to Atlantic salmon smolt migration success, we have little knowledge of the underlying nature of the specific components of spatial variation in migration success of Atlantic salmon smolts in riverine systems. Additionally, long time-series temporal data on migration success is lacking in the literature. To improve our understanding, there is need to examine individual movement patterns in finer detail (Drenner *et al*., 2012; Hussey *et al*., 2015; Welch *et al*., 2008; Klimley *et al*., 2013; Klinard *et al.*, 2019; Heupel *et al*., 2010; Hitt *et al*., 2011; Rowell *et al.,* 2015).

In this study, I used acoustic telemetry to investigate inter-annual migration success and the mechanisms that may influence migration success in River Derwent smolts, during their initial migration to sea, through the riverine environment. I had three main objectives to: 1) Assess the inter-annual temporal variation in migration success across three years; 2) Compare the spatial variation in smolt migration success through the River Derwent; and 3) Assess the potential biotic and environmental factors which are associated with riverine migration success.

Within these three general objectives, I tested four specific hypotheses related to smolt riverine migration: i) Loss rate is higher in river sections associated with anthropogenic development; ii) Successfully migrating smolts have a higher rate of movement than those that were not successful; iii) Migration duration is greater over longer river sections; and iv) Higher periods of average rainfall would increase rate of movement and decrease migration duration in a river section.

## 2.2 Methodology

### 2.2.1 Description of study site

The River Derwent catchment (Cumbria, North-West England) is 679km² in area and supports a population of wild Atlantic salmon. The River Greta, a tributary of the Derwent system, flows west through the town of Keswick where it intercepts the outflow of the lake, Derwentwater (54°36’07.1”N 3°09’10.1”W), to join the River Derwent. The River Derwent flows north, before flowing into Bassenthwaite Lake. Bassenthwaite Lake is the most northerly un-impounded lake in the Derwent catchment, it is 7.7km in length with a maximum depth of 21.3m. Upon exit of Bassenthwaite Lake, the River Derwent drains west flowing through the urbanised areas of Cockermouth and Workington before draining into the outer Solway Firth at the Port of Workington (54°38’58.2”N 3°34’07.9”W). The River Derwent is partially impounded by two large weirs, approximately 1.5km upstream of Workington harbour is Yearl Weir (~190m length) and 1.2km further upstream is Coops Weir (~90m length). These two weirs are currently the only river-spanning infrastructures along the River Derwent (Figure 2.1).

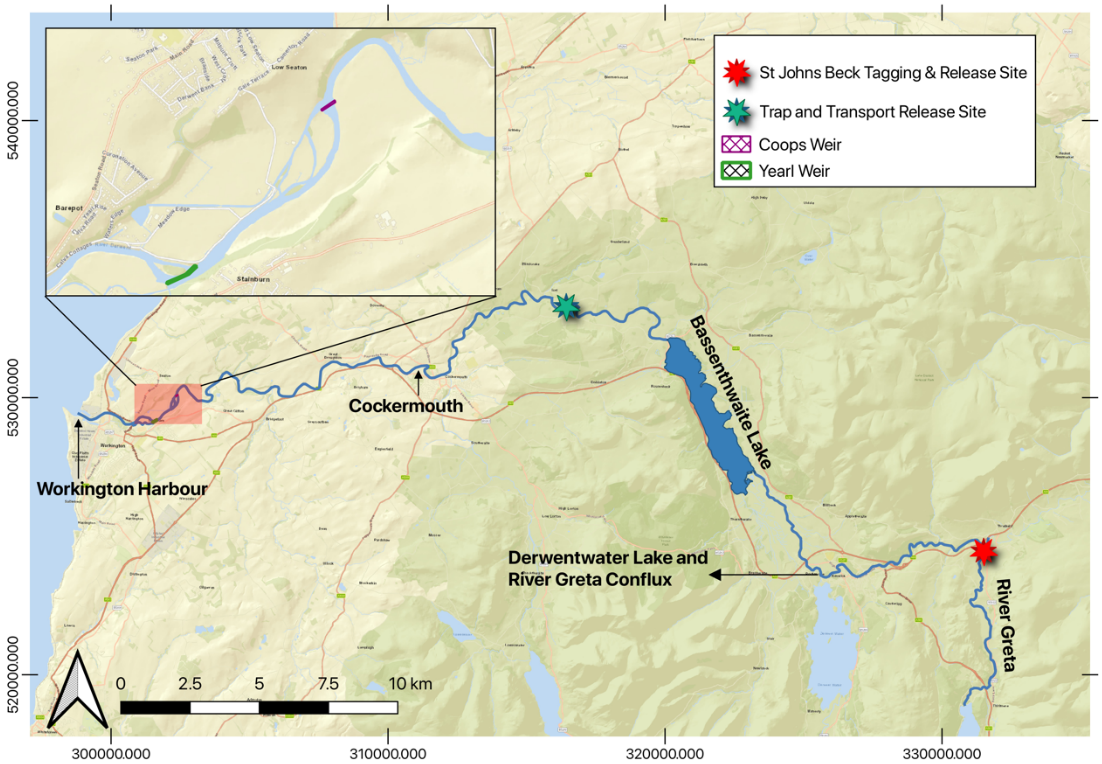


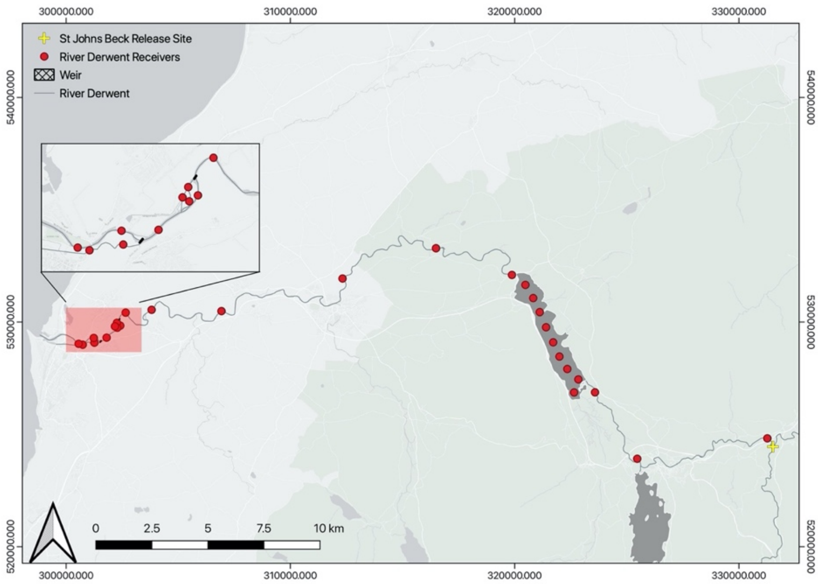

***Figure 2.1*** *River Derwent Catchment*

## 2.2.2 Acoustic receiver deployment

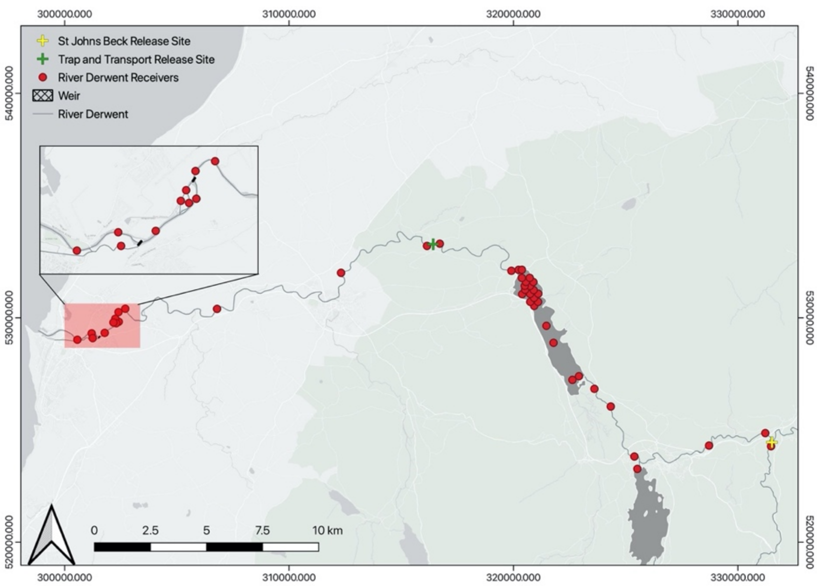
In order to track the seaward migration of Derwent smolts from the upper reaches of the Derwent catchment (St Johns Beck; 54°36'38.1"N 3°03'42.0"W) to the river discharge point into the Solway Firth at the Workington harbour, acoustic telemetry was used. Fixed receivers were placed throughout the River Derwent in three consecutive years (2020 – 2022). In 2020, 27 receivers were deployed (Figure 2.2$^{A}$), 44 in 2021 (Figure 2.2$^{B}$) and 24 in 2022 (Figure 2.2$^{C}$), respectively. Receivers deployed comprised of two types (VR2W and VR2Tx), both operating at 69kHz (Innovasea Ltd., Nova Scotia, Canada). Receivers were attached to a mooring comprised of a vertical steel rod attached on a 20–40kg weight. All river receivers were attached by chain to the riverbank, where suitable, for added security. Within

Bassenthwaite Lake in 2020, receivers were deployed ca.1m above the bed of the lake, attached to a subsurface buoy (to keep them upright) and weighed down by ca.40kg weights with an additional surface buoy attachment to aid in recovery. In 2021, all receivers were attached to a vertical steel rod welded to a steel weight (30–40kg) with a surface buoy attachment included. No receivers were deployed in Bassenthwaite Lake as part of the 2022 study.

A)




B)



C)

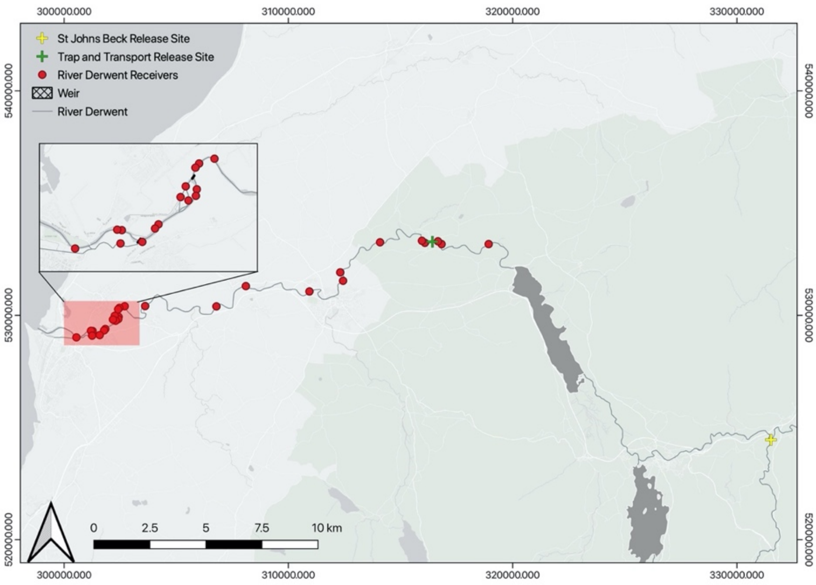



***Figure 2.2*** *Receiver placement throughout the River Derwent, across a three-year study period. A in 2020 (n=27), B in 2021 (n=44), C in 2022 (n=24).*

### 2.2.3 Smolt capture and acoustic tagging procedure

Between 2020 and 2022 Atlantic salmon smolts were captured during spring (April to May) using a 1.2m rotary screw trap during the downstream migration, at St Johns Beck, Threkheld (54°36’38.1”N 3°03’42.0”W). In 2020, 100 fish were tagged between 1st and 5th May, in 2021 150 were tagged between 14th April and 5th May and finally in 2022 150 smolts were tagged between 5th May and 25th May. Across the three study years, in additional to a rotary screw trap, a fyke net was used to increase catches. All trapping apparatus were checked and emptied daily to ensure smolts did not remain trapped for extended periods of time. Fish captured were anaesthetized by immersing them in a bucket containing MS222 (Tricaine Methane sulfonate) and sodium bicarbonate solution (0.6g/6L river water for each). It took approximately three minutes for smolts to lose equilibrium (stage three of anaesthesia) which is required for the tagging procedure to be conducted. Fork length ($L_F$, mm) and weight (g) were examined, and only fish greater than 130mm $L_F$ and 20g weight were tagged. Additionally, scale samples were taken. All surgical equipment was disinfected using

Reprodis/distilled water (1:20 ratio) and rinsed with distilled water. During surgery, fish were given low level anaesthesia (0.125g/2L) and river water was constantly applied across the gills to ensure fish remained sedated. A 10mm ventral incision was made anterior to the pelvic girdle. A V7-2L (69kHz) coded transmitter (VEMCO Ltd, 7mm diameter, 1.7g in air) was surgically placed inside the peritoneal cavity. The V7-2L tags had a nominal delay of 18–45 seconds and an estimated tag life of ca.75 days. The incision was closed by applying two interrupted surgeon knots with 4/0 Ethilon nylon sutures. Smolts were then placed into a recovery container on land for approximately 20 minutes to ensure normal swimming behaviour was exhibited (equilibrium restored). Fish were then placed into a river perforated container downstream from the rotary screw trap with good water flow throughout and given a further 40 minutes recovery.

#### 2.2.3.1 Release group

Tagged fish were released at two different release sites in 2021 and 2022, either at the trapping site or at a site further downstream during daytime hours. This was to ensure that a large enough sample size of fish reached the lower catchment of the River Derwent and to increase the probability of ultimate river migration success.

In 2020 100% of tagged smolts were released immediately downstream of the trap at St Johns Beck. In 2021, 62% (*n=93*) of tagged individuals were released at St Johns Beck, the remaining 38% (*n=57*) were transported to be released in the river downstream of Bassenthwaite Lake. In 2022 100% (*n=115*) of fish captured and tagged at St Johns Beck were transported downstream of Bassenthwaite Lake, these are to be referred to as Trap and Transported release group (TT). All fish released at St Johns Beck are subsequently referred to as the St Johns Beck release group (SJB).

For the transportation, fish were allowed 40+ minutes of recovery in a perforated holding tank St Johns Beck, then in 2021 tagged fish (*n=57*) were placed into a large transport box with continuous aeration. In 2022 tagged fish (*n=115*) were placed in large bags and filled with oxygen and sealed before transportation. In both years smolts were transported ca.25km from St Johns Beck to a release site downstream of Bassenthwaite Lake (54°41'14.7"N 3°17'52.3"W). The journey took an average of 25 minutes. Smolts were transported in groups of at least five to minimise predation risk once released. Fish were transported on six days in 2021 and eight days in 2022. All fish were checked at the release site for any signs of stress or poor swimming ability. Fish were placed into an in-river recovery container and given 30 minutes in flowing water to recover before final release.

### 2.2.4 Ethical statement

All tagging was conducted by a personal licence holder (UK Home Office PIL 70/8794) using procedures which complied with the UK Home Office regulations and UK Home Office project licence number PP0483054. Replacement, reduction, and refinement was considered for this study. All fish were cared for, and monitored, throughout the procedure where stress and suffering were reduced at all times.

### 2.2.5 Statistical analysis

#### 2.2.5.1 False detection filtering

Data analysis was conducted using R software version *4.0.2* (R Core Team, 2019). In order to ensure all detections were real detections, filtering for false detections was conducted using the R package *Glatos* (Holbrook *et al*., 2018; Pincock, 2012) which filtered using the short-interval criterion. Short-interval criterion filters all single detections that occurred at one receiver station within a fixed duration which is set at 30 times the average signal delay of the tag (in this study this duration was 840 seconds) (Hayden *et al*., 2016; Kneebone *et al*., 2014; Lilly *et al*., 2021, 2022) those detections above this set duration period were deemed false, additionally, signals detected during a duration which is less than the tags minimum signal delay (18 seconds) were deemed false (Hanssen *et al*., 2022).

In total, in 2020, 1.02% of detections were considered false, therefore, 1,533,102 detections were used for analyses. In 2021, 0.71% of detections were considered false, therefore, 1,251,308 detections were used for analyses. Finally, in 2022, 0.14% of detections were considered false, therefore, 842,137 detections were used for analyses.

#### 2.2.5.2 Descriptive analysis

Descriptive data from across the three-year study period were derived from the R package *Actel* (Flávio & Baktoft, 2021). Flávio & Baktoft (2021) state that *Actel* provides a systematic conditional pipeline to filter and analyse acoustic telemetry data in a reproducible fashion, for fish moving between receiver arrays. It also allows for detection efficiency estimations to be made for each receiver station. Additionally, *Actel* allows diel movement patterns to be observed by defining the arrival time recorded at each individual receiver.

#### 2.2.5.3 Migration success estimates

To assess migration success rates, survival likelihood through different riverine sections over the downstream migration route were calculated in *Actel* (Flávio & Baktoft, 2021). Those individuals that were detected at the last riverine receiver

(54°38’47.1”N 3°32’34.7”W) were deemed to be successful river migrants. Riverine migration success per km (%.km$^{-1}$) was calculated as the proportion of fish which were successful in reaching the finale River Derwent receiver, divided by the direct minimum distance travelled (MDT). Due to the release groups migrating across different distances (St Johns Beck smolts MDT=ca.49.12km, Trap and Transported smolts MDT=ca.24km) groups were not compared against each other and only St Johns Beck release group 2020 and 2021 were compared and similarly, Trap and Transport release group 2021 and 2022 migration success rates were compared. The MDT to the final River Derwent receiver is based on the minimum river distance from the first riverine receiver where smolts could be detected to the final River Derwent receiver.

In order to examine spatial variability in migration success, the river was split into three sections for analysis purposes (Figure 2.3). Section 1 extended ca.12.52km from the St Johns Beck release site (54°36’38.1”N 3°03’42.0”W) to the entrance of the river to Bassenthwaite Lake (54°37’51.4”N 3°11’06.4”W). Section 2 stretched ca.7.15km from Bassenthwaite Lake entrance point to the lake outflow (54°40’39.1”N 3°14’36.9”W). Finally, section 3 for the St Johns Beck release group smolts covered ca.29.44km from the lake outflow to the final River Derwent receiver. For fish from the Trap and Transport release group, the total distance travelled was ca.23.77km. Riverine migration success rate per section (%) was calculated as the proportion of fish which were successful in reaching the final section receiver, migration success rate per distance of that section (%.km$^{-1}$) was calculated as the proportion of fish which were successful in reaching the finale section receiver divided by the direct MDT.

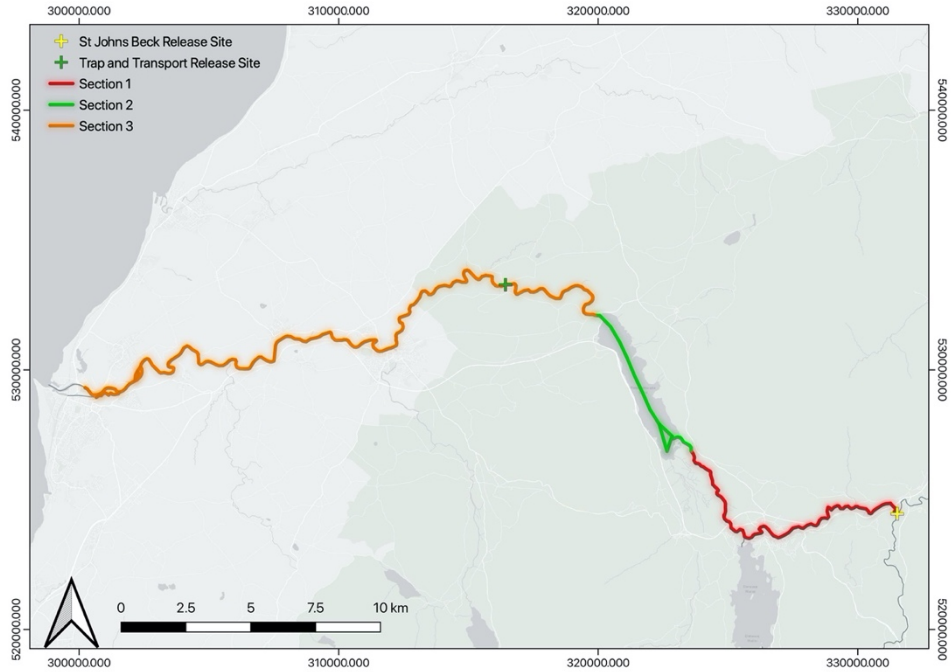



***Figure 2.3*** *Section divisions across River Derwent catchment. Section 1=12.52km, Section 2=7.15km and Section 3=29.45km for St Johns Beck released smolts and 23.77km for Trap and Transported released smolts.*

The detection efficiency of river acoustic receivers was not always 100% due to ambient noise, fast water currents increasing smolt speed and potential submerged barriers, such as logs and therefore, efficiency must be assessed when providing estimates of survival (Halfyard *et al*., 2013; Lilly *et al*., 2022). Efficiency is assessed by the number of smolts detected at a downstream receiver as a proportion of those not detected at the receiver upstream. In the River Derwent, there are a number of alternative river channels and thus alternative routes that could have allowed for migration were taken into consideration when detection efficiency was calculated.

#### 2.2.5.4 Non-residency events

To establish the number of individual movements undertaken by each fish between receiver stations during River Derwent migration, non-residency events were calculated using the R package *Vtrack* (Campbell *et al*., 2012) RunresidenceExtraction function. This function provides timestamps for each receiver and is used to determine the duration of riverine migration.

Once the non-residency event function in R was conducted it provided smolt rate of movement (ROM). ROM in meters per second ($m.s^{-1}$) was calculated for riverine migration by dividing the MDT (m) by the total duration (seconds) taken to migrate from one receiver to another. Release groups were split for analysis to compare the St Johns Beck release group (2020–2021) and the Trap and Transport release group smolts (2021–2022).

#### 2.2.5.5 Modelling

##### 2.2.5.5.1 Migration success rate

A general linear model (GLM) was tested to establish if river section or year impacted riverine migration success rate.

*Initial model:*

*glm(Migration Success Rate ~ river section + year)*

Significant factors highlighted by the GLM where further investigated for significant categorical factors. The R package *multcomp* (Hothorn *et al.*, 2016) was used for ANOVA testing with Post Hoc Tukey HSD Test in order to compare potential differences within categorical data sets (e.g., river section).

##### 2.2.5.5.2 Survival

General linear modelling (GLM) was undertaken to determine if biotic factors such as fork length ($L_F$, mm), release group (St Johns Beck or Trap and Transport), and day of year contributed to successful migration. For analysis, only data collected in 2021 was used due to it including both release groups. The GLM was fitted with a binomial error structure and the identity link function using the R Package *lme4* (Bates *et al*., 2014). Survival (dependent variable) was coded as 1 for fish detected on a receiver or 0 for an assumed failed migration.

*Initial model:*

*glm(Survival ~* $L_F$ *+ Day of Year + Release group, family = binomial (link = "identity"))*

Furthermore, in order to establish if year would be statistically significant in understanding the temporal disparities in survival, release group was split prior to modelling and a GLM of survival was conducted on St Johns Beck release group (2020–2021) (SJB) and a separate GLM was conducted on Trap and Transported released smolts (TT) (2021–2022).

*Initial models;*

*glm(Survival ~* $L_F$ *+ Year+ Day of Year, data= SJB, family = binomial (link = "identity"))*

*and*

*glm(Survival ~* $L_F$ *+ Year+ Day of Year, data= TT, family = binomial (link = "identity"))*

2.2.5.6 <u>ROM</u>

In order to determine if Rate of Movement (ROM) ($m.s^{-1}$) was being impacted by biotic factors such as $L_F$ (mm), release group (St Johns Beck or Trap and Transport), river section, day of year and year, a general linear mixed model was constructed using the R package *lme4* (Bates *et al*., 2014). The GLMM was fitted with a gamma error structure and log link function with ROM being the dependent variables and FishID as a random effect.

*Initial model:*

*glmer(ROM ~ River Section + Release Group +* $L_F$ *+Day of Year + Year (1|TRANSMITTERID) , family = Gamma(link = "log")*

2.2.5.7 Environmental predictors

Hourly water flow discharge ($m^3/s$) data was provided by the Ouse Bridge gauging station (54°40′41″N, 003°14′41″W). In order to investigate the impact water flow had on the survival rate of migrating smolts and if water flow discharge impacted ROM between receiver stations, hourly water flow discharge data ($m^3/s$) was modelled. Using a general linear model (GLM) with the R package *lme4* (Bates *et al*., 2014), survival was fitted with a binomial error structure and the identity link function. Survival (dependent variable) was coded as 1 for fish detected on a receiver or 0 for an assumed failed migration. ROM was modelled using a generalised linear mixed model (GLMM) with ROM being the dependent variables and FishID as a random effect. Year was also included for both models.

*Initial model for survival:*

*glm(Survival ~ Water Flow + ROM + Year, family = binomial (link = "identity"))*

*Initial model for ROM:*

*glmer(ROM ~ Water Flow + Year + (1|TRANSMITTERID) , family = Gamma (link = "log")*

## 2.3 Results

### 2.3.1 Tagging summary

In total, 365 Atlantic salmon smolts were tagged between 2020-2022. $L_F$ (mm), weight (g) and tag burden (%) averages are summarised in Table 2.1.

***Table 2.1*** *Summary data for River Derwent tagged Atlantic salmon smolts between 2020–2022. Summary of mean $L_F$ (mm), weight (g) and tag burden (%) for each year and release group: SJB- St Johns Beck release group, TT-Trap and Transport release group. Tag burden is calculated by dividing the weight of the tag in air (1.7g) by the weight of the individual* 100.*

| Year | $L_F$ (mm) ± SD (range) | Weight (g) ± SD (range) | Tag Burden (%) ± SD (range) |
|---|---|---|---|
| **2020 (SJB)** | 139.4 ± 0.65 (130–157) | 27.89 ± 0.42 (21.4–41.4) | 5.1 ± 0.07 (3.5–6.7) |
| **2021 (SJB)** | 141.9 ± 8.4 (130–164) | 29.4 ± 5.5 (21.5–44.5) | 4.9 ± 0.61 (3.6–6.1) |
| **2021 (TT)** | 141.0 ± 7.7 (130–164) | 29.8 ± 5.1 (21.5–44.5) | 4.8 ± 0.55 (3.6–6.1) |
| **2022 (TT)** | 138.7 ± 6.6 (130–161) | 27.4 ± 4.1 (21.2–40.4) | 5.1 ± 0.5 (3.9–6.2) |

### 2.3.2 Migration success

Out of all tagged smolts, 8% in 2020 (*n=8*), 27.3% in 2021 (*n=41*) and 41.7% in 2022 (*n=48*) were deemed to have made a successful river migration, having been detected at the final River Derwent receiver, located at Workington harbour, thus indicating likely entrance into the Solway Firth. Within section 1 (Figure 2.3), riverine migration success was particularly low. In 2020, only 32% (*n=32*) of smolts made a successful migration through section 1 (thus, 68% failed to migrate through this area) this had a migration success rate of 2.55%.km$^{-1}$. In contrast, 2021 migration success in section 1 was 64.5% (*n=60*) with a migration success rate of 5.15%.km$^{-1}$ (Figure 2.4, Table 2.2). In 2022 all smolts were released at the start of section 3, thus there is no measure of migration success for this section in 2022.

For the *32* individuals that migrated into Bassenthwaite Lake (Section 2/Figure 2.3) in 2020, only 47% (*n=15)* of individuals successfully migrated through the lake ($6.57\%.km^{-1}$ migration success rate). Similarly, in 2021, *60* individuals successfully entered Bassenthwaite Lake, 65% (*n=39*) of individuals successfully migrating out of Bassenthwaite Lake (migration success rate of $9.09\%.km^{-1}$) (Figure 2.4, Table 2.2).

Section 3 was the longest section, at ca.29.44km for St Johns Beck released smolts and ca.23.77km for Trap and Transported released smolts (Figure 2.3). In 2020, 53% (*n=8*) out of *15* smolts which entered section 3 made a successful migration, which gave a migration success rate of $1.8\%.km^{-1}$ (thus, 46.6% failed to migrate through this area). In 2021 46.1% (*n=17*) of smolts from St Johns Beck release group made a successful migration ($1.56\%.km^{-1}$ migration success rate) through this area. For Trap and Transported smolts, in 2021, 42.1% (*n=23*) of smolts had a successful riverine migration through section 3, making it to Workington harbour ($1.77\%.km^{-1}$ migration success rate). Nevertheless, in 2022 there was a migration success rate of $1.75\%.km^{-1}$ with 41.7% (*n=48*) making a successful migration through section 3 (thus, 58.2% migration failure). Across both years where Trap and Transport was conducted there was relatively similar success rates and failure ($\%.km^{-1}$), which is likely due to initial post tagging mortality affects (data is summarised in Table 2.2 and shown in Figure 2.4).

***Table 2.2*** *Summary table of section migration success rates (%) and migration success rate per km ($\%.km^{-1}$) for Atlantic salmon smolts tagged between 2020 – 2022 on the River Derwent. Release group: SJB- St Johns Beck release group, TT-Trap and Transport release group.*

| Year | Section 1 | Section 2 | Section 3 |
|---|---|---|---|
| **2020 (SJB)** (*n=100*) | 32 ($2.55\%.km^{-1}$) | 47 ($6.57\%.km^{-1}$) | 53 ($1.8\%.km^{-1}$) |
| **2021 (SJB)** (*n=93*) | 64.5 ($5.15\%.km^{-1}$) | 65 ($9.09\%.km^{-1}$) | 46.1 ($1.56\%.km^{-1}$) |
| **2021 (TT)** (*n=57*) | - | - | 42.1 ($1.77\%.km^{-1}$) |

| | | | |
|---|---|---|---|
| **2022 (TT)** (*n=115*) | - | - | 41.7 (1.75%.km$^{-1}$) |

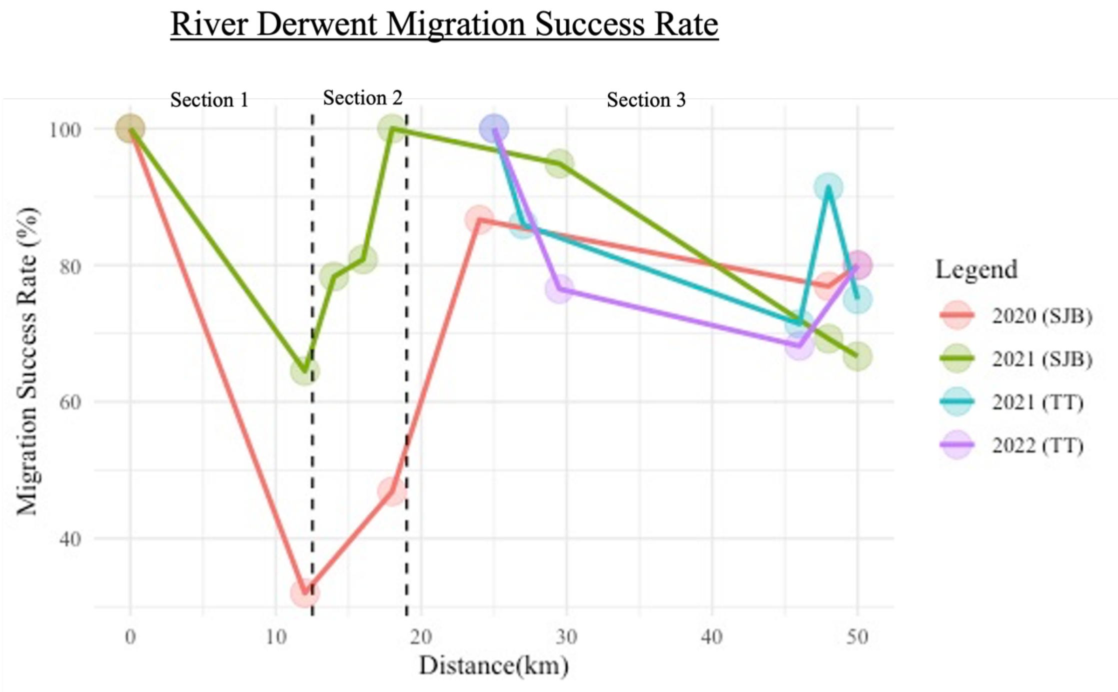



***Figure 2.4*** *Migration success rate (%) of Atlantic salmon smolts migrating through each analysis section across the three years of the study (2020–2022) through the River Derwent. Release group: SJB- St Johns Beck release group, TT-Trap and Transport release group.*

The modelling of migration success rate across three years showed section as a significant factor ($p$=0.004) on migration success rates of Atlantic salmon smolts through the River Derwent. This was strongly driven by migration success in sections 1 and 2 (section 1; $p$=0.02, section 2; $p$=0.02, section 3; $p$=0.07). Additionally, year was not found to be significant ($p$=0.7) (Figure 2.4). Fish $L_F$ did not predict migration success through a section ($p$=0.92). However, release group was a significant predictor ($p$=0.002). Due to only 2021 having both release groups present, release group data was compared using 2021 data only to see if St Johns Beck release group had a different total migration success rate compared to the Trap and Transported released smolts. Looking at full riverine migration success, Trap and Transported smolts migration success rate was significantly higher ($p$=0.006). In 2021, 42% ($n=23$) of the individuals from the Trap and Transport release group made a successful river migration, compared to 19% ($n=17$) of the individuals from smolts released in the St Johns Beck release group.

In order to understand the temporal disparities of migration success along the River Derwent, modelling showed that for smolts released at St Johns Beck in 2020 and 2021, Year was not significant in predicting survival ($p$=0.47, $p$=0.08). However, smolts released from the Trap and Transport release group were found to have significantly higher migration success in 2022 ($p$=0.02) compared to 2021 ($p$=0.54) (Table 2.3).

***Table 2.3*** *Summary table of the temporal variation of migration success rate (%) across two release groups. Release group: SJB- St Johns Beck release group, TT-Trap and Transport release group.* * significance level (<0.05).

| Year | Migration Success (MSR %) | *p value* |
|---|---|---|
| **2020 (SJB)** | 8 (8%) | 0.470 |
| **2021 (SJB)** | 17 (19%) | 0.088 |
| **2021 (TT)** | 23 (42%) | 0.541 |
| **2022 (TT)** | 48 (41%) | 0.028* |

### 2.3.3 Rate of movement

Modelling ROM through the River Derwent showed that there was spatial and temporal variability in the ROM of migrating smolts. Mean rates of movement for all sections across the three years are summarised in Table 2.4.

***Table 2.4*** *Summary table of section migration rate of movement (ROM) (m.s$^{-1}$) and km per day$^{-1}$ taken to migrate for Atlantic salmon smolts tagged between 2020 – 2022 on the River Derwent. Release group: SJB- St Johns Beck release group, TT-Trap and Transport release group.*

| Year | Section 1 | | Section 2 | | Section 3 | |
|---|---|---|---|---|---|---|
| | ROM (m.s-$^{1}$) | km.day$^{-1}$ | ROM (m.s-$^{1}$) | km.day$^{-1}$ | ROM (m.s-$^{1}$) | km.day$^{-1}$ |
| **2020 (SJB)** | 0.012 | 0.9 | 0.038 | 3.29 | 0.094 | 8.18 |
| **2021 (SJB)** | 0.024 | 2.09 | 0.017 | 1.47 | 0.051 | 4.44 |
| **2021 (TT)** | - | | - | | 0.058 | 4.94 |
| **2022 (TT)** | - | | - | | 0.020 | 1.73 |

Spatial variability in ROM was noted through the sections. Section 1 showed the slowest ROM along the River Derwent (Table 2.4). Both section 2 and 3 were significantly faster (*p*=0.0001). But when analysing the differences, section 3 was substantially slower than section 2 when taking into account section size (Table 2.4, Table 2.5).

Release Group was found to significantly predict ROM, whereby St Johns Beck released smolts were significantly faster than Trap and Transported release smolts across the three years (*p*=0.0001) across the whole of the River Derwent. Additionally, smolts that were released later in the tagging season per year had a higher ROM (*p*=0.001). Fork length was significant in predicting ROM (*p*=0.018) whereby larger smolts had a faster ROM compared to smaller smolts across both release groups (Table 2.5).

***Table 2.5*** *Rate of Movement (ROM) (m.s$^{-1}$) generalised linear mixed model output, displaying significant predictors of ROM using p value, T value and overall Effect Size for Atlantic salmon smolts tagged between 2020-2022 on the River Derwent. Release group: SJB- St Johns Beck release group.*

| Predictor of ROM | *p value* | *T value* | Effect Size |
|---|---|---|---|
| **Section 1 (Intercept)** | | -275.93 | 0 |
| **Section 2** | 0.0001 | 198.06 | 99.95 |
| **Section 3** | 0.0001 | 139.32 | 9.45 |
| **Day of Year** | 0.001 | 149.12 | 1.01 |

| | | | |
|---|---|---|---|
| **Release Group: SJB** | 0.0001 | 170.96 | 16.91 |
| **Fork Length ($L_F$, mm)** | 0.018 | 11.15 | 0.98 |

2.3.4 Environmental predicators of survival and rate of movement

To determine if environmental factors were predictors of smolt survival and the ROM during their downstream migration water flow discharge and year were modelled.

Year was a significant predictor for ROM ($p$=<0.001). When looking further into how flow rate impacts on ROM, an ANOVA and Post Hoc Tukey test were performed and found the year 2021 was significant ($p$=<0.001) which coincides with high rainfall noted during 2021 smolt tagging. However, flow discharge ($m^3/s$) did not predict smolt migration success in the River Derwent ($p$=0.221).

## 2.4 Discussion

### 2.4.1 Migration success

The probability of Atlantic salmon smolts successfully migrating through riverine systems at a sensitive life cycle stage is low (Aarestrup & Koed, 2003; Halfyard *et al.*, 2012; Thorstad *et al.*, 2012a). Multiple interacting factors are a probable cause of low migration success rates found throughout literature (Flávio *et al.*, 2020), though migration success is likely to be geographically specific. Moore *et al.* (1995) reported migration success through the River Conwy (Wales) to be as high as 97%. Additionally, studies conducted on the River Skjern (Denmark) by Dieperink *et al.* (2002) also reported a high migration success rate of 89%. The recorded overall smolt migration success in the River Derwent was substantially lower (8%, 41%, 48%) in the three-years studied, though Flávio *et al.* (2020) recorded low migration success rates of Atlantic salmon smolts on rivers Tea and Minho (Portugal). Flavio *et al.*

(2020) found migration success to be below 55% across a three-year study period with the lowest period of 30% migration success. Likewise, Lothian *et al*. (2018) conducted an acoustic telemetry study along the River Deveron (Scotland) finding migration success rates declined along the River Deveron with only 40% survival (0.41%.km$^{-1}$). It has been suggested that increased migration success rates are correlated with relatively longer riverine migration distances (Lothian *et al*., 2018). This is simply not the case for River Derwent smolts and suggests differing migration success rates could be a factor of varying catchment attributes with differing physical and encironment characteristics. Nevertheless, literature remains limited as to the potential temporal and spatial differences throughout riverine systems which may be contributing to declines in migration success rates of Atlantic salmon smolts.

The study presented here shows exceedingly strong evidence of spatial variation in migration success rates of Atlantic salmon smolts. Throughout the three sections of the River Derwent, distinctive patterns of migration success are prevalent across the three-year study period. Calculated migrations success rate (%.km$^{-1}$) along the River Derwent indicates there may be considerable pressures existing within section 1 and 2 leading to assumed tag loss, which Trap and Transported released smolts avoided.

It is possible that the potential tagging effects “tag burden” impacted on smolt migration success estimates during initial migration through section 1. Brown *et al*. (2011) and Wilson *et al*. (2017) proposed tag loss during the riverine phase is due to altering behaviours by delaying growth, reducing swimming speeds and consistently lowering activity levels (Zale *et al*., 2005; Welch *et al*., 2007; Rechisky & Welch, 2010) which corresponds with the reduced ROM experienced within section 1. However, Newton *et al*. (2016) found no associated effects of increased tag burden and Atlantic salmon smolt fork length. It is possible larger smolts have the ability to increase rate of movement throughout the riverine environment, reducing predation risk and increasing migration success rate estimates in comparison to smaller sized smolts. Though, in this study fork length did not predict migration success rate through the River Derwent, unlike other studies such as Flávio *et al*. (2020) which found that large smolts were more likely to be successful than smaller smolts (also: Chaput *et al*., 2019; Davidsen *et al*., 2009; Flávio *et al*., 2019; Jepsen *et al*., 1998). In this study only smolts above a minimum fork length and weight threshold were tagged, therefore there is the possibility of size bias playing a role in the lack of association between smolt fork length and migration success estimates recorded.

Section 2 presented a low migration success rate per km for both 2020 and 2021 smolts (2020: 47%.km$^{-1}$, 2021: 65%.km$^{-1}$). Bassenthwaite Lake is a large standing water and lakes are commonly associated with inhibiting migratory success due to the lack of directional currents which smolts require to initiate migration and reduce navigational error (Honkanen *et al*., 2018). Often migration success is low in natural standing waters due to the increased migration duration, incurring increased energy expenditure costs and predation pressures. Honkanen *et al*. (2021) found a migration failure rate of 24.6%.km$^{-1}$ within Loch Garve (Scotland). However, other studies have found migration success to be exceedingly lower than UK based studies (0.3 to 9.4%.km$^{-1}$) (Thorstad *et al*., 2012a), leading us to assume migration success through standing waters is geographically/regionally specific, and further investigation into the key differences is required.

Section 3 was the longest riverine stretch throughout the River Derwent study system and was found to have the high migration success rates in comparison to the previous two sections. St Johns Beck smolts were found to have a success rate of 53% (1.8%. km) in 2020 and 31.5% (1.56%.km$^{-1}$) in 2021. Trap and Transported smolts had a high success rate in 2021 of 42.1% (1.77%.km$^{-1}$) and 41.7% (1.75%.km$^{-1}$) in 2022.

The trap and transportation of smolts around Bassenthwaite Lake provided evidence in allowing for the assumption that the reduction in km to migrate faced by smolts is associated with increased migration success rates found along the River Derwent. Trapping of migrating smolts and transporting around high migration failure zones (bottleneck zones) is a common mitigation strategy since 1970's (Chapman *et al*., 1997). However, trap and transport studies have primarily focused on hatchery reared fish, and growing concerns of long-term effects on wild populations are becoming more prevalent. Such concerns include potential disruption to smolting, increased predation pressures at release site and altered phenology which has the ability to reduce overall smolt size which can impair vigilance when entering high salinity environments (Chapman *et al*., 1997; Muir *et al*., 2006; Tipping, 1998). Nevertheless, Muir *et al*. (2006) assessed chinook salmon (*Oncorhynchus tshawytscha,* Walbaum 1792) mortality rates when undergoing transportation as a proposed management strategy and reported approximately 100% survival during transport around the Bonneville dam (Columbia), providing evidence to suggest transporting fish around associated bottleneck zones associated with high migration failure is a viable way to increase immediate freshwater survival rates. Trap and transport conducted on the River Derwent saw survival rates remain high in 2021 (42%) and 2022 (41%) in comparison to St Johns Beck smolts released in 2020 (8%) and 2021 (19%). Our findings correlate with that of Lilly *et al*. (2022) where Atlantic salmon smolts which were transported around Loch Lomond appeared to increase overall survival likelihood, particularly in the Clyde Estuary ($n$=18; 3.32%.km$^{-1}$) compared to ‘naturally’ released smolts ($n$=11; 2.83%.km$^{-1}$). However, it should be noted studies evaluating return rates of transported fish are disproportionately low when compared to natural migrants (Muir *et al.*, 2006). This allows for the assumption that trap and transported smolts are at a disadvantage due to lack of imprinting and physiological preparation for their marine migration (Keefer *et al.*, 2008; Rechisky *et al.*, 2012; Mills, 1994; Muir *et al.*, 2006). Migration into marine environment requires physiological and morphological preparation (Keefer *et al.*, 2008) may be compromised in trap and transported fish. Studies have found size disparities between river migrants (SJB) and transported migrants (TT), with river migrants having a $L_F$ 6–8mm longer than transported migrants (Muir *et al.*, 2006). This is assumed to be as a result of transported fish skipping large riverine sections which provide opportunities to feed and increase body condition (Jutila & Jokikokko, 2008). Further investigation into the long-term effects and return rate impacts of trap and transported methods of Atlantic salmon is required before it can be regarded as a safe enhancement measure to increase a populations size and future success. Though, based on the size disparity between the riverine sections it would be concluded that avoidance of section 1 and 2 would promote increased survival ratios of Atlantic salmon smolts.

### 2.4.2 Mechanisms of migration failure

Smolt migration failure may be associated with increased anthropogenic modifications through the riverine system, resulting in habitat fragmentation. Previous research found a migration failure rate of 37% for Atlantic salmon smolts when passing over a partial passable barrier under certain environmental conditions (i.e high water discharge), with 75% of the migration failure being of immediate effect, post impact (Thorstad *et al.*, 2012a). This demonstrates the potential impact on smolt migration when faced with anthropogenic river-spanning infrastructure such as the weirs at Workington. Aarestrup & Koed (2003) detailed the impact of two weirs along River Salten and found 53% of Atlantic smolts survived weir passage though indicated delays and predation were a leading cause of losses. Much like natural standing waters, in-river barriers increase migration delays, reduce rate of movement and are a potential bottleneck zone for high predation pressures.

One of the leading mechanisms associated with mortality is increased predation pressure by avian and piscine species (Thorstad *et al*., 2012b; Koed *et al*., 2006; Jepsen *et al*., 2010, 2000, 1988) which is a common source of mortality within rivers (Carter *et al*., 2001; Dieperink *et al*., 2002; Heggenes & Borgstrom, 1988; Hvidsten & Møkkelgjerd, 1987; McCormick *et al*., 1998; Thorstad *et al*., 2012a). The Derwent catchment supports a variety of predatory fish, e.g., pike (*Esox lucius,* Linnaeus 1785), brown trout (*Salmo trutta,* Linnaeus 1785), and a variety of avian species. One of the most common species along the River Derwent is cormorants (*Phalacrocorax carbo carbo,* Linnaeus 1785). Moreover, researchers have found a correlation between in-river barriers and increased predation rates and smolt stress (Koed *et al*., 2002; Thorstad *et al*., 2008). Chavarie *et al*. (2022) measured smolt predation during migration along the Endrick Water, Scotland using an active tracking approach and found avian predators to be the main cause of mortality (42%), though considerable piscivorous fish predation was also recorded (14%).

R Package *Actel* (Flávio & Baktoft, 2021) provided substantial evidence to help aid in determining levels of bird predation of Derwent smolts across the three-year study. Smolts which were found to migrate considerable distances with a rate of movement unsustainable for natural migration were removed from analysis from the point prior to the excessive move. This was commonly found within section 1 prior to Bassenthwaite Lake entry. Smolts were found to rapidly appear upstream (ca.12km) from their final monitoring point (Bassenthwaite Lake entrance). Lothian *et al*. (2018) states that we must assume that when smolts are not detected throughout the riverine array after tagging, that they did not return upstream as a result of de-smolting. Initial migration is time sensitive, when morphological, behavioural, and physiological pre-adaptions of individuals occur, smolts have a limited amount of time in which to exit their riverine system (Hoar, 1976; McCormick *et al*., 1998).

### 2.4.3 Rate of movement

The ROM ($m.s^{-1}$) of migration Atlantic salmon smolts across the three-year study period alluded to spatial variation and also inter-annual variation in the River Derwent. ROM was found to be considerably slower in section 1 across the two years when smolts migrated through this system, though ROM in 2020 ($0.012m.s^{-1}$) was considerably slower than 2021 findings ($0.024m.s^{-1}$). ROM within Bassenthwaite Lake was significantly lower in 2021 than in 2020 (2020: 0.038, 2021: $0.0170m.s^{-1}$). ROM was predominately higher in section 3 compared to other sections. ROM is often accelerated when nearing the marine environment as smolt physiological development matures (Whalen *et al*., 1999; Stich *et al*., 2015). For Trap and Transported smolts which covered a distance of 23.77km along the River Derwent, smolts migrating in 2021 had a mean ROM of $0.05m.s^{-1}$ ($4.94km.day^{-1}$), under similar environmental pressures 2022 smolts had a speed of $0.02m.s^{-1}$ ($1.73km.day^{-1}$). St Johns Beck released smolts which travelled 29.44km were considerably faster compared to the Trap and Transport release group, where in 2020 smolts were found to travel at $0.094m.s^{-1}$ ($8.18km.day^{-1}$) and $0.05m.s^{-1}$ ($4.44km.day^{-1}$) in 2021. It is plausible that smolts which were transported had a lower ROM through section 3 due to lagged tagging effects which may have reduced swimming speeds and consistently loweried activity levels (Zale *et al.*, 2005; Welch *et al.*, 2007; Rechisky & Welch, 2010; Wilson *et al.*, 2017).

Additionally, it is plausible that high flow regimes recorded during 2021 contributed to a greater mean ROM of Atlantic salmon smolts in section 1 and section 3. Researchers have speculated that increased flow regimes may impact smolt migration by the following processes: 1) smolts utilise current- to increase speed, reducing the overall duration spent in the riverine environment; 2) reducing visibility in the water column; and 3) increasing the number of smolts simultaneously migrating downstream (Hvidsten *et al.*, 1995; Jonsson & Jonsson, 2009). This coincides with the significant findings of the ROM model regarding flow regimes during 2021.

The ground speed ($km.day^{-1}$) of Atlantic salmon smolt downstream migration has been found to vary considerably between populations in recent literature, with the predominant influences on increase rate of movements being river discharge and photoperiod (Martin *et al.*, 2009; McCormick *et al.*, 1998; Rand *et al.*, 2006; Thorstad *et al.*, 2012a). The ground speed of the River Derwent smolts differed both spatially and temporally. Section 1 recorded ground speeds of $0.9km.day^{-1}$ in 2020 and $2.09km.day^{-1}$ in 2021. Section 2 ground speed in 2020 was $3.29km.day^{-1}$ and $1.47km.day^{-1}$ in 2021, all of which is deemed to be at the lower end of the range reported by previous studies, which range from 0.2 to $60km.day^{-1}$ (Thorstad *et al.*, 2012a). In section 3, 2020 ground speeds were $8.18km.day^{-1}$, in 2021 $4.44km.day^{-1}$ for St Johns Beck released smolts and $4.94km.day^{-1}$ for Trap and Transported smolts in 2021, though in 2022 ground speed was drastically slower at $1.73km.day^{-1}$. It is most likely that migration speed in the study was heavily influenced by water discharge at the time of migration where flow rate was found to significantly impact ROM in the lower sections of the River Derwent.

## 2.5 Conclusion

This study increases current knowledge on riverine migration of wild Atlantic salmon smolts and mortality of smolts throughout the River Derwent and around potential bottleneck zones. The work also provides evidence that Atlantic salmon smolts exhibited a higher mortality rate during the initial migration phase through section 1, though temporal and spatial variation was observed be occurring throughout the River Derwent catchment, a finding that has not been observed in other Atlantic salmon populations. Smolts also experienced a greater swimming velocity within the lower catchment regions, potentially accelerating towards marine environments when smolting pre-adaptions and external factors are optimal. This is the first description of Atlantic salmon smolt behaviour and swimming trajectories throughout the River Derwent. Future research should focus on determining the underlying mechanisms of smolt mortality and the further elucidate to the temporal and spatial differences within the catchment.

# *Chapter 3:* Investigating the Behaviour of Atlantic salmon smolts through Bassenthwaite Lake.


**Abstract**

The anadromous Atlantic salmon, (*Salmo salar,* Linnaeus 1785) is listed in Annex II of the European Union's Habitats Directive and has seen a dramatic decline throughout its range. We know from a few recent studies that migration success through natural lakes is often poor but not how universal that effect might be or how and why it happens. The potential drivers associated with lake survivor likelihood are unclear, so in this study we use acoustic telemetry to examine phenotypic, behavioural and environmental factors that distinguish successful lake migrants from unsuccessful lake migrants through Bassenthwaite Lake, Cumbria. We also determine if we can identify an area in which cues are just right for smolt exit from a lake which is referred to as "Goldilocks Zone". Similar to other studies we found high tag loss within the lake (33%, *n=20*). Migration speeds throughout the lake were similarly slow in Bassenthwaite Lake ($0.16 m.s^{-1}$) when compared to other studies conducted in UK lakes. Individual migration trajectories also frequently diverted away from the lake exit. No evidence of phenotypic (fork length: $p$=0.417), behavioural ($p$=0.28) or environmental (wind direction: Easterly; $p$=0.32, Westerly; $p$=0.76) effects that distinguished successful from unsuccessful smolts were identified. This suggests that migration success in Bassenthwaite Lake was random, which supports the findings of other acoustic telemetry studies. We determined that the "Goldilocks Zone" is applicable to Bassenthwaite Lake at an average estimated minimum distance of 0.72 ± 0.6km (mean ± SD; range: 0.13–1.24) from the lake exit, though it remains unclear if the "Goldilocks Zone" is applicable to all standing waters or if its specific to only natural lake systems.

*Key words: Atlantic salmon, Standing Waters, Smolts, Migration, Impact, Direction, Telemetry*

## 3.1 Introduction

Migration is commonly described as a regular seasonal movement pattern across different temporal and spatial scales (Roshier & Reid, 2003). During migration, species transition across different environments, undergoing varied periods of residency within a habitat, which is dependent on the current life stage and species (Mueller & Fagan, 2008; Avgar *et al*., 2014; Lilly *et al*., 2021). Migration is often driven by opportunities to increase foraging and growth potential, resulting in increased likelihood of higher fecundity (Hendry *et al*., 2004; Dingle & Drake, 2007; Avgar *et al*., 2014; Mueller & Fagan, 2008; Tamario *et al*., 2019; Lucas & Baras, 2001; Quinn & Myers, 2004). High costs are commonly associated with migration, including, for example, increased predation pressure (Mueller & Fagan, 2008; Alerstam *et al*., 2003; Horton *et al*., 2020; Vogel *et al*., 2021; Lilly *et al*., 2021. Understanding the risks that are associated with particular elements of a species' migration behaviour can be important for effective management.

The Atlantic salmon, *Salmo salar,* Linnaeus 1785, is an anadromous fish which undergoes long-distance migrations between freshwater and saltwater environments (Limburg & Waldman, 2009; Gilbey *et al*., 2021; Thorstad *et al*., 2008). Seaward migration is an important life stage (Mueller & Fagan, 2008; Thorstad *et al*., 2012b; Avgar *et al*., 2014), however, it is associated with high mortality rate in this species, especially within the riverine migration phase. Atlantic salmon have shown rapid declines throughout their range over several decades (ICES, 2018; Chaput, 2012; Russell *et al*., 2012; Condron *et al*., 2005; Adams *et al*., 2022a,b) and have since been declared as 'Near Threatened' on the ICUN Red List (2023). CEFAS (2019) reported an 88% decline of Atlantic salmon caught from all methods in England and Wales. One stressor that has been shown to have an effect on salmon populations is habitat fragmentation by disrupting connectivity to important areas which support different life stages (Richter *et al*., 1997; Lucas & Baras, 2001; Deinet *et al*., 2020). Anthropogenic riverine habitat fragmentation is common in Great Britain, with 97% of riverine networks being fragmented by the construction of artificial river-spanning infrastructure such as hydropower dams, low head weirs and culverts (Jones *et al*., 2019; Rosenberg *et al*., 2000; Lucas & Baras, 2001; Baguette *et al*., 2013; Pringle, 2001) which impede fish movements. However, not only is river spanning infrastructure a barrier to movement by anadromous fish, but a number of natural features may also prevent or delay riverine migration. One of these is natural standing waters such as lakes, which have been associated with low migration success, as fish navigate through these natural features to reach the marine environment (Honkanen *et al*., 2018, 2021; Limburg & Waldman, 2009; Nunn & Cowx, 2012; Lilly *et al*., 2021).

Large standing waters like lakes are an important habitat for Atlantic salmon (Kennedy *et al*., 2018), providing key habitat for juvenile stages, providing an area for temperature regulation and important feeding areas for juveniles (Hartman 1973; Halvorsen & Jørgensen, 1996; Hutchings *et al*., 2019). Previous examining riverine migration of Atlantic salmon smolts, has shown that directional water flow is used to aid navigation as the fish tend to travel passively with the current, though there is also evidence of active swimming during riverine migration (Honkanen *et al*., 2021; Lacroix *et al*., 2004a,b; Svendsen *et al*., 2007; Davidsen *et al*., 2009; Fängstam, 1993; Lilly *et al*., 2021). Thus, it is likely that large standing bodies of water impose a risk to successful riverine migration, in that natural standing waters often lack directional currents and are likely to provide less useful directional cues (Honkanen *et al*., 2018). Many studies have shown that the rate of movement (ROM) through standing waters in salmon smolts is much slower in comparison to migration along the rest of the river system. Honkanen *et al*. (2018) studied the movements of Atlantic salmon smolts within Loch Lomond, Scotland, and found that smolts were travelling on average at ~$0.05m.s^{-1}$, (a relatively slow rate of travel compared with river migration) and that the migration failure rate was as high as 60% and high migration failure rates have also been shown in other studies (Aarestrup *et al*., 1999; Berry, 1934; Bourgeois & O'Connell, 1988; Jepsen *et al*., 1998; McCormick *et al*., 1998; Thorpe *et al*., 1981; Honkanen *et al*., 2021; Lilly *et al*., 2021). The high loss rates within lakes necessitates further for research into the fine scale behavioural movements of smolts within standing water environments.

It has been shown that migration through natural standing waters is not unidirectional, with smolts often undertaking long and convoluted migrations. Lilly *et al*. (2021) for example found a salmon smolt that travelled an estimated 250km in total to cover a direct route of ca.9km through Loch Lomond. Furthermore, it is not uncommon for smolts to show frequent directional movements away from the exit point of the lake (Honkanen *et al*., 2018; Lilly *et al*., 2021). It has been proposed that these seemingly random movements around standing waters will increase the energy expenditure costs of smolt migration and increases the risk of predation (Hanssen *et al*., 2022; Honkanen *et al*., 2018, 2021; Jepsen *et al*., 1998). However, we have a limited understanding of the cues and behaviours smolts require to successfully migrate through standing waters (Hanssen *et al*., 2022; Honkanen *et al*., 2018; Lennox *et al*., 2021). This understanding is required to provide mitigation for future construction of artificial standing waters to ensure migration success is not impeded.

Lilly *et al*. (2021) analysed the point in which cues are "just right" for smolt exit from Loch Lomond and referred to this zone as "Goldilocks Zone", and in that study this occurred when smolts entered an area approximately 1.75 ± 0.80km (mean ± SD; range: 1.19–4.27) from the outflowing River Leven. Within that zone, 67% of smolts made a direct movement into the outflowing River Leven (and thus out of the standing water). A total of 29% of smolts made frequent movements within the Goldilocks Zone and also made distinctive backwards movements, back into Loch Lomond (that is away from the entrance to the draining river) before eventually exiting the lake. The remaining 4% did not exit the lake successfully. Additionally, Lilly *et al*. (2021) assessed if smolt fork length was a significant predictor of migration success through the lake and found no correlation, despite that other work has previously suggested that larger smolts are more likely to be successful migrants due to their increased ability to endure long distance migrations and evade predators (Kennedy *et al*., 2007; Tucker *et al*., 2016; Lilly *et al*., 2021). No other study has looked into applying the Goldilocks Zone concept to different lake systems.

Passive acoustic telemetry is a relatively new technique which allow for the investigation fish migration patterns, site fidelity, diel movement patterns and predation events (Heupel *et al*., 2010; Hitt *et al*., 2011; Rowell *et al.,* 2015; Hussey *et al*., 2015; Honkanen *et al*., 2018, 2021; Hanssen *et al*., 2022; Lilly *et al*., 2021). Relatively few studies have utilised acoustic telemetry techniques in standing waters to assess smolt migration success rates, migration behaviours, smolt ROM and cues associated with successful exit (i.e., Aarestrup *et al*., 1999; Honkanen *et al*., 2018; Thorstad *et al*., 2011; Lilly *et al*., 2021).

In this study, I used acoustic telemetry to investigate migration through Bassenthwaite Lake, Cumbria. Bassenthwaite Lake (7.15km in length) is the most northern lake situated along the River Derwent catchment. We assess migration success rates of River Derwent smolts and describe their migration behaviours through Bassenthwaite Lake. Additionally, I looked to see if the Goldilocks Zone can also be identified in Bassenthwaite Lake and if it is geographically different to that described for Loch Lomond and lake specific. In addition, I looked to see if smolt characteristics (i.e., fork length) is a significant predictor in migration success through natural standing waters.

There are four main hypotheses in this study: i) Migration failure rate in Bassenthwaite Lake is consistent in magnitude with other standing water studies in the UK (~60%); ii) Larger smolts ($L_F$, mm) have higher migration success through Bassenthwaite Lake than smaller smolts; iii) Both successful and unsuccessful migrating smolts exhibit indirect migration trajectories in Bassenthwaite Lake; and iv) Smolts which enter the Goldilocks Zone are more likely to orientate towards Bassenthwaite Lake outlet.

## 3.2 Methodology

### 3.2.1 Description of study site

The River Derwent catchment (Cumbria, North-West England) is 679km$^2$ in area and supports a population of wild Atlantic salmon. The River Greta, a tributary of the Derwent system, flows west through the town of Keswick where it intercepts the outflow of Derwentwater Lake, (54°36’07.1”N 3°09’10.1”W), to join the River Derwent. The River Derwent flows north, before entering Bassenthwaite Lake. Bassenthwaite Lake is the most northerly un-impounded lake in the Derwent catchment, it is 7.7km in length, with a maximum depth of 21.3m. Upon exiting Bassenthwaite Lake, the River Derwent drains west flowing through the urbanised areas of Cockermouth and Workington, where two low-head weirs (Coops and Yearl Weir) are present, before draining into the outer Solway Firth at the Port of Workington (54°38’58.2”N 3°34’07.9”W) (Figure 3.1).

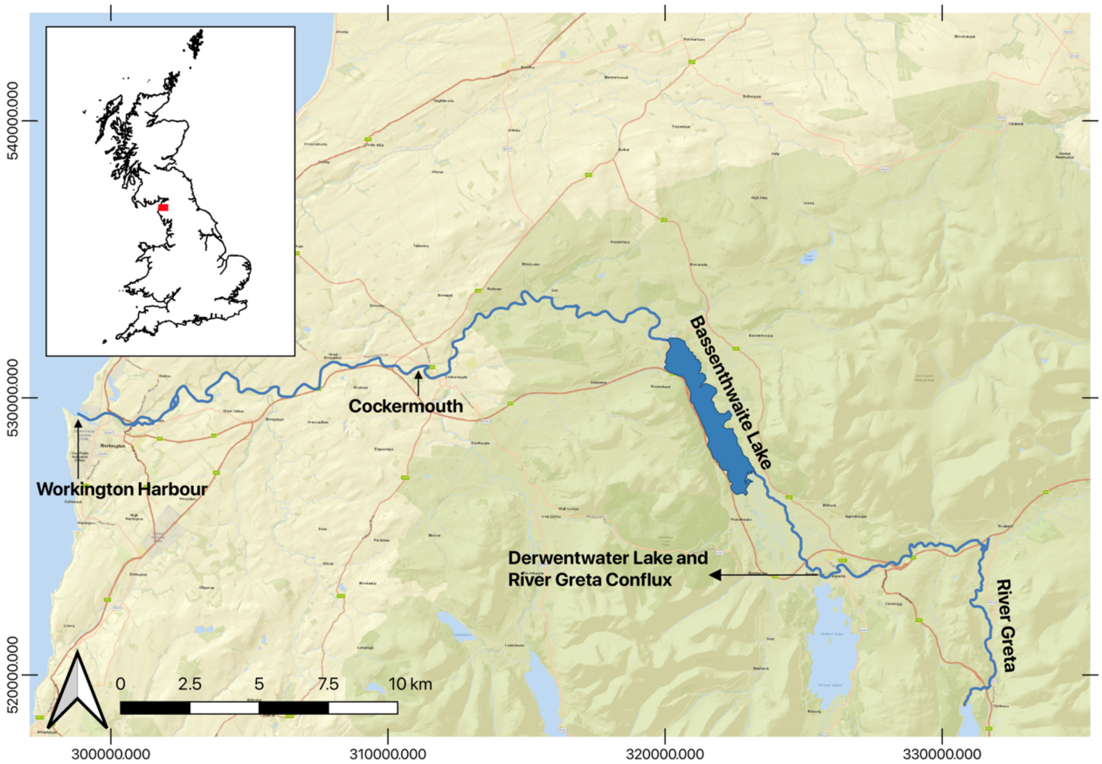



***Figure 3.1*** *River Derwent Catchment*

### 3.2.2 Acoustic receiver deployment

Acoustic receivers were deployed in the River Greta and River Derwent in order to track the seaward migration of Atlantic salmon smolts from the upper reaches of the Derwent catchment (St Johns Beck; 54°36’38.1”N 3°03’42.0”W) (Figure 3.2). Receivers deployed comprised of two types (VR2W and VR2Tx), both operating at 69kHz (Innovasea Ltd., Nova Scotia, Canada). Receivers deployed in 2021 in the river consisted of VR2W’s (Greta: $n$=$2$, Derwent: $n$=$4$) and VR2Tx’s (Greta: $n$=$1$), while acoustic receivers deployed in Bassenthwaite Lake consisted of only VR2Tx's (*n=22*) (Figure 3.1). Acoustic receivers were deployed through the River Greta, River Derwent and Bassenthwaite Lake from 23rd March 2021 to March 25th 2021. Acoustic receivers were deployed in a grid-like system in 2021 to increase our understanding of small-scale spatial movements within the lake and positions were chosen based on published literature range testing results (Newton *et al*., 2016, 2021). Receivers within both the River Greta and River Derwent were attached to a mooring comprised of a vertical steel rod attached on a 20–40kg weight. All river receivers were attached by chain to the riverbank where suitable, for added security. In Bassenthwaite Lake in 2021, all receivers were attached to a vertical steel rod welded to a steel weight (30–40kg) with a surface buoy attachment included. All acoustic receivers were recovered on 8th August 2021 and it was noted receivers were moved from their original position though the date of this remained unknown, thus, analysis was conducted from the receivers' position when collected.

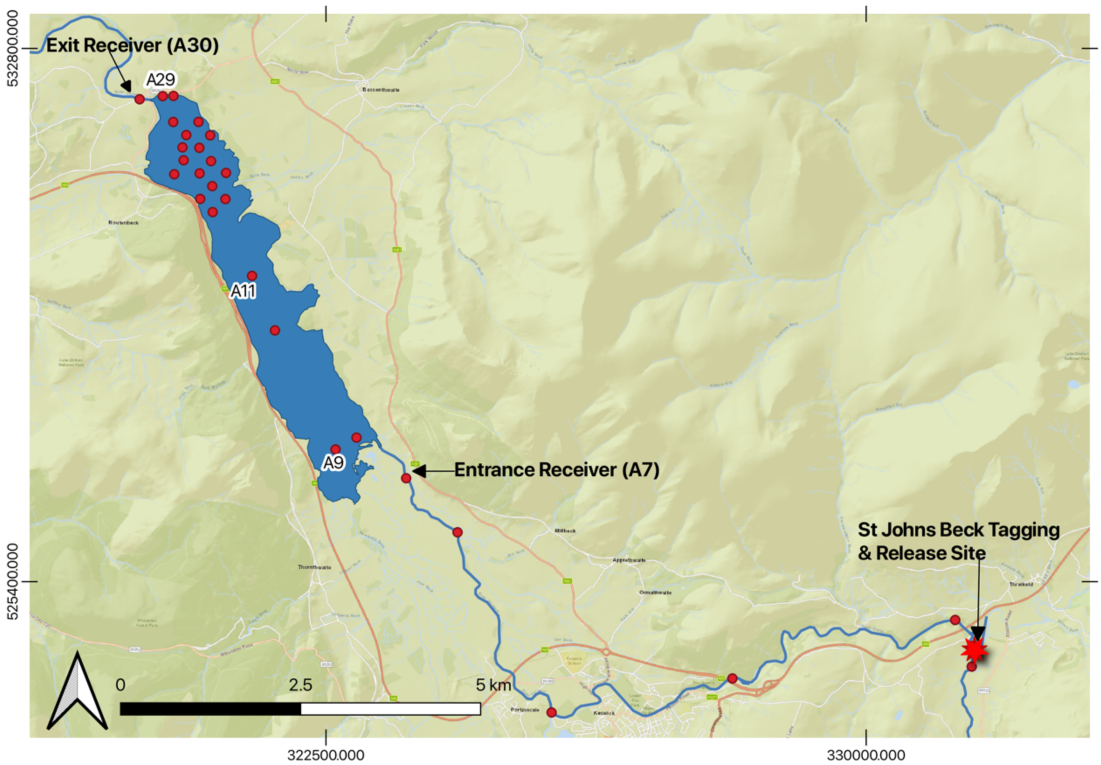



***Figure 3.2*** *Map illustrating receiver layout throughout Bassenthwaite Lake consisting of VR2Tx's (n=22) and VR2W's (n=2) receivers, positioned at both the entrance and exit of Bassenthwaite Lake.*

### 3.2.3 Smolt capture and acoustic tagging procedure

Atlantic salmon smolts were captured during spring (April to May 2021) during their downstream migration using a 1.2m rotary screw trap, at St Johns Beck, Threkheld (54°36’38.1”N 3°03’42.0”W). In 2021, *93* fish were tagged between 14$^{th}$ April and 5$^{th}$ May. In addition to a rotary screw trap, a fyke net was used to increase catches. All trapping apparatus was checked and emptied daily to ensure smolts did not remain in the trap for extended periods of time. Fish captured were anaesthetized by immersing them in a bucket containing MS222 (Tricaine Methane sulfonate) and sodium bicarbonate solution (0.6g/6L river water for each). It took approximately three minutes for smolts to lose equilibrium (stage three of anaesthesia) which is required for the tagging procedure to be conducted. Fork length ($L_F$, mm) and weight (g) were determined, and only fish greater than 130mm $L_F$ and 20g weight were tagged. Additionally, scale samples were taken. All surgical equipment was disinfected using Reprodis/distilled water (1:20 ratio) and rinsed with distilled water. During surgery, fish were given low level anaesthesia (0.125g/2L) and river water was constantly applied across the gills to ensure fish remained sedated. A 10mm ventral incision was made anterior to the pelvic girdle. A V7-2L (69kHz) coded transmitter (VEMCO Ltd, 7mm diameter, 1.7g in air) was surgically placed inside the peritoneal cavity. The V7-2L tags had a nominal delay of 18–45 seconds and an estimated tag life of ca.75 days. The incision was closed by applying two interrupted surgeon knots with 4/0 Ethilon nylon sutures. Smolts were then placed into a recovery container on land for approximately 20 minutes to ensure normal swimming behaviour was exhibited (equilibrium restored). Fish were then placed into a perforated river container downstream from the rotary screw trap with good water flow throughout and given a further 40 minutes recovery before being released.

### 3.2.4 Ethical statement

All tagging was conducted by a personal licence holder (UK Home Office PIL 70/8794) using procedures which complied with the UK Home Office regulations and UK Home Office project licence number PP0483054. Replacement, reduction, and refinement was considered for this study. All fish were cared for and monitored, throughout the procedure where stress and suffering were reduced at all times.

### 3.2.5 Statistical analysis

#### 3.2.5.1 False detections

All analysis was conducted using R software *version 4.2.3* (R Core Team, 2019). Using raw VEMCO receiver data, all data was filtered to only include fish tagged in 2021. Additionally, from the filtered detections, a further filter to remove false detections was conducted using the package *Glatos* (Holbrook *et al*., 2018) using the short-term interval criterion. Short-interval criterion filters all single detections that occurred at one receiver station within a fixed duration which is set at 30 times the average signal delay of the tag (in this study this duration was 840 seconds (s)) (Hayden *et al*., 2016; Kneebone *et al*., 2014; Lilly *et al*., 2021, 2022). Detections above this fixed duration period were deemed false detections. Additionally, signals detected within a duration which is less than the tag's minimum signal delay (18s) were also deemed false detections and removed from further analysis (Hanssen *et al*., 2022). 0.96% of detections were considered false and removed, therefore, 853,352 detections were used for analyses.

#### 3.2.5.2 Descriptive analysis

Descriptive results from 2021 data were calculated using the R package *Actel* (Flávio & Baktoft, 2021), which provides a systematic conditional pipeline to filter and analyse acoustic telemetry data in a reproducible fashion, for fish moving between receiver arrays. It also allows for detection efficiency estimations to be made for each receiver station. Additionally, *Actel* allows diel movement patterns to be observed by defining the arrival time recorded at each individual receiver using the *circular* R package (Agostinelli & Lund, 2022; Jammalamadaka & SenGupta, 2001).

#### 3.2.5.3 Timing of migration

Using the *r.test* function in the *CircStats* package (Lund & Agostinelli, 2018) a Rayleigh test of uniformity was performed to determine if migration both into and out of Bassenthwaite Lake 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).

#### 3.2.5.4 Migration success and failure

To assess migration success and failure rate, a smolt was deemed to be a successful lake migrant if it was first detected entering the lake (54°37'50.9"N 3°11'06.0"W) and later detected at the first receiver in the river flowing out of Bassenthwaite Lake (54°40'39.3"N 3°14'37.7"W). Unsuccessful migrants were detected entering the lake but not subsequently detected at the Bassenthwaite Lake outflow receiver. These categories of migration success were calculated using descriptive data from the R package *Actel* (Flávio & Baktoft, 2021) output. Migration success rate per km ($\%.km^{-1}$) was calculated as the percentage of successful migrating smolts (using *Actel* output), divided by the direct minimum distance travelled (MDT) through Bassenthwaite Lake (7.15km). This was also repeated on unsuccessful migrants using the percent of unsuccessful smolts divided by the direct MDT of Bassenthwaite Lake.

The detection efficiency of acoustic receivers across Bassenthwaite Lake varied and was not always 100% due to receiver layout and ambient noise from recreational lake activities, therefore, efficiency was assessed to provide estimates of survival (Halfyard *et al*., 2013; Lilly *et al*., 2022). Efficiency was assessed as the number of smolts detected at any downstream receiver expressed as a proportion of those not detected at the receiver upstream. Due to the range of receivers throughout Bassenthwaite Lake, there is the possibility that fish were not detected on any given receiver due to placement, this was taken into consideration when detection efficiency was calculated.

#### 3.2.5.5 Phenotype

To determine if migration success or failure rates were related to Atlantic salmon smolt phenotype, three metrics were used: this included fork length ($L_F$, mm), weight (g) and tag burden (%). Tag burden was calculated by dividing the weight of a tag in air (1.7g) by the weight of the tagged Atlantic salmon smolt x 100 (Brown *et al*., 2012).

General linear modelling (GLM) was undertaken to determine if phenotypic factors such as $L_F$ (mm), weight (g) and tag burden (%) contributed to successful migration. Additionally, smolt average rate of movement (ROM) was analysed to see if smolt ROM contributed to migration success. The GLM was fitted with a binomial error structure and the identity link function using the R Package *lme4* (Bates *et al*., 2014). Survival (dependent variable) was coded as 1 for fish detected on a receiver which exits Bassenthwaite Lake or 0 for an assumed failed lake migration.

*Initial model:*

*glm(Survival ~ $L_F$ + Weight + Tag Burden + ROM, family = binomial (link = "identity")*

#### 3.2.5.6 Centre of activity

To analyse Atlantic salmon smolt behaviour, centre of activity (COA) was calculated both for successful and unsuccessful lake migrants to determine the location of smolt activity within Bassenthwaite Lake, using the *Animal Tracking Tool* in R package *Vtrack* (Udyawer *et al*., 2018). COA positions are a mean two-dimensional position measure (providing latitude and longitude) of a smolt determined through weighting the detections of a smolt between adjacent acoustic receivers which have non-overlapping ranges during a specified duration of time (Simpfendorfer *et al*., 2002; Espinoza *et al*., 2015; Lilly *et al*., 2021). The duration used for determining COA positions in this study was 15 minutes. This was determined using the methods outlined in Villegas-Rios *et al*. (2015) using data from smolts that were deemed successful and migrated out of Bassenthwaite Lake ($n=40$). COA position data was further used to calculate non-residency events (Campbell *et al*., 2012), behavioural metrics and space used in Bassenthwaite Lake. A non-residency event was defined as the movement of an individual between two COA positions which was calculated using *RunResidenceExtraction* function in the *Vtrack* package in R (Campbell *et al*., 2012).

#### 3.2.5.7 Space use

In order to evaluate Atlantic salmon smolt space use of Bassenthwaite Lake, core (50%) and extended (90%) home ranges (Brownian Bridge Kernel Utilisation Distribution (BBKUD)) were calculated using the *Animal Tracking Tool* in R package *Vtrack* (Udyawer *et al*., 2018).

Using previously defined methodology (Lilly *et al*., 2021), the final migration trajectory of successful smolts was extracted based on a direct migration pathway from Bassenthwaite Lake into the River Derwent. The mean distance from which successful smolts initiated a direct migration pathway out of Bassenthwaite Lake and into the River Derwent at the northern exit point was determined by using the *ComputeDistance* function in the R package *Vtrack* (Campbell *et al*., 2012), 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 Derwent) were, at this point presumed to be "just right" (Lilly *et al*., 2021).

#### 3.2.5.8 Comparisons of space use

The comparison between the size of core (50% BBKUD) and extended (95% BBKUD) home ranges of successful and unsuccessful migrants were made using a Wilcoxon rank sum test.

To determine if the Goldilocks Zone served as a defined 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 of movements that resulted in movement southwards and thus away from the lake exit and out of this zone, using a paired Wilcoxon signed-rank test.

In order to determine if space use of Atlantic salmon smolts was predominately along the easterly or westerly side of the lake within the Goldilocks Zone, the zone was split into two groups: Easterly (E) or Westerly (W). Using the Non-residency detections on receivers within the Goldilocks Zone, smolt detections were allocated to either E or

W dependent on where they were detected within the Goldilocks Zone. A Wilcoxon signed-rank test was conducted to compare the space use of both successful and unsuccessful smolts. Additionally, in order to determine if environmental factors such as wind (o) is a significant predictor in space use within the Goldilocks Zone, wind direction was modelled hourly. Using the package *Circular* (Agostinelli & Lund, 2022), wind direction was converted into degrees and tested using the *Watson.test ()* function to determine if the circular data differed from a specified reference direction (in this case 0 degrees). Using Non-residency detections on receivers within the Goldilocks Zone, wind direction in degrees were matched to the specific timestamp of each detection in hours. A generalised linear mixed model (GLMM) was constructed using the R package *lme4* (Bates *et al*., 2014) fitted with a binomial error structure and the identity link, where space use (dependent variable) was coded as E for fish detected within the easterly half or W for those detected in the westerly half, using FishID as a random effect.

*Initial model:*

*glmer(Space Use ~ Wind Direction + (1|FISHID) , family = Binomial(link = "identity")*

## 3.3 Results

### 3.3.1 Tagging summary

In total, *93* Atlantic salmon smolts were tagged in 2021. The mean recorded $L_F$ (mm) of smolts tagged at St Johns Beck in 2021 was 141.9 ± 8.4 (mean ± SD; range: 130 - 164), weight (g) was 29.4 ± 5.5 (mean ± SD; range: 21–5-44.5) and tag burden (%) was 5.3 ± 0.91 (mean ± SD; range 3.5–7.0).

### 3.3.2 Migration failure rate

From the *93* smolts that were successfully tagged at St Johns Beck, only 64% (*n=60*) successfully migrated the river distance of 12.5km and entered Bassenthwaite Lake (river loss rate of 2.87%.$km^{-1}$). Of the *60* individuals that successfully entered Bassenthwaite Lake, 66% (*n=40*) individuals successfully migrated out of the lake. Therefore, there was a loss rate of 9.3%.$km^{-1}$ in Bassenthwaite Lake.

The mean $L_F$ of successful Atlantic salmon lake migrants (*n=40*) was 142.4 ± 7.99 mm (mean ± SD; range:131–164) and for unsuccessful lake migrants (*n=20*) mean $L_F$ was 138.7 ± 7.13mm (mean ± SD; range:130–159). A binomial regression model (GLM) testing the influence phenotypic factors on migration success through the lake was conducted. Both weight and tag burden were highly correlated with $L_F$, so for analysis only $L_F$ was used. Migration success was not dependent on smolt $L_F$ ($p$=0.41), however, smolt rate of movement (ROM) did significantly predict migration success ($p$=0.001) with those smolts that had a greater ROM being more likely to be successful lake migrants.

### 3.3.3 Migration timing

Successful lake migrants had an estimated mean rate of movement (ROM) of 0.16 ± 0.05m.$s^{-1}$ (mean ± SD; range: 0.13-0.27) over a mean travel duration of 6 ± 5 days (mean ± SD; range: 1–35). Migration into Bassenthwaite Lake (*n=60*) was dependent on the time of the day (entrance: Rayleigh test; *r.bar* = 0.34, $p$=< 0.01) and occurred primarily during the night and early morning hours between 20:00 and 05:00am, with a mean time of movement being 00:30am. No smolts were found to migrate into Bassenthwaite Lake between 06:00am and 17:30pm British Summer Time (BST, GMT + 1) (Figure 3.3).

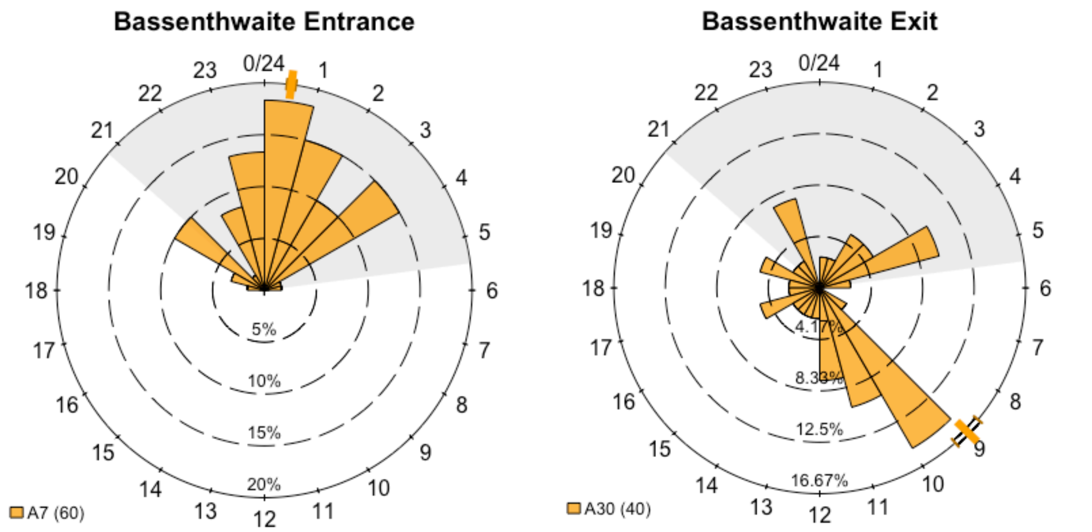



***Figure 3.3*** *Circular plots generated using R package 'Actel' using the plotTimes() function depicting the hour (British Summer Time; BST) when smolts both entered Bassenthwaite Lake at receiver A7 (n=60) and exited (n=40) Bassenthwaite Lake at receiver A30.. The mean time of movement is highlight within the outer circle. Each bar sum to 100%. The number of smolts included in the analysis are presented. The shaded zone indicates the average sunset and sunrise which occurred during May - June 2021.*

However, smolt departure from Bassenthwaite Lake (*n=40*) was not dependent on the time of the day (entrance: Rayleigh test; *r.bar* =0.19, *p*=0.96), with smolts found to exit the lake at varied times of day. The mean time of movements out of the lake was 09:00am British Summer Time (BST, GMT + 1) (Figure 3.3).

### 3.3.4 Home range

Successful (*n=40*) and unsuccessful (*n=20*) lake migrants did not differ in their space use of Bassenthwaite Lake, utilising both the lower, middle and upper regions of the lake. Using the BBKUD of both successful and unsuccessful lake migrants, a Wilcoxon sum rank test confirmed there was no significant difference between average core (50%) space use distributions of successful (4.68 ± 2.33km$^{-2}$) and unsuccessful lake migrants (4.42 ± 2.97km$^{-2}$) (*p*=0.56). Additionally, there was no significant difference in the average extended (90%) space use distributions of successful (7.98 ± 6.03km$^{-2}$) and unsuccessful lake migrants (8.02 ± 7.66km$^{-2}$)

($p$=0.35). Examples of BBKUD space use of successful and unsuccessful smolts can be found in Figure 3.5.

### 3.3.5 Migration trajectories

Successful lake migrants (*n=40*) travelled on average an estimated minimum total distance (km) of 56.11 ± 30.28 (mean ± SD; range: 8–125.09) and were detected for 6 ± 5 days (mean ± SD; range: 1–35) in the lake. Both successful and non-successful lake migrants displayed varied directional migration pathways throughout and utilised both the lower (southern), middle and upper (northern) regions of the lake. There was no distinct migration trajectory through Bassenthwaite Lake that was unique to successful lake migrants. Smolt lake migration duration, ROM and migration direction differed across successful smolts; for example one smolt (ID: 43122) after entering Bassenthwaite Lake took a southern migration pathway, being detected on (A9, Figure 3.2) and spent ca.2 days within the southern region of the lake before making a direct exit out of Bassenthwaite Lake, having travelled a total distance of 19.97km over 2.48 days in total with an average ROM of 0.08m.s$^{-1}$ (Figure 3.4a). This fish had an overall greater 50% BBKUD in the northern region of Bassenthwaite Lake than the mid or south regions (Figure 3.5a). Another successful individual (ID: 35928) also took an initially southern migration pathway and then migrated north. Within the northern region, smolt ID:35928 reached the most northernly receiver prior to the lake exit (A29, Figure 3.2), although it displayed a complex movement behaviour (not unidirectional) travelling both forward and backwards across a minimum estimated distance of 80.60km, taking this individual 5.9 days at an average ROM of 0.19m.s$^{-1}$ (Figure 3.4b); its BBKUD was predominately within the middle and southern region of Bassenthwaite Lake (Figure 3.5b). Lastly, smolt ID:43087 was the only smolt found to take a northern trajectory once it migrated into Bassenthwaite Lake, it showed rapid forwards and backwards migration behaviour when migrating within the southern region on the lake, travelling an estimated minimum distance of 58.5km over 4.04 days at a ROM of $0.18m.s^{-1}$ (Figure 3.4c); it had a BBKUD predominantly within the middle and southernly regions (Figure 3.5c).

Unsuccessful smolts also displayed varied migration pathways before assumed loss within the lake, though a vast proportion of time was spent within the southern region of the lake. After exiting the River Derwent and entering Bassenthwaite Lake, one smolt (ID: 43081) took a southern trajectory, although it did explore the northern regions before making a backwards movement and remaining at A11 which is within the middle region of the lake. This smolt then made multiple attempts to exit the lake and being detected on the final lake receiver (A29, Figure 3.2). In total this smolt travelled an estimated maximum distance of 87.5km at a ROM of $0.16m.s^{-1}$ (Figure 3.4d); its BBKUD was within the middle and upper southern region of the lake (Figure 3.5d). A second smolt (ID: 43076) remained in the south of the lake and had a BBKUD only within the southerly region of the lake, travelling an estimated maximum distance of 53km at a ROM of $0.04m.s^{-1}$ (Figure 3.4e/3.5e). Lastly, one smolt (ID: 43116), like the majority of smolts, took a southernly trajectory before migrating north, though this smolt travelled an estimated maximum distance of 247km at a ROM of $0.05m.s^{-1}$. This smolt primarily migrated within the northern region of the lake (Figure 3.5f) where it displayed complex migration behaviours which were not unidirectional, though it ultimately did not successfully migrate out of Bassenthwaite Lake (Figure 3.4f).

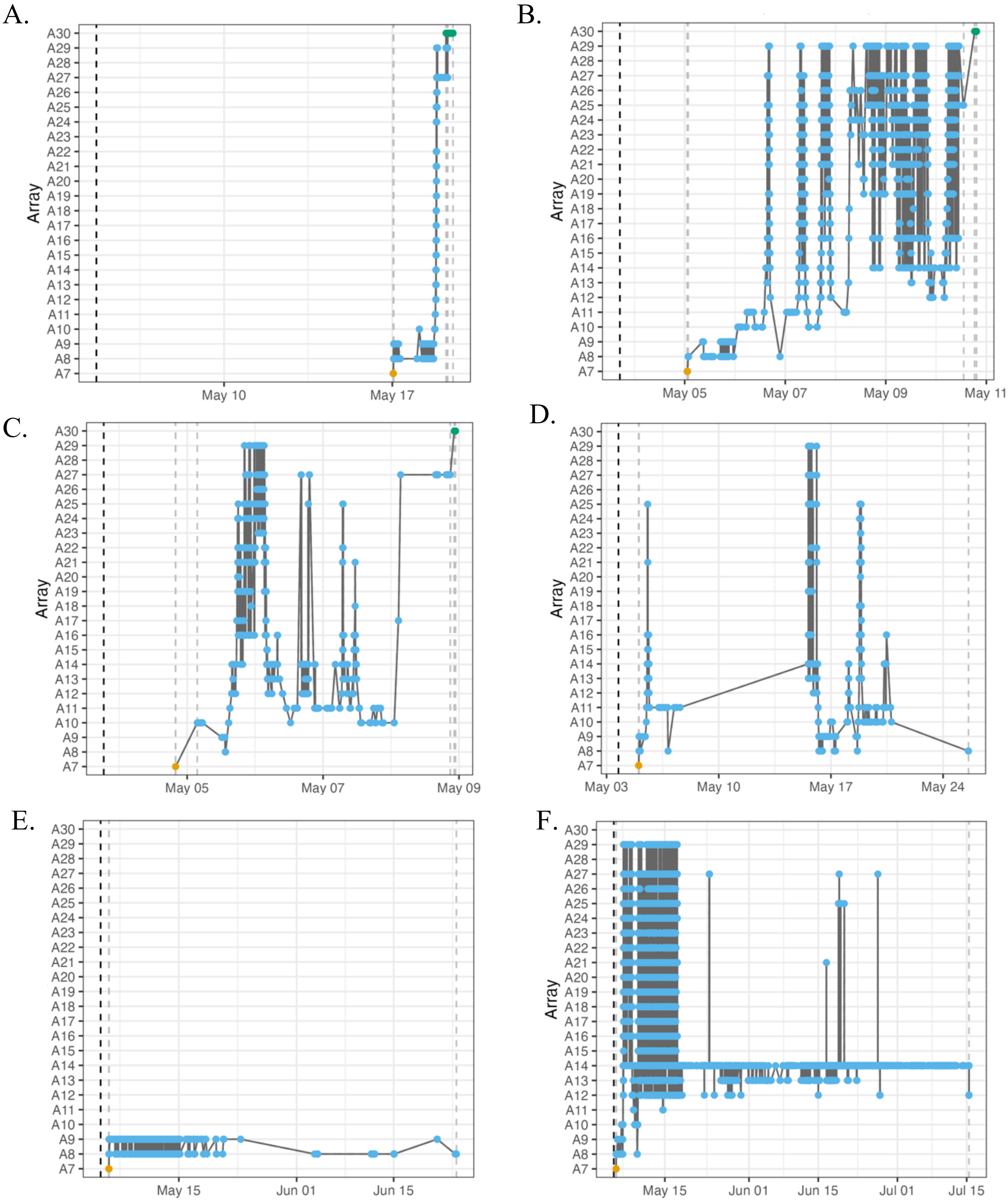



***Figure 3.4*** *Individual detection plots generated using Actel, plotDectections() function, showing successful (3.4a-c) and unsuccessful smolts (3.4d-f). The vertical dashed lines show time in which smolts entered Bassenthwaite Lake, whereas the vertical grey dashed lines detail the assigned movements when exiting or assumed tag loss from the study site. The dots represent when a fish was detected at a given receiver, orange for the first receiver (A7) and green for the exit receiver (A30) all those detailed in blue are receivers deployed across Bassenthwaite Lake. All detection plots detail individual timestamps. Receivers are found along the y axis.*

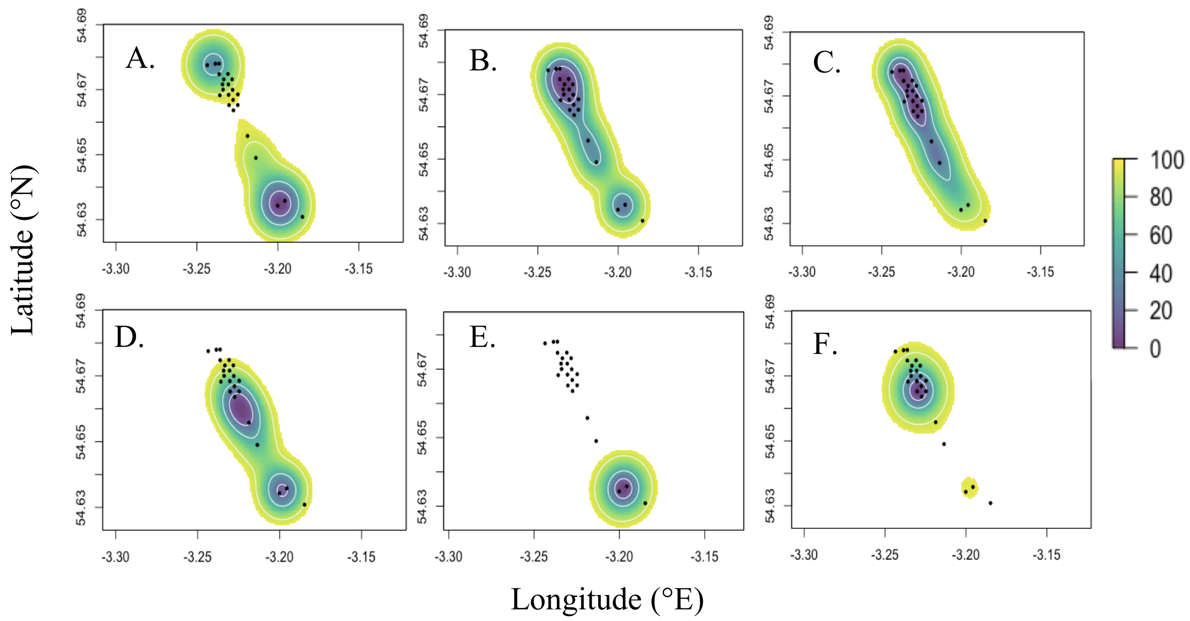



***Figure 3.5*** *Examples of comparison of activity spaces between successful (n=40)(3.5a-c) and unsuccessful (n=20)(3.5d-f) lake migrates across Bassenthwaite Lake. Centres of activity (15-minute time step, coloured crosses) Minimum convex polygons (broken coloured polygons) and Brownian Bridge Kernel Utilisation Distributions (50% contour = filled dark polygons; 90% contour = filled light polygons). Black points represent receiver locations of both VR2Tx's and VR2W's deployed throughout Bassenthwaite Lake.*

### 3.3.6 <u>Goldilocks Zone</u>

Once smolts re-entered the River Derwent at the northern exit point of Bassenthwaite Lake, they were deemed as successful lake migrants, with four individuals later detected re-entering the lake (smolt IDs: 35891, 35921, 35927, 43131). For all successful lake migrants (*n=40*), movement into the River Derwent occurred at a mean estimated minimum distance (km) of 0.72 ± 0.6 (mean ± SD; range: 0.13–1.24) away from the exit point. We define this point as representing the outer bounds of the Goldilocks Zone (Lilly *et al*., 2021). These direct exit trajectories out of the Goldilocks Zone and into the River Derwent, took a mean duration (hrs) of 3 ± 15.6 (mean ± SD; range: 0.89–46.3). Once fish entered the Goldilocks Zone, 95% (*n=38*) remained within the Goldilocks Zone, making non-unidirectional movements throughout the zone prior to migrating out of Bassenthwaite Lake. The remaining 5% (*n=2*) of smolts made a southern migration, leaving the zone and moving further away from the exit of Bassenthwaite Lake. Within the Goldilocks Zone, successful Atlantic salmon smolts ($n=40$) made a number of complex migration trajectories which were not unidirectional (12.4 ± 13.8 (range; 1–19)) that resulted in southerly migration (backwards movement) out of the Goldilocks Zone (7.5 ± 1.9 (range; 1–13)) (paired Wilcoxon signed rank test; $W$=85, $p$=0.02). Additionally, 70% ($n=14$) of unsuccessful lake migrants did enter the Goldilocks Zone, and thus entry into the zone did not guarantee successful migration out of the lake. We define the outer bounds of the Goldilocks Zone in Figure 3.6.

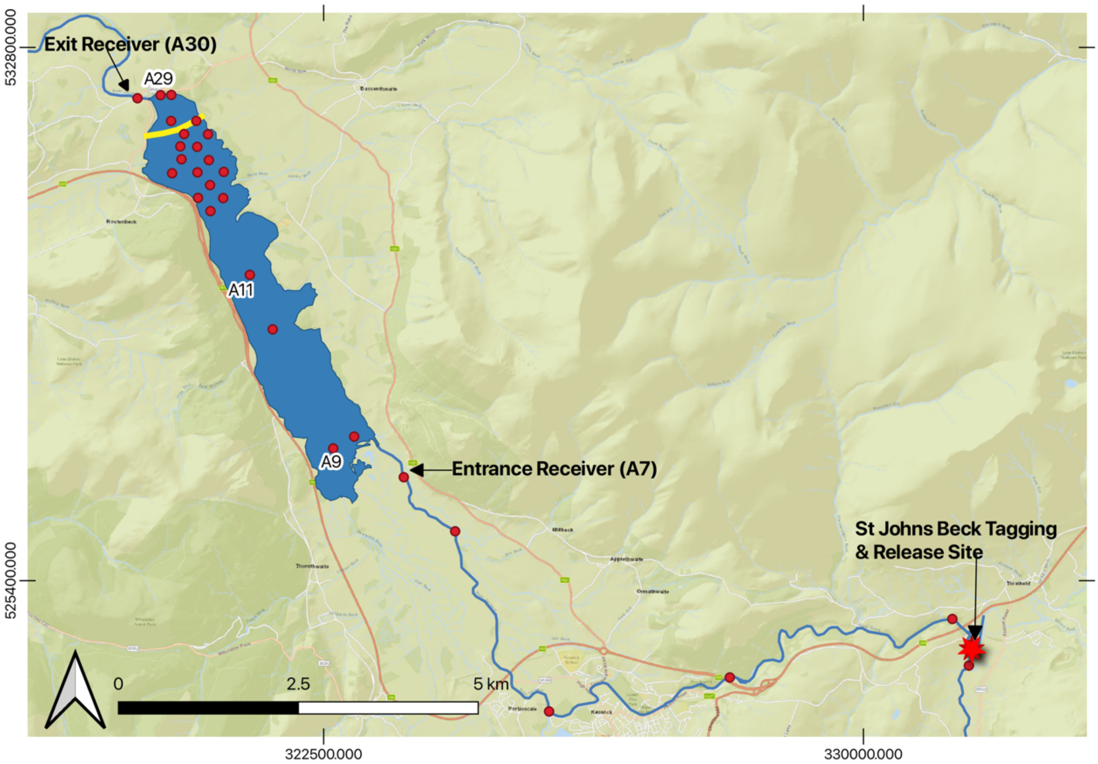



*__Figure 3.6__ The Goldilocks Zone is represented by the area above the yellow line. The outer boundary of the Goldilocks Zone was defined as the mean distance (mean ± SD; 0.72 ± 0.6km) that successful smolts (n=40) engaged in their final movements into the River Derwent.*

Atlantic salmon space use was not found to be significantly predicted by wind direction at the time of detection ($p$=0.28) and the Wilcoxon sum rank test confirmed there was no significant difference between space use of successful and unsuccessful lake migrants using the easterly half ($W$=45, $p$=0.32) or the westerly half ($W$=19, $p$=0.76) within the Goldilocks Zone.

## 3.4 Discussion

Previous research has highlighted the high loss rates which are found to commonly occur in natural standing waters; up to 88% loss has been recorded (Jepsen *et al*., 1998). Here we provide evidence that the loss rate of Atlantic salmon smolts in the Bassenthwaite Lake is consistent with previous studies (Aarestrup *et al*., 1999; Berry, 1934; Thorpe *et al*., 1981; Bourgeois & O'Connell, 1988; Honkanen *et al*., 2021; Lilly *et al*., 2021). Atlantic salmon smolts tagged and released in 2021 (*n=93*) showed a low likelihood of successful lake migration through Bassenthwaite Lake, with only 43% (*n=40*) being detected entering the River Derwent at the northern end of Bassenthwaite Lake (exit). Loss rate prior to entering Bassenthwaite Lake was high when comparing to other UK riverine systems. In a 2020 baseline study in this system, the loss rate in the River Derwent prior to entering Bassenthwaite Lake (a distance of 12.5km) was as high as 70% (migration loss rate of 5.59%.km$^{-1}$). In 2021 there was a considerable increase in survivorship, but migration loss rate was still considered high at 35.5% (migration loss rate of 2.8%.km$^{-1}$) which is consistent with loss rate findings from studies for example in the Endrick Water, Scotland (Honkanen *et al*., 2018; 3.17%.km$^{-1}$, Lilly *et al*., 2021; 3.25%.km$^{-1}$) and also in Lough Erne, Northern Ireland (Kennedy *et al*., 2018; 0 and 9.4%.km$^{-1}$) which are all similar to previous levels observed in a range of other river systems 0.3–7.0%.km$^{-1}$ (Thorstad *et al*., 2012a). Recent studies have highlighted potential reasons for smolt mortality within riverine systems showing that there can be high rates of avian and piscine predation (Chavarie *et al*., 2022). The high loss rates of Atlantic salmon smolts occurring in Bassenthwaite Lake may partly also be associated with predation pressures within natural standing waters. Both goosanders (*Mergus merganser,* Linnaeus 1785) and cormorants (*Phalacrocoracidae carbo carbo,* Linnaeus 1785) are known to target salmon smolt spring migration periods (Boström, 2013; Falkegård *et al*., 2023). Thus, disruption of key foraging behaviour of these avian species may result in an increased likelihood of successful smolt migration outcomes within both riverine and natural standing water environments (Hawkes *et al*., 2013; Kennedy & Greer, 1988). However, a study conducted through the Lough Erne catchment, Northern Ireland by Kennedy *et al*. (2018) postulated that high rates of assumed tag loss was associated with piscine predation attributed to pike (*Esox lucius,* Linnaeus 1785) which are also found to be present in Bassenthwaite Lake, where behaviour of pike predation has been noted as such in smolt ID: 43076 (Figure 3.5e) where slow latitudinal movements within a small area were recorded. The termination of detections from an unsuccessful individual may also be attributed to a variety of factors, such as poor detection efficiency, tag loss, tag failure, mortality due to predation by another aquatic predator or stress induced by the capture and acoustic tagging procedure (Cooke *et al*., 2011; Klinard & Matley, 2020; Lilly *et al*., 2021).

Migration from the River Derwent into Bassenthwaite Lake was found to take place primarily during night hours, correlating with other studies (Kennedy *et al*., 2018; Haraldstad *et al*., 2017; Ibbotson *et al*., 2011, 2006), which is thought to be a predator avoidance strategy. This is a consistent pattern observed by smolts migrating through Norwegian lakes and Loch Lomond, Scotland (Hanssen *et al*., 2022; Haraldstad *et al*., 2017; Kennedy *et al*., 2018; Lilly *et al*., 2021). However, if this is a predator avoidance strategy used by Derwent smolts, their slow speeds upon entry (minimum estimates) and lack of unidirectional migration throughout Bassenthwaite Lake would likely diminish the benefits of migrating during night hours and energy expenditure costs are likely to increase due to increased duration in environments where there is lack of currents aiding in migration, further delaying exit from the lake (Jepsen *et al*., 1998) and ultimately impacting on lake survivorship. Virtanen & Forsman (1987) reported maximum sustainable smolt swimming speeds of $0.50m.s^{-1}$, which is well above the minimum estimated average swimming speeds detected in Bassenthwaite Lake here. Successful lake migrants from 2021 migrated at an estimated average swimming speed of $0.16m.s^{-1}$ over 5.85 days. This finding is consistent with Scottish lake migrants from two studies, where Lilly *et al*. (2021) reported smolts travelled at a minimum estimated average speed of $0.13m.s^{-1}$ over 5.23 days in Loch Lomond, Scotland and Honkanen *et al*. (2018) reported minimum estimated average migration speed through three lakes in Scotland varied between 0.09 and $0.15m.s^{-1}$. The observed slow minimum estimated average swimming speed could be due to either of two possibilities: 1) the lack of unidirectional movements in Bassenthwaite Lake where smolts did not take the most direct route to exit the lake upon entrance and were not moving in a straight line between receivers, though this could be due to receiver layout ; or 2) the assumed slow average speeds (minimum estimates) may be because of potential predator loss and with tags are being detected in either the predators' stomach or after expulsion and are within range of receivers on the lake bed (Lilly *et al*., 2021). Migration behaviour in Bassenthwaite Lake of both successful and unsuccessful smolts appeared not to be unidirectional, although once smolts entered an area within ~0.7km from the lake exit, smolts were found to have a higher possibility of successful exit, which is referred to as Bassenthwaite Lake's Goldilocks Zone. This finding could suggest the Goldilocks Zone is present in all standing waters regardless of size, and thus, investigations incorporating the Goldilocks Zone theory should be explored across a variety of lake/standing waters to determine if the Goldilocks Zone is more widely applicable.

Surface currents are important to Atlantic salmon smolts migrating within the riverine environment (Hedger *et al*., 2008; Lothian *et al*., 2018; Mcilvenny *et al*., 2021; Thorstad *et al*., 2012b) providing energy saving navigational cues and directing them downstream (Newton *et al*., 2021; Silva *et al*., 2020; Coutant, 2001; Montgomery *et al*., 2000; Silva *et al*., 2011). However, researchers postulate that in habitats where currents are mostly lacking, such as in natural standing bodies of water, surface currents are largely driven by wind (Svendsen *et al*., 2007, Mcilvenny *et al*., 2021). However, though surface currents may be wind driven in Bassenthwaite Lake, the results from this study suggest they may not be strong enough for smolts to follow (both successful and unsuccessful). This could also be a result of receiver layout and wind data being poor, therefore quality information to detect the effect of wind on migration trajectories in Bassenthwaite is lacking. We found that space utilisation in the lake was random, and we can hypothesise this is because there are a lack of cues or poor-quality cues available to lake migrants, which provide no direct pathway to exit these systems.

## 3.5 Conclusion

Based on the evidence of this study, we can conclude that survivorship likelihood of individual Atlantic salmon smolts in Bassenthwaite Lake is very likely random and does not appear to be dependent on fish phenotype, behaviour characteristics or environmental factors (wind direction). Our study provided evidence to suggest the Goldilocks Zone is applicable to Bassenthwaite Lake although it is still unclear if the Goldilocks Zone is more widely applicable to all standing waters or if its specific to only natural lake systems. Determining the cues associated with successful migration through these natural standing systems is required to aid in conservation and habitat protection of migrating smolts.

# *Chapter 4:* Assessing spatial pathway choice of Atlantic salmon smolts during seaward migration across weirs in the River Derwent, Cumbria.


## Abstract

One of the leading causes of Atlantic salmon declines is increased habitat fragmentation, particularly through the construction of artificial river-spanning infrastructure such as low-head weirs. Throughout England and Wales there are approximately 66,381 river-spanning obstacles, indicating that greater than 97% of English and Welsh river networks are fragmented. One such fragmented river is the River Derwent, Cumbria, where two low-head weirs are located in the Workington area (Coops Weir and Yearl Weir). The downstream migration and migration failure rates of Atlantic salmon smolts were studied in this area across a three-year period (2020-2022) with 365 smolts tagged using V7-2L (69kHz) coded transmitters and released in two groups: St Johns Beck and Trap and Transported. Migration failure rates of tagged smolts differed across the weirs, with Coops Weir having a failure rate of 2.24-9%.$km^{-1}$ and between 0–32.2%.$km^{-1}$ for Yearl Weir. These findings are considerably higher than those reported in other studies and with overall riverine failure rates analysed within the River Derwent. Additionally, there was little disparity in migration failure rates between St Johns Beck and Trap and Transport release smolts. Both temporal and spatial differences were found to occur across both weirs when analysing migration failure rate. Duration spent above the weirs was random, with water flow discharge ($m^3/s$) having no significant impact on the time spent there. Additionally, evidence was found to suggest that smolts had the ability to choose their migration routes away from the main water channel, although time spent above the weirs and route choice was random. It remains unclear whether migration failure rate was due to lack of preparedness for salinity environments, injury or disorientation/stress as a result of passage or predation.

*Key words: Atlantic salmon, fragmentation, smolt, downstream migration, weir*

## 4.1 Introduction

Habitat fragmentation, which limits the connectivity between adjacent habitats is one of the leading causes of salmonid population declines (Ceballos & Ehrlich, 2002; Baguette *et al*., 2013; Richter *et al*., 1997; Lucas & Baras, 2001; Deinet *et al*., 2020). The increase in riverine construction of artificial river-spanning infrastructure such as low-head weirs, dams and hydro facilities are have a particularly adverse effect on species with complex life cycles, which require to move between habitats for particular life stages to be facilitated (Jager *et al*., 2001; Cote *et al*., 2009; Branco *et al*., 2012; Hill *et al*., 2019). It has been estimated that throughout England and Wales there are approximately 66,381 river spanning obstacles, indicating greater than 97% of English and Welsh river networks are fragmented (Jones *et al*., 2019).

Atlantic salmon, *Salmo salar,* Linnaeus 1785*,* are highly mobile anadromous fish which has been found to be highly vulnerable to riverine habitat fragmentation both during upstream and downstream migration (Newton *et al*., 2018; Baras *et al*., 1994; Lucas & Frear, 1997; Jager *et al*., 2001; O'Hanley & Tomberlin, 2005; Kemp *et al*., 2008). Literature has highlighted the impact that large scale infrastructure (>5m hydraulic head height) has had on downstream migrating Atlantic salmon (Gowans *et al*., 2003; Antonio *et al*., 2007; Meixler *et al*., 2009; Branco *et al*., 2012; Newton *et al*., 2018) and other migrating species. This increases the importance of current mitigation and legislation measures, by requiring that all EU member states ensure that fish passage is enabled through all aspects of the EU Water Framework Directive (Directive 2000/60/EC), and EU Eel Regulation (EC No. 1100/2007) (Newton *et al*., 2018). The literature regarding the impact of low-head river-spanning infrastructure on fish migration is relatively sparse. It is assumed that barriers such as weirs may present significant obstacles to migrating Atlantic salmon and thus impact on migration success (Lucas and Frear, 1997; Ovidio and Philippart, 2002; O'Connor *et al*., 2006). This simply may not be the case for all river spanning infrastructure, however.

Weir structures are commonly found across UK river networks, where they provide a means of flood prevention, hydropower production, water discharge measures, boat navigation and fish farm production (Gauld *et al*., 2013; Havn *et al*., 2020; Newton e*t al*., 2018; Lothian *et al*., 2018). Such structures have not only been found to impact upon essential life stage movements of migrating species, but weir presence can also alter the water flow, temperature, sediment and nutrient movements throughout the riverine environment (Antonio *et al*., 2007; Branco *et al*., 2012; Gauld *et al*., 2013). The biological consequences for Atlantic salmon resulting from weir presence is still debated.

The increased energy expenditure of both adult and juvenile anadromous fish has been found to negatively impact on seasonal migration success (Gowans *et al*., 2003; Caudill *et al*., 2007; Frank *et al*., 2009; Dodd *et al*., 2018). A study conducted in Denmark found increased delays and assumed mortality in migrating Atlantic salmon in rivers with obstacles (Aarestrup & Koed, 2003). Additionally, studies conducted in Australia found other anadromous species such as Murray cod (*Maccullochella peeli*, Mitchell 1838) and golden perch (*Macquaria ambigua*, Richardson 1845) showed a reluctance to move past low-head weir infrastructure when migrating downstream (O'Connor *et al*., 2006) where delays in migration were associated with mortality. Not only have low head weirs impacted on energy expenditure and passage reluctance, but other behaviours have also been observed (Garcia de Leaniz, 2008; Newton et al., 2016, 2019; Shaw, 2013; Rahel & McLaughlin, 2018). For example, when salmon smolts enter accelerated flow fields, their behaviour adapts to orientate into the current to establish better control of movement and reduce injury (Hansen & Jonsson, 1985; Davidsen *et al*., 2005).

Successful passage across weir structures relies on a combination of water discharge, fish characteristics (e.g., body size (fork length) and species) and various environmental conditions which create discrete periods when fish passage is successful (Kemp & O'Hanley, 2010) . The balance of the specific river flow regimes is essential for successful passage: if water levels are too low, movement of fish over a weir is impeded, conversely, elevated flow levels can have negative effects, particularly upstream of the weir itself. When flow is above the weir construction height, it can exceed the swimming capability of fish (Fraser *et al*., 2015; KLTAP, 2015; Dodd *et al*., 2018), incurring potential injury and increased stress responses in Atlantic salmon. Additionally, Havn *et al*. (2020) found that weir mortality was predominately caused by the physical damage sustained by an individual during weir passage resulting from the physical properties of the weir itself (i.e., height or length) and the energy expenditure costs associated with crossing it.

In this study, I used acoustic telemetry to investigate the behaviour of Atlantic salmon smolts as they made their downstream migration to sea. Specifically we examine the time taken for migrating smolts from the River Derwent to pass across two low-head weir structures. The study had three main objectives and these were to; 1) Assess the inter-annual variation in migration failure rate across three years from two release group (St Johns Beck and Trap and Transport); 2) Compare the spatial variation in smolt migration failure rates across two weirs (Coops Weir and Yearl Weir); and 3)

Assess the potential biotic and environmental factors which are associated with successful weir passage.

Within these three general objectives, we tested four specific hypotheses related to smolt migration across the two weirs: i) Loss rate is equal across both weirs (Coops Weir and Yearl Weir) and release groups (St Johns Beck and Trap and Transport); ii) Smolts which have a prolonged migration delay above the weir will seek alternative migration pathways; iii) High flow conditions will allow for smolts to migrate across both weirs more quickly; and iv) Migration success across a weir is fork length dependent.

## 4.2 Methodology

### 4.2.1 Description of study site

The River Derwent catchment (Cumbria, northwest England) has an area of 679 km² in area and supports a population of wild Atlantic salmon. The River Greta, a tributary of the Derwent system, flows west through the town of Keswick where it intercepts the outflow of the Derwentwater Lake (54’36’0”.1”N 3’09’1”.1”W), to join the River Derwent. The River Derwent flows north, before flowing into Bassenthwaite Lake. Upon exit of Bassenthwaite Lake, the River Derwent drains west flowing through the urbanised areas of Cockermouth and Workington. At Workington the River Derwent is partially impounded by two low-head weirs (Coops Weir and Yearl Weir). Coops Weir has an approximate width of ~90m and was designed to feed various mills (Salmon Hall, Seaton Mill) and Barepot reservoir, though all are currently unused by industry at present. Coops Weir comprises two ‘alternative’ routes, containing good flow, with attractive characteristics (more sheltered, good cover substrates (bouldering)) though both small channels contain a small weir. Located ca.1.2km downstream is Yearl Weir (~190m Width) designed to divert water to Workington Mill (Soapery Beck) which is also unused by industry at present. The Yearl Weir comprises one 'alternative' route (Soapery Beck) which contains stagnant water where there is limited flow and high siltation throughout. The River Derwent drains ca.1.5km west to Workington harbour before draining into the outer Solway Firth (54'38'5".2"N 3'34'0".9"W) (Figure 4.1).

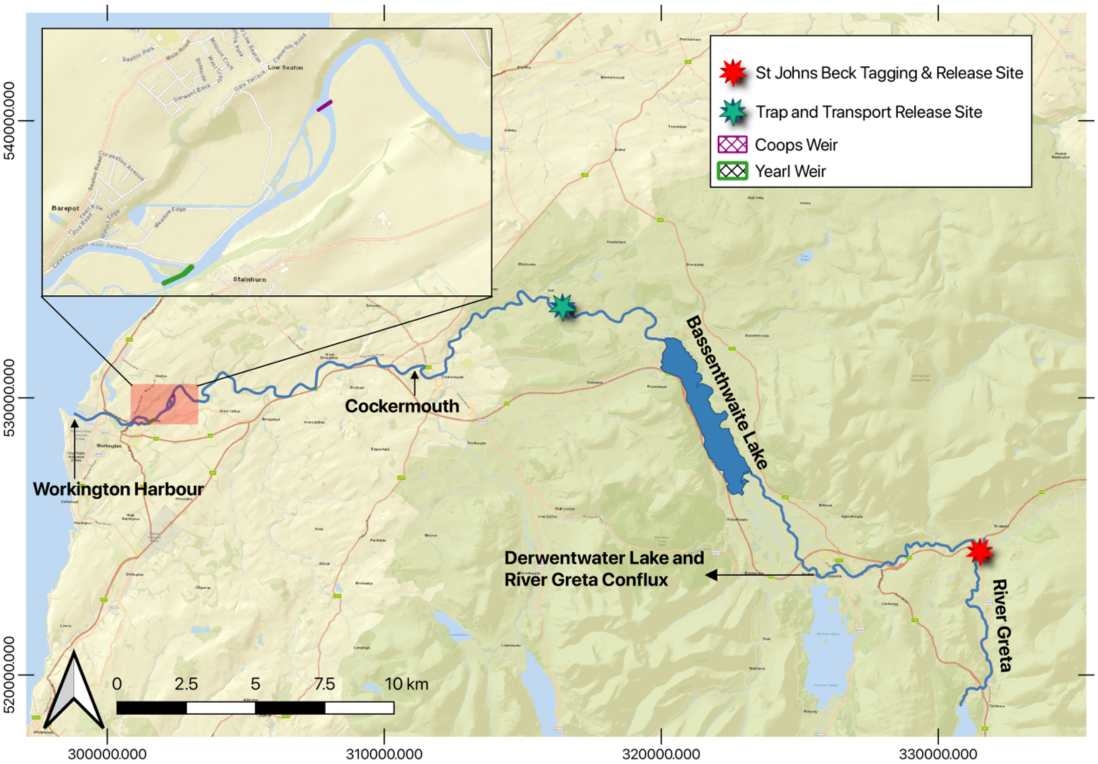


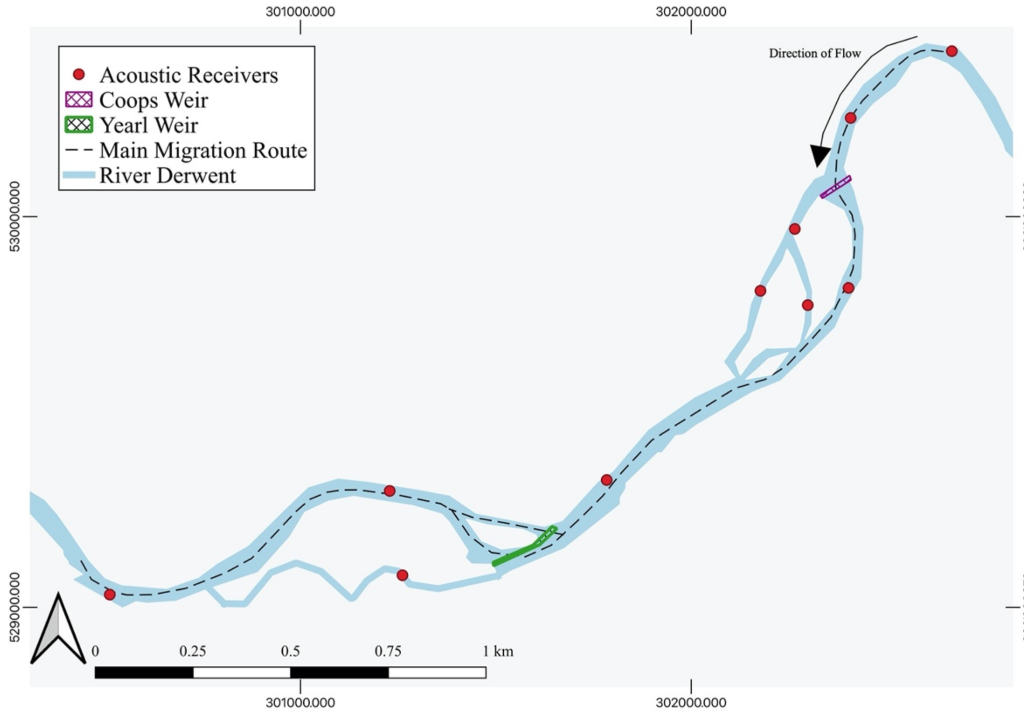

***Figure 4.1*** *River Derwent Catchment*

### 4.2.2 Acoustic receiver deployment

In order to track the seaward migration of Derwent smolts migrating across two low-head weirs structures in the Derwent catchment (Coops Weir: 54'39'2".1"N 3'30'5".6"W, Yearl Weir; 54°38'52.2"N 3°31'36.3"W) to the river discharge point into the Solway Firth at the Workington harbour, acoustic telemetry was used. Fixed receivers were placed in the main weir channels ("main routes") and all possible alternative channels ("alternative routes") in the River Derwent during three consecutive years (2020–2022). In 2020 and 2021, ten receivers were deployed in the same fixed positions (Figure 4.2[A]) and in 2022 ten receivers were deployed and placed in the same position as previous years, with an additional five receivers deployed to increase detection efficiency (Figure 4.2[B]), respectively. Receiver positions were chosen based on published literature range testing results (Newton *et al*., 2016, 2021). Receivers deployed comprised of two types (VR2W and VR2Tx), both operating at 69kHz (Innovasea Ltd., Nova Scotia, Canada). Receivers were attached to a mooring comprised of a vertical steel rod attached on a 20–40kg weight. All river receivers were attached by chain to the riverbank, where suitable, for added security.

Coops Weir is the more upstream river spanning structure, located approximately 44.63km (direct minimum distance travelled; MDT) downstream from the St Johns Beck release location and 19.29km (MDT) from the Trap and Transport release location. Yearl Weir is located 1.30km downstream from Coops Weir, thus 45.93km from the St Johns Beck release site and 20.59km from the Trap and Transport release site.

A)




B)

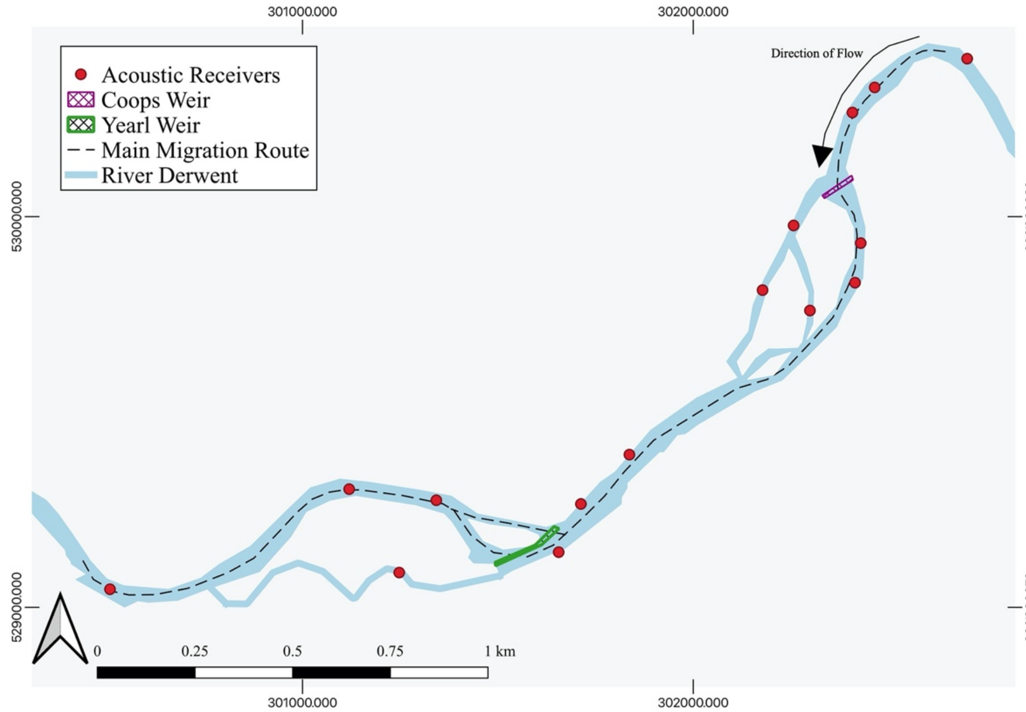



***Figure 4.2*** *Map illustrating acoustic receive layout between 2020 (A), 2021 (A) and 2022 (B), analysing Atlantic salmon smolt downstream migration. --- refers to the minimum estimate main route across the weir in which smolts are hypothesised to take. All river routes not mapped out are referred to as alternative routes (Coops Weir; n=2, Yearl Weir; n=1).*

### 4.2.3 Smolt capture and acoustic tagging procedure

Between 2020–2022 Atlantic salmon smolts were captured during spring (April to May) using a 1.2m rotary screw trap during the downstream migration, at St Johns Beck, Threkheld (54’36’3”.1”N 3’03’4”.0”W). In 2020, 100 fish were tagged between 1st and 5th May, in 2021 150 were tagged between 14th April and 5th May and finally in 2022 150 smolts were tagged between 5th May and 25th May. Across the three study years, in addition to a rotary screw trap, a fyke net was used to increase catches. All trapping apparatus was checked and emptied daily to ensure smolts did not remain in the trap for extended periods of time.

Fish captured were anaesthetized by immersing them in a bucket containing MS222 (Tricaine Methane sulfonate) and sodium bicarbonate solution (0.6g/6L river water for each). It took approximately three minutes for smolts to lose equilibrium (stage three of anaesthesia) which is required for the tagging procedure to be conducted. Fork length ($L_F$, mm) and weight (g) were measured and only fish greater than 130mm $L_F$ and 20g weight were tagged. Additionally, scale samples were taken. All surgical equipment was disinfected using Reprodis/distilled water (1:20 ratio) and rinsed with distilled water. During surgery, fish were given low level anaesthesia (0.125g/2L) and river water was constantly applied across the gills to ensure fish remained sedated. A 10mm ventral incision was made anterior to the pelvic girdle. A V7-2L (69kHz) coded transmitter (VEMCO Ltd, 7mm diameter, 1.7g in air) was surgically placed inside the peritoneal cavity. The V7-2L tags had a nominal delay of 18–45 seconds and an estimated tag life of ca.75 days. The incision was closed by applying two interrupted surgeon knots with 4/0 Ethilon nylon sutures. Smolts were then placed into a recovery container on land for approximately 20 minutes to ensure normal swimming behaviour was exhibited (equilibrium restored). Fish were then placed into a river perforated container downstream from the rotary screw trap with good water flow throughout and given a further 40 minutes recovery.

#### 4.2.3.1 Release group

In 2020, 100% of tagged smolts were released immediately downstream of the trap at St Johns Beck. Tagged fish were released at two different release sites in 2021 and 2022, either at the trapping site or at a site further downstream. This was to ensure that a large enough sample size of fish reached the lower catchment of the River Derwent and to increase the probability of ultimate river migration success. In 2021, 62% (*n=93*) of tagged individuals were released at St Johns Beck, the remaining 38% (*n=57*) were transported downstream of Bassenthwaite Lake to be released back into the River Derwent at the village Isle (54'41'1".7"N 3'17'5".3"W). In 2022 100% of fish captured and tagged at St Johns Beck were transported downstream of Bassenthwaite Lake, these are to be referred to as Trap and Transport release group (TT). All fish released at St Johns Beck are subsequently referred to as the St Johns Beck release group (SJB) (refer to Figure 4.1 for release sites).

Fish that were transported were given a minimum of 40 minutes of recovery from the tagging procedure in a perforated holding tank in St Johns Beck. In 2021 the recovered tagged fish (*n=57*) were placed into a large transport box with continuous aeration. In 2022 the tagged fish (*n=115*) were placed in large bags and filled with oxygen and sealed before transportation. In both years smolts were transported ca.25km from St Johns Beck to a release site downstream of Bassenthwaite Lake. The journey took an average of 25 minutes. Smolts were transported in groups of at least five to minimise predation risk once released. Fish were transported over six days in 2021 and eight days in 2022. All fish were checked at the release site for any signs of stress or poor swimming ability. Fish were placed into an in-river recovery container and given 30 minutes in flowing water at the release site to recover before final release.

### 4.2.4 Ethical statement

All tagging was conducted by a personal licence holder (UK Home Office PIL 70/8794) using procedures which complied with the UK Home Office regulations and UK Home Office project licence number PP0483054. Replacement, reduction, and refinement was considered for this study. All fish were cared for, and monitored, throughout the procedure where stress and suffering were reduced at all times.

### 4.2.5 Statistical analysis

#### 4.2.5.1 False detection filtering

Data analysis was conducted using R software version *4.0.2* (R Core Team, 2019). In order to ensure all detections collected from VEMCO receivers were real detections, filtering for false detections was conducted using the R package *Glatos* (Holbrook *et al*., 2018; Pincock, 2012) which filtered using the short-interval criterion. Short-interval criterion filters all single detections that occurred at one receiver station within a fixed duration which is set at 30 times the average signal delay of the tag (in this study, this duration was 840 seconds (s)) (Hayden *et al*., 2016; Kneebone *et al*., 2014). Detections above this fixed duration period were deemed false. Additionally, signals detected twice during a period which is less than the tags minimum signal delay (18s) were also deemed false (Hanssen *et al*., 2022). In 2020 0.05% of detections were considered false, therefore, 38,053 detections were used for analyses. In 2021, 0.18% of detections were considered false, therefore, 247,235 detections were used for analyses. Finally, in 2022, 0.1% of detections were considered false, therefore, 489,396 detections were used for analyses.

#### 4.2.5.2 Non-residency events

To establish the number of individual movements undertaken by each fish between receiver stations during River Derwent migration, non-residency events were calculated using the R package *Vtrack* (Campbell *et al*., 2012) *RunresidenceExtraction* function. A non-residency event is the movement of a smolt from one fixed positioned receiver to another either downstream or upstream. This function provides timestamps for each receiver and is used to determine the duration and overall success of the riverine migration.

#### 4.2.5.3 Residency events

In order to estimate the overall duration spent at any given receiver, residency events were calculated in *Vtrack* (Campbell *et al.,* 2012; Breece *et al.,* 2018). A residency event is defined as at least two consecutive detections of a smolt at an individual receiver where it had not previously been detected or where it was not detected at a single receiver for a period of greater than 60 minutes (Newton *et al*., 2021). Release groups were split for analysis to compare the St Johns Beck release group (2020-2021) and the Trap and Transport release group smolts (2021-2022).

#### 4.2.5.4 Descriptive analysis

Using the R package *Actel* (Flávio & Baktoft, 2021), descriptive data were calculated for the three-year study period. Flávio & Baktoft (2021) state that *Actel* provides a systematic conditional pipeline to filter and analyse acoustic telemetry data in a reproducible fashion, for fish moving between receiver arrays. It also allows for detection efficiency estimations to be made for each receiver station and observing diel movement patterns by defining the arrival time recorded at each individual receiver.

The detection efficiency of river and weir acoustic receivers is not always 100% due to ambient noise, fast water currents increasing smolt speed and potential submerged barriers, such as logs and therefore, efficiency must be assessed when providing estimates of survival (Halfyard *et al*., 2013; Lilly *et al*., 2022). Efficiency is assessed by the number of smolts detected at a downstream receiver as a proportion of those not detected at the receiver upstream. Across each River Derwent weir there are a number of alternative routes that could have allowed for successful migration, and these were taken into consideration when detection efficiency was calculated.

#### 4.2.5.4 Migration failure across weirs

Migration failure rate of Atlantic salmon across each weir was calculated using R package *Actel* (Flávio & Baktoft, 2021). Smolts which were detected on a receiver upstream of the weir but not detected on any receiver downstream of the weir or on an alternative route receiver were deemed unsuccessful weir migrants (%). Migration failure per km (%.km$^{-1}$) was calculated as the proportion of fish which were unsuccessful in reaching a receiver downstream of a weir divided by the direct minimum distance travelled (MDT). Both release groups were assessed together to compare potential release group affects at weir structures. Both weirs include alternative routes and therefore smolts which were detected on any alternative route receiver but not later detected on any downstream receiver of all possible exit routes was deemed unsuccessful. In order to determine if migration failure rate incurred at weirs is structure specific, the two weirs were assessed separately.

General linear modelling (GLM) was undertaken to see if abiotic factors such as year, release group (St Johns Beck or Trap and Transport), and day of year contributed to successful migration. Release group was split prior to modelling and a GLM of survival was conducted on St Johns Beck release group (2020-2021) (SJB) and a separate GLM was conducted on Trap and Transported released smolts (TT) (2021-2022). The GLM was fitted with a binomial error structure and the identity link function using the R Package *lme4* (Bates *et al*., 2014). Survival (dependent variable) was coded as 1 for fish detected on a receiver or 0 for an assumed failed migration.

*Initial models;*

*glm(Survival ~ Year + Day of Year, data=SJB, family = binomial (link = "identity"))*

*and*

*glm(Survival ~  Year + Day of Year, data= TT, family = binomial (link = "identity"))*

4.2.5.5 Smolt phenotype

To determine if migration success or failure rates were related to Atlantic salmon smolt phenotype, three metrics were used: this included fork length ($L_F$, mm), weight (g) and tag burden (%) which was calculated by dividing the weight of a tag in air (1.7g) by the weight of the tagged Atlantic salmon smolt (Brown *et al*., 2012). General linear modelling (GLM) was undertaken to determine if phenotypic factors such as $L_F$, weight and tag burden contributed to successful weir migration. The GLM was fitted with a binomial error structure and the identity link function using the R Package *lme4* (Bates *et al*., 2014). Survival (dependent variable) was coded as 1 for fish detected on a receiver below the weir or 0 for an assumed failed weir migration. Both Coops Weir and Yearl Weir were analysed separately.

*Initial model:*

*glm (Survival ~ $L_F$ + Weight + Tag Burden, family = binomial (link= "identity")*

4.2.5.6 Timing of migration

Using the *r.test* function in the *CircStats* package (Lund & Agostinelli, 2018) a Rayleigh test of uniformity was performed to determine if arrival at the receiver situated directly above the weir and the receiver either situated immediately below the weir or in an alternative route, were 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).

4.2.5.7 Duration

Biotic factors such as $L_F$ (mm), weight (g), tag burden (%), release group (St Johns Beck or Trap and Transport) and year were modelled using a general linear model, constructed using the R package *lme4* (Bates *et al*., 2014) to determine the significant difference each factor had on duration above the weir. The GLM was fitted with a gamma error structure and log link function with duration being the dependent variable.

*Initial model:*

*glm(duration ~ $L_F$ + Weight + Tag Burden + Release Group + Year, family = Gamma(link = "log")*

4.2.5.8 Route choice

Two logistic regression models (GLM) were tested to establish if route choice was impacted by the average duration (hrs) (residency event) above each weir. The GLM's were fitted with a binomial error structure and logit link function with route choice being the dependent variable. The dependent variable represents a categorical outcome with two possible values: 1 for choosing the main migration route and 0 for choosing any alternative route. Year was also added to assess the temporal disparities in route choice of Atlantic salmon smolts.

*Initial model:*

*glm(Route Choice ~ Duration + Year, family = binomial (link = "logit")*

Additionally, Chi-Squared tests were undertaken per weir to help determine if the observed frequencies of migration choice differ significantly from what would be expected by chance.

#### 4.2.5.9 Environmental factor analysis

Hourly water flow discharge ($m^3/s$) data was provided by the Seaton Mill gauging station (54°39′02″N, 003°31′19″W) for the main stem of the river which is situated ca.1km downstream of Coops Weir and 0.3km upstream of Yearl Weir. In order to investigate the impact that water flow had on migration success rates across the weir and if water flow discharge impacted duration spent above the weir, hourly water flow discharge data ($m^3/s$) was modelled from the main route only. Using a general linear model (GLM) with the R package *lme4* (Bates *et al*., 2014) survival was fitted with a binomial error structure and the identity link function. Survival (dependent variable) was coded as 1 for fish detected on a receiver or 0 for an assumed failed migration. Duration (hrs) was modelled with duration being the dependent variable with a gamma error structure and log link function. Year was also included for both models.

*Initial model for survival:*

*glm(Survival ~ Water Flow + Duration + Year, family = binomial (link = "identity"))*

*Initial model for duration:*

*glm(Duration ~ Water Flow + Year, family = Gamma(link = "log"))*

Significant factors highlighted by the GLM where further investigated for significant categorical factors. The R package *multcomp* (Hothorn *et al*., 2016) was used for ANOVA testing with Post Hoc Tukey HSD Test in order to compare potential differences within categorical data sets (e.g., Year).

## 4.3 Results

### 4.3.1 Tagging summary

In total, 365 Atlantic salmon smolts were tagged between 2020-2022. $L_F$ (mm), weight (g) and tag burden (%) averages are summarised in Table 4.1.

***Table 4.1*** *Summary data for River Derwent tagged Atlantic salmon smolts between 2020-2022. Summary of mean $L_F$ (mm), weight (g) and tag burden (%) for each year and release group: SJB- St Johns Beck release group, TT-Trap and Transport release group. Tag burden is calculated by dividing the weight of the tag in air (1.7g) by the weight of the individual *100.*

| Year | $L_F$ (mm) ± SD (range) | Weight (g) ± SD (range) | Tag Burden (%) ± SD (range) |
|---|---|---|---|
| **2020 (SJB)** (*n=100*) | 139.4 ± 0.65 (130-157) | 27.89 ± 0.42 (21.4-41.4) | 5.1 ± 0.07 (3.5–6.7) |
| **2021 (SJB)** (*n=93*) | 141.9 ± 8.4 (130-164) | 29.4 ± 5.5 (21.5-44.5) | 4.9 ± 0.61 (3.6-6.1) |
| **2021 (TT)** (*n=57*) | 141.0 ± 7.7 (134-150) | 29.8 ± 5.1 (21.5-44.5) | 4.8 ± 0.55 (3.6-6.1) |
| **2022 (TT)** (*n=115*) | 138.7 ± 6.6 (130-161) | 27.4 ± 4.1 (21.2- 40.4) | 5.1 ± 0.5 (3.9-6.2) |

### 4.3.2 Weir migration failure rate

In 2020, 9% (*n=9*) smolts were detected above Coops Weir. 88% (*n=8*) smolts were later detected downstream and deemed successful. In 2021, 31% (*n=29*) of smolts from the St Johns Beck release group and 63% (*n=36)* of Trap and Transported smolts were detected above the weir. Of these, 96% (*n=28*) of St Johns Beck released smolts and 91% (*n=33*) of Trap and Transport released smolts were deemed successful in crossing the weir (deemed unsuccessful: SJB 4%, TT 9%). Finally, in 2022 only 52% (*n=60*) smolts were detected above Coops Weir and of those fish, 98% (*n=59*) were deemed successful weir migrants.

In 2020, 8% *(n=8)* smolts were detected above Yearl Weir. 100% (*n=8*) of these smolts were later detected downstream and therefore deemed successful. In 2021, 96% (*n=28*) smolts from the St Johns Beck release group and 91% (*n=33*) of Trap and Transported smolts were detected above the weir. Of these, 60% (*n=17*) of St Johns Beck released smolts and 69% (*n=23*) of Trap and Transport released smolts were deemed successful in crossing the weir (deemed unsuccessful: SJB 40%, TT 31%). Finally, in 2022 98% (*n=59*) smolts were detected above Yearl Weir and of those, 81% (*n=48*) smolts were deemed successful weir migrants. Results of migration rates for both Coops Weir and Yearl Weir are summarised in Table 4.2.

***Table 4.2*** *Summary table of the number of smolts detected (n=) and the estimated migration success rate (%) for Atlantic salmon smolts tagged between 2020-2022 across both Coops Weir and Yearl Weir. Release group: SJB-St Johns Beck release group, TT-Trap and Transport release group.*

| Year | Above Coops Weir | Below Coops Weir | Above Yearl Weir | Below Yearl Weir |
|---|---|---|---|---|
| **2020 (SJB)** | *n=9* | *n=8* (88%) | *n=8* | *n=8* (100%) |
| **2021 (SJB)** | *n=29* | *n=28* (96%) | *n=28* | *n=17* (60%) |
| **2021 (TT)** | *n=36* | *n=33* (91%) | *n=33* | *n=23* (69%) |
| **2022 (TT)** | *n=60* | *n=59* (98%) | *n=59* | *n=48* (81%) |

Results of the migration failure rate across weirs GLM found that day of year smolts were released was significant ($p$=<0.0001) in predicting passage. Smolts released later each year have a greater success rate compared to those released at the beginning of the tagging season. A chi-squared test of independence also concluded this ($X^2$=0.05, $p$=0.004).

### 4.3.3 Migration route choice

From the successful smolts which migrated across Coops Weir in 2020 (*n=8*, 88%), no fish were detected using an alternative route, thus, all 88% are assumed to have passed over the weir itself on the main river stem. In 2021, not all smolts were found to utilise the main migration route across the weir, with three individuals from both groups (total *6*) taking an alternative route around Coops Weir while 90% (*n=55*) of successful smolts chose to cross via the main weir route. Additionally, in 2022, 18% (*n=11*) smolts took an alternative route around Coops Weir and the remaining 82% (*n=48*) took the main weir route. All smolts which took an alternative route in 2021 and 2022 were successful in reaching the Yearl Weir. A chi-squared test of independence was run to test whether year significantly impacted on route choice chosen by smolts an found route choice was not significantly different between years ($X^2$=2.10, $p$=0.34).

Of the successful smolts which migrated across/around Yearl Weir in 2020, only 12.5% (*n=1*) of smolts utilised an alternative route, thus 87.5% (*n=7*) of smolts chose to cross via the main weir route. In 2021, 5.8% (*n=1*) of smolts from St Johns Beck release group and 17.39% (*n=3*) of smolts from Trap and Transport release group took an alternative route around Yearl Weir. Therefore 94% (*n=16*) of St Johns Beck smolts and 82.6% (*n=20*) of Trap and Transported smolts choose to take the main weir route in 2021. Additionally, in 2022, out of the *48* successful smolts none were found to take an alternative route around Yearl Weir. All smolts which took an alternative route in 2020 and 2021 were successful in reaching the final River Derwent receiver, located ca.0.7km above the exit into the Solway Firth. A chi-squared test of independence tested to see if year significantly impacted on route choice around/across Yearl Weir found there was no significant difference between years

($X^2$=5.35, $p$=0.06). Results of route choice across/around both weirs are summarised in Table 4.3.

***Table 4.3** Summary table of the number of smolts detected (n=) and the estimated migration route choice rate (%) for Atlantic salmon smolts tagged between 2020-2022 across both Coops Weir and Yearl Weir. Release group: SJB- St Johns Beck release group, TT-Trap and Transport release group. Percentage for alternative and main routes taken is calculated using successful smolts only. Chi-squared ($X^2$) Statistical tests results included for both weirs testing the significance of year (p).*

| **Year** | **Coops Weir** | | **Yearl Weir** | |
|---|---|---|---|---|
| | Main Route Taken | Alternative Route Taken | Main Route Taken | Alternative Route Taken |
| **2020 (SJB)** | *n=8* (100%) | *n=8* (0%) | *n=7* (87.5%) | *n=1* (12.5%) |
| **2021 (SJB)** | *n=25* (89%) | *n=3* (11%) | *n=16* (94.2%) | *n=1* (5.8%) |
| **2021 (TT)** | *n=30* (90%) | *n=3* (10%) | *n=20* (82.6%) | *n=3* (17.4%) |
| **2022 (TT)** | *n=48* (82%) | *n=11* (18%) | *n=48* (100%) | *n=0* (0%) |
| **Chi-squared ($X^2$)** | *2.10* | | *5.35* | |
| ***p* value** | *0.34* | | *0.06* | |

When comparing the weir migration success rates, based on the above findings, total migration success rate across Coops Weir equalled to 95.5%, however, Yearl Weir was found to have a much lower migration success rate of 75%, with year not being regarded as a significant factor.

### 4.3.4 Does duration have an impact on route choice?

The study examined whether the duration (hrs) spent above each weir had any significance in determining the route choice for smolts either across or around the weir. It was found that across the three-year period combined, average duration spent above Coops Weir had no significance in determining the route chosen (Chi-Squared test: $X^2$=0.74, $p$=>0.05; Main route: $p$=0.33, Alternative route: $p$=0.85) (Table 4.4).

***Table 4.4** Summary of average duration (hrs) spent above Coops Weir and the significance in duration determining smolt route choice ($X^2$, p) across or around Coops Weir between 2020-2022. Release group: SJB- St Johns Beck release group, TT-Trap and Transport release group.*

| **Year** | **Duration (hrs) ± SD (range)** | **Chi- Squared ($X^2$)** | **p value (*p*)** |
|---|---|---|---|
| | Combined (three- year period) | 0.74 | >0.05 |
| **2020 (SJB)** | 0.35 ± 0.53 (0.05–1.69) | | |

| | | | |
|---|---|---|---|
| **2021 (SJB)** | 0.98 ± 2.51 (0.02–10.77) | | |
| **2021 (TT)** | 1.29 ± 2.71 (0.03–12.98) | | |
| **2022 (TT)** | 0.25 ± 0.80 (0.01–6.34) | | |
| | | Main Route | 0.33 |
| | | Alternative Route | 0.85 |

Similarly, duration spent above Yearl Weir did not have significance in determining migration route choice across all three study years combined (Chi-Squared test: $X^2$=0.367, $p$=>0.05; Main route: $p$=0.96, Alternative route: $p$=0.82) (Table 4.5). However, when comparing weirs, average time spent above Yearl Weir was approximately 1.3 hrs longer compared to Coops Weir across all three years.

***Table 4.5*** *Summary of average duration (hrs) spent above Yearl Weir and the significance in duration determining smolt route choice ($X^2$, p) across or around Yearl Weir between 2020 - 2022. Release group: SJB- St Johns Beck release group, TT-Trap and Transport release group.*

| **Year** | **Duration (hrs) ± SD (range)** | **Chi- Squared ($X^2$)** | **p value (*p*)** |
|---|---|---|---|
| | Combined (three- year period) | 0.367 | >0.05 |
| **2020 (SJB)** | 2.93 ± 6.47 (0.20–18.24) | | |
| **2021 (SJB)** | 1.67 ± 4.61 (0.09-18.51) | | |
| **2021 (TT)** | 1.64 ± 3.01 (0.28–12.37) | | |
| **2022 (TT)** | 0.29 ± 0.38 (0.02–1.91) | | |
| | | Main Route | 0.96 |
| | | Alternative Route | 0.82 |

### 4.3.5 Environmental influences on route choice

To determine if environmental factors were predictors of route choice and duration at both Coops Weir and Yearl Weir, water flow discharge ($m^3/s$) and year were modelled. Across both weirs, water discharge differed significantly across years ($p$=<0.001). Further testing by ANOVA and Post Hoc Tukey test were performed, finding water discharge significantly differed in 2021 ($q$=4.22, $\alpha$=0.05, $p$=<0.001) where smolts faced greater discharge rates ($m^3/s$) compared to the years 2020 and 2022. This coincides with high rainfall noted during the 2021 study season. However, when analysing the impact of flow on duration spent above both weirs, it was found flow discharge ($m^3/s$) did not predict the duration spent above Coops Weir ($p$=0.13) or Yearl Weir ($p$=0.49). Based on the findings, overall duration spent above both weirs was random and not impacted by flow discharge at the time of migration, however, as stated in section 4.3.4, individuals had a greater duration above Yearl Weir compared to Coops Weir.

### 4.3.6 Phenotype

A binomial regression model (GLM) testing the influence of phenotypic factors on migration success across Coops Weir and Yearl Weir was conducted separately. Both weight and tag burden were highly correlated with smolt $L_F$, so for the analyses only $L_F$ was used. Smolt $L_F$ (mm) of both successful and unsuccessful migrants across Coops Weir and Yearl Weir are summarised in Table 4.6.

***Table 4.6*** *Summary data for successful and unsuccessful Coops Weir and Yearl Weir migrants between 2020-2022. Summary of mean $L_F$ (mm) for each year and release group: SJB- St Johns Beck release group, TT-Trap and Transport release group.*

| **Year** | **Coops Weir** | | **Yearl Weir** | |
|---|---|---|---|---|
| | Successful<br>Mean $L_F$ (mm) ± SD (range) | Unsuccessful<br>Mean $L_F$ (mm) ± SD (range) | Successful<br>Mean $L_F$ (mm) ± SD (range) | Unsuccessful<br>Mean $L_F$ (mm) ± SD (range) |
| **2020 (SJB)** | 141.3 ± 5.44 (134–149) | 142 | 141.3 ± 5.44 (134–149) | - |
| **2021 (SJB)** | 141.9 ± 7.47 (130–164) | 150 | 141.9 ± 7.47 (130–164 | 141.7 ± 7.43 (130 -164) |
| **2021 (TT)** | 140.9 ± 6.57 (130–159) | 141.3 ± 6.89 (130–159) | 140.9 ± 6.57 (130–159) | 140.9 ± 6.66 (130-159) |
| **2022 (TT)** | 139.1 ± 7.04 (130–161) | 145 | 139.1 ± 7.04 (130-161) | 141.1 ± 7.45 (131-161) |

Migration success across Coops Weir was not dependent on smolt $L_F$ ($p$=0.66). However, $L_F$ in years 2021 and 2022 did significantly predict smolts route choice (2021; $p$=0.001, 2022; $p$=0.02). Larger smolts were more likely to utilise alternative routes away from the main migration pathway across Coops Weir compared to smaller smolts. Migration success across Yearl Weir was also found not to be dependent on smolt $L_F$ ($p$=0.82). $L_F$ did not significantly predict route choice around Yearl Weir ($p$=0.49), thus smolts migrating through the alternative route around Yearl Weir was random.

### 4.3.7 Migration timing

Variations in the diurnal patterns of migrating smolts across Coops Weir in different years were observed (Figure 4.3). In 2020 and 2022, migration was not significantly dependent on time of day (Rayleigh test; 2020: *r.bar*=0.68, $p$=0.49, 2022: Rayleigh test; *r.bar*=0.97, $p$=0.86). In 2021, migrating smolts across Coops Weir showed a divergence, with trap and transported smolts migration being significantly determined by a clear nocturnal preference (Rayleigh test; *r.bar*=0.27, $p$=< 0.01).

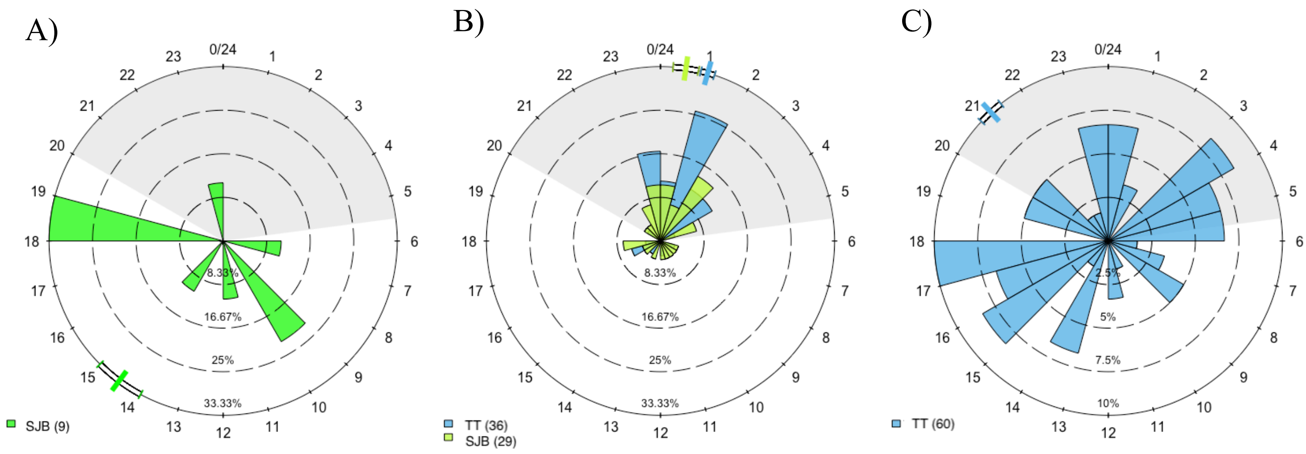



***Figure 4.3*** *Circular plots generated in Actel using the plotTimes() function depicting the hour (British Summer Time; BST) when smolts migrated across Coops Weir. The mean time of movement is highlight within the outer circle. Each bar sum to 100%. The number of smolts included in the analysis are presented. The shaded zone indicates the average sunset and sunrise which occurred during May- June. St Johns Beck (SJB) released smolts are shown in green and Trap and Transport (TT) are displayed in blue. A: 2020 (SJB; n=9), B: 2021 (SJB; n=29, TT; n=36), C: 2022 (TT; n=60).*

Conversely, in the case of migration across Yearl Weir, results demonstrated both similarities and slight differences when compared to Coops Weir diurnal passage patterns (Figure 4.4). Migration across Yearl Weir in 2020 and 2022 were not significantly dependent on time of day (Rayleigh test; 2020: *r.bar*=0.72, $p$=<0.22/2022: Rayleigh test; *r.bar*=0.66, $p$=0.78). Though in 2022, the meantime of movement across Yearl Weir was at 02:15am compared to 21:15pm at Coops Weir. Nevertheless, weir passage timing across Yearl Weir in 2022 was still predominately random. In 2021, both release groups exhibited different diurnal patterns. Trap and Transported smolts were significantly more likely to have a nocturnal preference (Rayleigh test; *r.bar*=0.33, *p*=0.03).

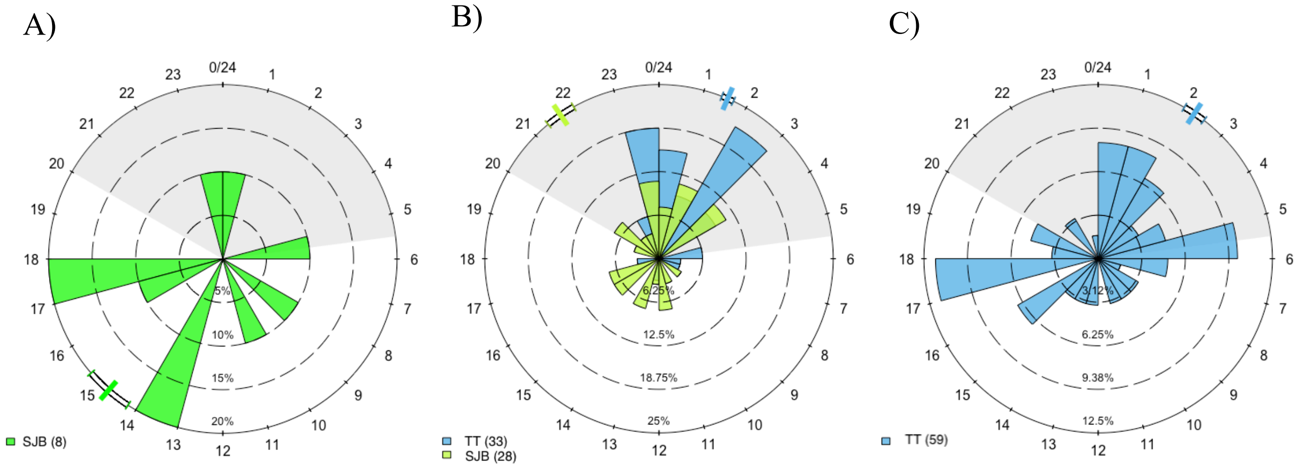



***Figure 4.4*** *Circular plots generated in Actel using the plotTimes() function depicting the hour (British Summer Time; BST) when smolts migrated across Yearl Weir. The mean time of movement is highlight within the outer circle. Each bar sum to 100%. The number of smolts included in the analysis are presented. The shaded zone indicates the average sunset and sunrise which occurred during May-June. St Johns Beck (SJB) released smolts are shown in green and Trap and Transport (TT) are displayed in blue. A: 2020 (SJB; n=8), B: 2021 (SJB; n=28, TT; n=33), C: 2022 (TT; n=59).*

In the year 2021, both Coops Weir and Yearl Weir exhibited analogous outcomes, notably with respect to the behaviour of smolts released from the trap and transport group. During this period, these smolts demonstrated a pronounced nocturnal preference. Though only differences observed in 2022 were that of the mean time of movement, it is notable that upon rigorous statistical examination, these differences did not attain a level of significance that could be considered statistically different, underlining the subtle variations characterising diurnal migration patterns during this specific year. Results of mean time of movement and statistical findings are summarised in Table 4.7.

*__Table 4.7__ Summary of Rayleigh test results of the diurnal migration patterns across Coops Weir and Yearl Weir between 2020-2022 of successful migrating smolts. Displaying mean time of movement (hrs:mm) for all three years and each release group: SJB- St Johns Beck release group, TT-Trap and Transport release group.*

| **Year** | **Coops Weir** | | **Yearl Weir** | |
|---|---|---|---|---|
| | Mean Time of Movement (am/pm) | Significances ( Rayleigh test: *r.bar*, *p)* | Mean Time of Movement (am/pm) | Significances ( Rayleigh test: *r.bar*, *p)* |
| **2020 (SJB)** | 14:30 pm | *r.bar* = 0.68, *p*= 0.49 | 14:30 pm | *r.bar* = 0.72, *p*= < 0.22 |
| **2021 (SJB)** | 00:30 am | *r.bar* = 0.43, *p*= 0.06 | 21:45 pm | *r.bar* = 0.98 , *p*= 0.87) |
| **2021 (TT)** | 01:00 am | *r.bar* = 0.27 , *p*= < 0.01 | 01:30 am | *r.bar* = 0.33 , *p*= 0.03 |
| **2022 (TT)** | 21:15 pm | *r.bar* = 0.97 , *p*= 0.86 | 02:15 am | *r.bar* = 0.66 , *p*= 0.78 |

## 4.4 Discussion

This study contributes to previous work and provides further evidence illustrating the migration failure rate of Atlantic salmon smolts during downstream migration, particularly where low head weirs are present (Havn *et al*., 2020; Newton *et al*., 2021). Migration failure rates in this study across two migration barriers (Coops Weir and Yearl Weir) were considerably higher when compared with other studies of riverine migration across barriers (Table 4.2) (Havn *et al*., 2020; Gauld *et al*., 2013; Aarestrup & Koed, 2003; Aarestrup *et al*., 1999; Baisez *et al*., 2011; Deng *et al*., 2015; Meixler *et al*., 2009; Hockersmith *et al*., 2003; Keefer *et al*., 2012; Muir *et al*., 2001, 2006; Raymond, 1979, 1988; Smith *et al*., 2002, 2006; Williams *et al*., 2001). A review of riverine migration literature found failure rate per km (%.km$^{-1}$) ranged between 0.3-7%.km$^{-1}$ (Davidsen *et al*., 2009; Dieperink *et al*., 2002; Koed *et al*., 2002, 2006; Martin *et al*., 2009; Moore *et al*., 1998; Thorstad *et al*., 2012a, 2012b). However, Gauld *et al*. (2013) found failure rate per km of salmonids when riverine barriers were present was within ranges observed in other studies (0.55-0.88%.km$^{-1}$). This is consent with the findings from the River Derwent study, showing migration failure rates within the observed ranged where Coops Weir was between 1.49-2.24%.km$^{-1}$ (successful weir migrant rate: 88-98%), though extremely high migration failure rates per km were experience at Yearl Weir, particularly in 2021 (0–32.2%.km$^{-1}$ (successful weir migrant rate: 60-100%)). Nevertheless, Havn *et al*. (2020) only found a 0.4%.km$^{-1}$ migration failure rate when observing smolt passage across a low-head weir structure on River Rhine, Germany. We can assume the variations in migration failure rates could be due to site specific geographical features, such as environmental fluctuations and predator assemblages and also a result of structure specific impacts. The reasons for migration failure in riverine systems, and in particular the River Derwent, still remain unclear and could be due to a lack of physiological preparedness for environmental transition between freshwater and brackish environments at the Yearl Weir or increased predation pressures (Järvi, 1989; Jepsen *et al*., 2006; Thorstad *et al*., 2012a; Newton *et al*., 2021).

During smolting, the fish go through morphological, physiological, and behavioural changes that prepare them for migration to the marine environment (Milner *et al*., 2003; Thorstad *et al*., 2012b; Zydlewski *et al*., 2014). Smolts that migrate across Yearl Weir immediately switch from freshwater to a brackish environment, therefore if poor physiological preparedness for entry into high salinity environments was a primary influence in migration failure patterns found at Yearl Weir then it can be assumed migration success is positively correlated with day of year which aligns with our findings ($X^2$=0.05, $p$=0.004). Previous research by Stich *et al*. (2015) and Newton *et al*. (2021) supports this notion, indicating that later migrating smolts may have already physiologically adapted themselves to succeed in high salinity environments. Therefore, our findings not only highlight the significance of the release date but also provide insights into the potential physiological adaptations that influence smolt survival during migration.

Additionally, not only do physiological pressures impact smolt passage success, but there is risk in delay above low-head weir structures where smolts may accumulate over time due to the stressful environment (Norrgård *et al*., 2013; Stich *et al*., 2015; Havn *et al*., 2020). Chanseau *et al*. (1999) found specific barrier features (i.e height) impacted on potential delays faced to migrating Atlantic salmon, where tall obstacles (>2.5m height) stalled migration for several days compared to small structures (<1.5m height) which saw <24 hrs delay. However, Newton *et al*. (2018) found the mean delay experienced by migrating Atlantic salmon smolts was not significantly different between an impacted (0.17hrs) and an unimpacted (0.16hrs) riverine stretch, although temporal variation in the delays experienced were significant. In addition, Renardy *et al*. (2021) reported that median cumulative crossing delays varied between 2.6hrs and 32.1hrs and was increased as the number of more barriers also increased in number. The potential for increased delays incurred at weirs will in turn possibly increase predation pressure through the aggregation of Atlantic salmon smolts in a relatively small area. Predation from piscine species such as pike (*Esox lucius, Linnaeus 1758*) and avian species such as the great cormorant (*Phalacrocorax carbo carbo, Linnaeus 1758*) are a common source of mortality at weir structures and are known to prey on Atlantic salmon smolts during spring migrations and in bottleneck zones where migration delays are prevalent (Havn *et al*., 2020; Dieperink *et al*., 2002; Jepsen *et al*., 1998, 2000; Carter *et al*., 2001; Heggenes & Borgstrom, 1988; Hvidsten & Møkkelgjerd, 1987; McCormick *et al*., 1998; Thorstad *et al*., 2012a). However, this was not the case at both River Derwent weirs because smolt duration of passage was not extended when compared with the free-flowing riverine stretch prior (Chapter 2, unpublished). Furthermore, Björnsson *et al*. (1995, 2010), McCormick (1994) and McCormick *et al*. (2000, 2007, 2002) noted migration is precisely timed with photoperiod and river discharge), though, this is simply not the case for River Derwent smolts. Water discharge rates from the main route only, had no significant impact on the duration smolts spent above weirs weir passage was random across the three study years. Studies regarding weir passage and timings remains extremely limited, with current knowledge mostly gained from non-impacted riverine systems. Fernandes *et al*. (2015) found migration out of riverine systems was random and occurred at various points throughout the day which is similar to patterns on the River Derwent. Research analysing time of day at which smolts approach hydro power structures aids in our understanding of time-of-day influences. Moore *et al*. (2018) found smolts migrated towards a hydro structure during nocturnal hours, thus we can assume again approach and passage times are structure and site specific, although further research into time-of-day influence on migration behaviours is required.

It is not uncommon for migratory fish to cross multiple obstructions across many riverine systems and the cumulative impact of the obstacles can be significant even when loss rate at each is low (Havn *et al*., 2020; Larinier, 2008; Norrgård *et al*., 2013; Newton *et al*., 2018). For example, in the River Derwent there are two weirs present (Coops and Yearl) and in 2022 the migration failure rate at Coops Weir was 2.24%.$km^{-1}$ and 15.32%.$km^{-1}$ at the Yearl Weir, thus the total migration failure rates for downstream migrating smolts to pass both riverine obstructions was 17.56%.$km^{-1}$, although this may be a minimum estimated failure rate. Increased failure rates observed may be a result of cumulative injuries incurred over time, which do not present themselves immediately post barrier passage. This alludes to the false narrative that smolts have been successful in the riverine environment when this is simply not the case, resulting in a proportional reduction in the number of returning spawning adults (Havn *et al*., 2020).

Across the three-year study period, a proportion (86.1%) of Atlantic salmon smolts that passed the Coops Weir migrated over the main weir channel instead of utilising an alternative route (13.9%) and therefore followed the main discharge channel. This was similar to Yearl Weir where 95.8% of smolts passed via the main route and only 4.2% took an alternative passage. The results from this study are comparable to other research suggesting that the proportion of smolts passing a weir is related to the proportion of water discharge available for passage (Hvidsten & Johnsen, 1997; Ruggles, 1980; Serrano *et al*., 2009). There are however, indications from this study to suggest that increased water flow did not determine pathway choice across/around weirs and that smolts have the ability to actively swim, choosing indirect routes where flow may not be as direct (Havn *et al*., 2017; Hedger *et al*., 2011; Mork *et al*., 2012; Økland *et al*., 2006; Ounsley *et al*., 2020).

## 4.5 Conclusion

Based on the evidence of this study we can conclude that low-head weirs present throughout the River Derwent are having an impact on migrating smolts, through increasing risk of migration mortality. We found the two weirs displayed varying migration failure rates, where the Yearl Weir had a greater negative impact on migrating smolts across a three-year study period, although this could be due to the lack of preparedness of smolts when migrating directly from freshwater to brackish water environments as smolts which migrated later (potentially more physiologically prepared) had a greater success rate. Additionally, it can be assumed that varying failure rates across weirs are location specific and not only due to the weir itself but due to potential abiotic factors such as environmental fluctuations and predator assemblages. Migration delays above the weirs were consistent with previous literature, although failure rates observed across the weirs demonstrated temporal and spatial differences. The work suggests that smolts had the ability to actively swim and choose their migration routes even if it was remote from the main water channel and regardless of duration spent above the weir.

# *Chapter 5*: Evidence of long-distance coastal sea migration of Atlantic salmon, *Salmo salar*, smolts from northwest England (River Derwent).

Green, A., Honkanen, H.M., Ramsden, P., Shields, B., del Villar-Guerra, D., Fletcher, M., Walton, S., Kennedy, R., Rosell, R., O'Maoiléidigh, N. and Barry, J. (2022). Evidence of long-distance coastal sea migration of Atlantic salmon, *Salmo salar*, smolts from northwest England (River Derwent). *Animal Biotelemetry*, **10**(1), 3.

**Note this chapter is published in Animal Biotelemetry*

*Data from this study is included in Lilly et al. (2023) Journal of Fish Biology 101(1) 265-283*

**Abstract**

Combining data from multiple acoustic telemetry studies has revealed that west coast England Atlantic salmon (*Salmo salar,* Linnaeus 1758) smolts used a northward migration pathway through the Irish Sea to reach their feeding grounds. 100 Atlantic salmon smolts were captured and tagged in May 2020 in the River Derwent, northwest England as part of an Environment Agency/Natural England funded project. Three tagged smolts were detected on marine acoustic receivers distributed across two separate arrays from different projects in the Irish Sea. One fish had migrated approximately 262km in ten days from the river mouth at Workington Harbour, Cumbria to the northernmost receiver array operated by the SeaMonitor project; this is the longest tracked marine migration of an Atlantic salmon smolt migrating from the United Kingdom. This migrating fish displayed behaviours which resulted in fast northward migration. The remaining two fish were detected on a receiver array operated by a third project: the Collaborative Oceanography and Monitoring for Protected Areas and Species (COMPASS). These detections further provide evidence that migration to reach marine feeding grounds of at least a

proportion of salmon smolts from rivers draining into the Irish Sea is northerly, although without a southern marine array it is impossible to conclude that this is the only route. The pattern of these detections would not have been possible without the collaborative efforts of three distinct and separately funded projects to share data. Further work is required to fully understand migration trajectories in this species on the west coast of the British Isles.

*Key words: Atlantic salmon, post-smolt, marine, migration, telemetry*

## 5.1 Background

For diadromous fish species, that migrate between marine and freshwater habitats, there is commonly very considerable disparity in knowledge about their ecology in different habitats (Klemetsen *et al*., 2003; Armstrong *et al*., 2018). For the anadromous Atlantic salmon (*Salmo salar,* Linnaeus 1758) there is a relatively good understanding of the ecology of the freshwater phase of the life cycle in published literature; this is in marked contrast to that of the marine phase (post-smolt) (Thorstad *et al*., 2012b; Barry *et al*., 2020; Flávio *et al*., 2020). In particular, we have only a limited comprehension of their marine habitat use and the migration pathways they use to migrate between their natal river and their marine foraging areas in both directions (Riley *et al*., 2014). The limited knowledge gathered for Atlantic salmon making their outwards marine migrations and the environments through which they migrate comes principally from two approaches: the capture of salmon at sea from either targeted (SALSEA-MERGE, 2012; CEFAS, 2019; Ahlbeck-Bergendahl *et al*., 2019) or opportunistic (Thorstad *et al*., 2012a) capture by fisheries vessels and from telemetry studies tracking fish tagged in freshwater to marine habitats (Barry *et al*., 2020; Went, 1973; Mork *et al*., 2012; Ounsley *et al*., 2020; Klimley *et al*., 2013; Lothian *et al*., 2018; Newton *et al*., 2018; Chaput *et al*., 2019).

The former study approach can provide important, spatially explicit, but point source data on the presence of migrating salmon (Hitt *et al*., 2011; Heupel *et al*., 2010; Rowell *et al*., 2015). This approach has shown us that salmon emanating from rivers in southern Europe migrate north to marine feeding grounds in the Norwegian Sea and/or to the north-west Atlantic, to the seas off west Greenland (Klemetsen *et al*., 2003; Thorstad *et al*., 2012b; Dunbar & Thomson, 1979). Using this approach however, it is difficult to reconstruct migration pathways and passage speeds, in part because it requires fish collection over an enormous spatial area from which pathways need to be inferred.

The telemetry approach applied to seaward migrating smolts has until now, mostly centred around tracking using acoustic technology. Acoustic telemetry studies, typically using fixed position, continuous monitoring acoustic receivers and fish tagged with acoustic transmitters, have rapidly become a common method to investigate fish migration patterns (large and small), site fidelity and diel and seasonal movements (Hitt *et al*., 2011; Heupel *et al*., 2010; Rowell *et al*., 2015) through both freshwater and marine environments. This technique has the advantage that it can provide highly precise spatial information and thus more precise migration pathways. The disadvantage, when this approach is used to track anadromous species migrating into marine systems, is that the financial and logistical costs of maintaining suitably positioned receivers increases exponentially with distance from the river from which individuals are being tracked. Collaboration amongst global and regional projects, often with differing primary aims, allow for fish migration information in the spatially extensive marine environments to be obtained in a more cost-effective way (Goulette *et al*., 2014; Gazit *et al*., 2013).

In one of the few studies to have looked at migration pathways of anadromous Atlantic salmon in the Irish Sea using acoustic telemetry, Barry and colleagues (Barry *et al*., 2020) analysed fish migrating from Castletown River and the River Boyne, both of which discharge into the west of the Irish Sea (on the east of Ireland). They found three Atlantic salmon smolts tagged in these tributaries were detected in the north Irish Sea, suggesting a northern trajectory after leaving the river mouth, taking them towards the North Channel, giving them access to the North Atlantic. Of these, one fish was detected on one of only two marine receivers, 250km to the north, approximately 30 days after leaving its natal river. This finding provided the first evidence of a northerly marine migration trajectory for Atlantic salmon migrating into the Irish Sea. However, because there was no southern marine receiver array, it was not possible to completely exclude the possibility of some southern migration occurring (Barry *et al*., 2020).

Here we provide a Telemetry Case Report on sea migrating Atlantic salmon from a river in north-west England discharging into the eastern Irish Sea. We show that Atlantic salmon smolts once entering the Irish Sea took a northern pathway suggesting a northern trajectory towards the North Channel, giving them access to the more open North Atlantic. We extend the maximum distance that a post-smolt Atlantic salmon has been tracked in acoustic studies in Europe to date. This study also demonstrates the need for both collaboration and data sharing between telemetry projects with alternative funding sources and project aims and for cross project detection compatibility to obtain maximum benefit from highly expensive, logistically demanding marine telemetry studies.

## 5.2 Methods

The River Derwent, Cumbria, North-West England, (catchment: 679km$^2$) supports a population of wild Atlantic salmon. As part of a multi-partner project, led by the University of Glasgow, 100 Atlantic salmon smolts were captured in May 2020 by rotary screw trap and fyke net in St Johns Beck, Threkheld (54°36'38.1"N 3°03'42.1"W), a tributary in the River Derwent which flows through Bassenthwaite Lake, before draining west into the outer Solway Firth at the Port of Workington (54°38'58.2"N 3°34'07.9"W) 50km from the trapping site. The smolts were tagged at the capture location under licence (UK Home Office PIL 70/8794) with V7-2L (69kHz) coded acoustic transmitters (VEMCO Ltd, 7mm diameter, 1.7g in air, average transmission delay of 45 seconds) and released during daylight hours. Acoustic receivers (VR2W and VR2Txs (VEMCO Ltd)) were deployed throughout the Derwent system (*n=29*) from the tagging site to where the river discharges to the open sea (see Figure 5.1). Two marine arrays were deployed. One, part of the Collaborative Oceanography and Monitoring for Protected Areas and Species (COMPASS) project, in the Irish Sea, comprised 22 VEMCO VR2ARs receivers, deployed as a curtain over 24km from Northern Ireland (54°53'18.6"N 5°39'24.1"W) to Scotland (54°58'12.0"N 5°18'54.2"W). The other, deployed by a different project, the SeaMonitor project, comprised of six VEMCO VR2ARs, deployed as a curtain over a distance of 2km from 55°20'25.0"N 6°34'06.1"W to 55°20'56.9"N 6°32'42.8"W (see Figure 5.2).

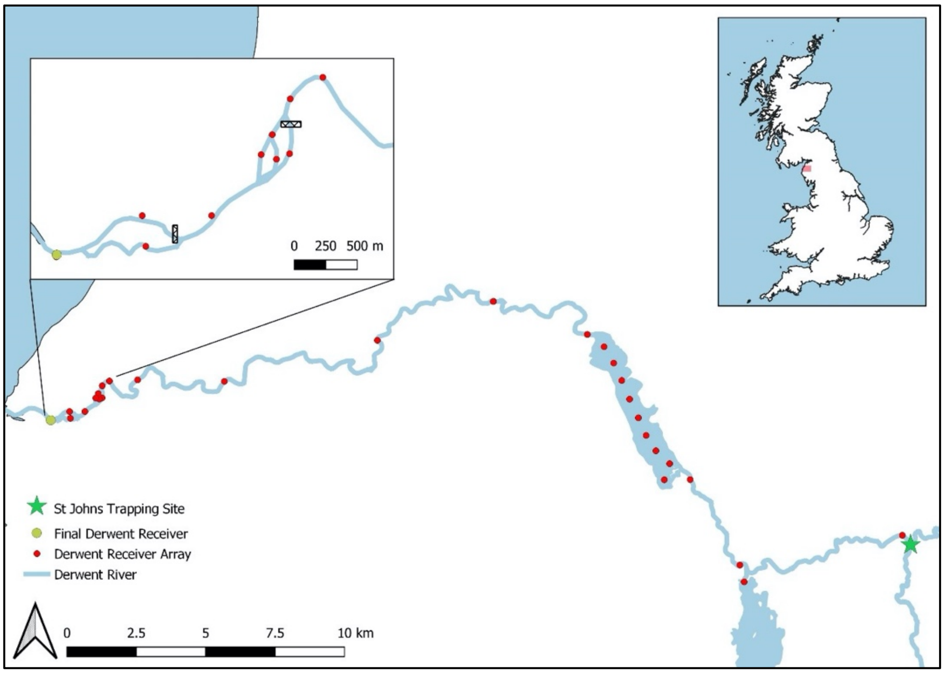



***Figure 5.1*** *Map showing the River Derwent Tracking Project receiver locations and the trapping and tagging site at St Johns Beck.*

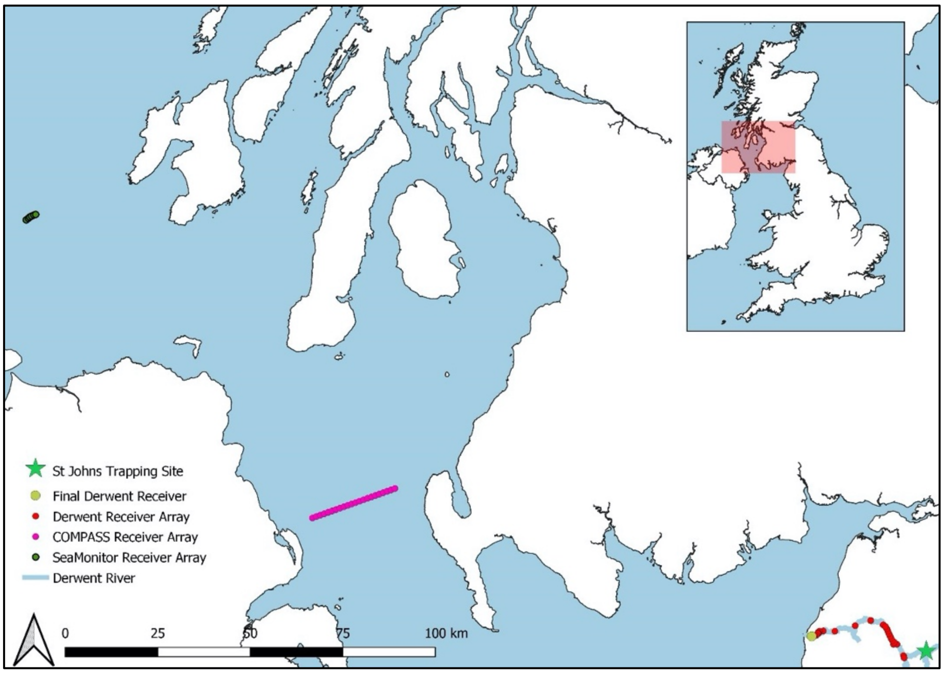


***Figure 5.2*** *The two marine curtain receiver arrays from the two distinct projects (COMPASS and SeaMonitor) alongside the smolt tagging site and Derwent system, Cumbria.*

## 5.3 Results

In total, 100 Atlantic salmon smolts were captured using in the upper reaches of the River Derwent, northwest England. The mean (± SD) fork length ($L_F$, mm) and mass (g) of tagged salmon smolts was 139.36 ± 0.65mm and 27.89 ± 0.42g (range: 157-130mm, 21.4–41.4g) respectively. The mean (± SD) tag burden (%) was 5.1% ± 0.07% (range: 3.5%-6.7%). Eight smolts (8% of those tagged) were detected at the last River Derwent receiver at the river mouth before Workington port (see Figure 5.2), equating to a river loss rate of 1.84%.km$^{-1}$. The mean migration speed of the eight successful migrants from the release site to the final receiver before sea entry was 0.4km.day$^{-1}$. The eight successful fish had a mean (± SD) $L_F$ and mass of 141.38 ± 5.10mm and 28.84 ± 3.11g compared to the unsuccessful salmon smolts (*n=92*) 139 ± 6.33mm and 27.48 ± 4.11g, respectively.

37.5% (*n=3*) of the salmon smolts that entered the marine environment were detected on receivers deployed across the Irish Sea. Two smolts (34946 and 34988) were detected on the COMPASS array and another smolt (34920) was detected on the SeaMonitor array. Unfortunately, the distances between receivers (ca.1km) exceed the presumptive detection ranges (ca.0.4km) (Newton *et al*., 2021) for both marine arrays, therefore it is plausible that more smolts may have passed both arrays undetected.

Tag 34946 was last detected entering Workington harbour from the river on 18th May 2020 at 16:34pm (UTC) and subsequently detected at both marine arrays. After approximately six days at sea, travelling a distance of approximately 138km, this fish was detected on the COMPASS array (54°57'16.2"N 5°22'48.5"W) on 31st May 2020 at 1:38am. This equates to a movement speed of 23 km.day$^{-1}$ or 1.72 body lengths per second (BL.s$^{-1}$). Seven detections were made of this fish at this site, providing confidence that this was not a false detection. This fish left this receiver location on 31st May 2020 at 1:46am and travelled in a westerly direction to be redetected again on the COMPASS array (54°56'34.5"N 5°25'44.2"W) on 31st May 2020 at 4:29am, after travelling a further 3.37km at 2.41BL.s$^{-1}$ (29.77 km.day$^{-1}$). There was only one detection on this receiver at this site (Figure 5.3, Table 5.1). Tag 34988 was last detected at Workington on 24th May 2020 at 15:58pm. After approximately nine days at sea, travelling a minimum distance of 137.8km, this smolt was detected on the COMPASS array (54°56'20.4"N 5°26'42.8"W) on the 3rd June 2020 at 12:49pm, having travelled at a speed of 15.3 km.day$^{-1}$ or 1.08BL.s$^{-1}$. Tag 34988 was detected six times on this receiver (Figure 5.4, Table 5.1).

Tag 34920 was last detected entering the marine environment on the 18th May 2020 at 16:34pm. Taking ten days to travel at sea, this smolt covered a distance of 262km (26.2 km.day$^{-1}$) at a speed of 1.97BL.s$^{-1}$. This smolt was the only smolt from the River Derwent tracking project to be detected only on the SeaMonitor array (55°34'02.1"N

6°56'50.5"W). This smolt must have passed the area of the COMPASS array without being detected. This fish was detected twice on the SeaMonitor array (Figure 5.5, Table 5.1).

***Table 5.1*** *2020 Tagged Atlantic salmon smolt characteristics and migration speed metrics for individuals detected at the COMPASS and SeaMonitor marine receivers.*

| **Smolt Tag Number** | **Date Tagged** | $L_F$ **(mm)** | **W (g)** | **Tag Burden (%)** | **Estimated distance travelled before marine detection (km)** | **Migration Speed** | | | | **Array Detection** |
|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | | Km.day$^{-1}$ | m.s$^{-1}$ | BL.s$^{-1}$ | Days at sea | |
| **34920** | 2020-05-01 | 146 | 31.4 | 4.5 | 261.88 | 26.2 | 0.2876 | 1.9701 | 10 | SeaMonitor |
| **34946** | 2020-05-02 | 143 | 30.7 | 4.6 | 138.01 | 23 | 0.2457 | 1.7184 | 6 | COMPASS |
| **34988** | 2020-05-03 | 149 | 32.3 | 4.3 | 137.75 | 15.3 | 0.1616 | 1.0843 | 9 | COMPASS |

The overall net movement of all three River Derwent salmon smolts was northwards as registered in the marine receiver arrays. Thus, fish effectively must have taken an initially westly trajectory towards the Irish coast once they left the riverine environment, followed by a northerly trajectory towards the North Channel (Figure 5.3 to 5.5, Table 5.1). Without a southern receiver array, we cannot completely exclude the possibility of southern migration occurring initially for these fish or others that were not detected.

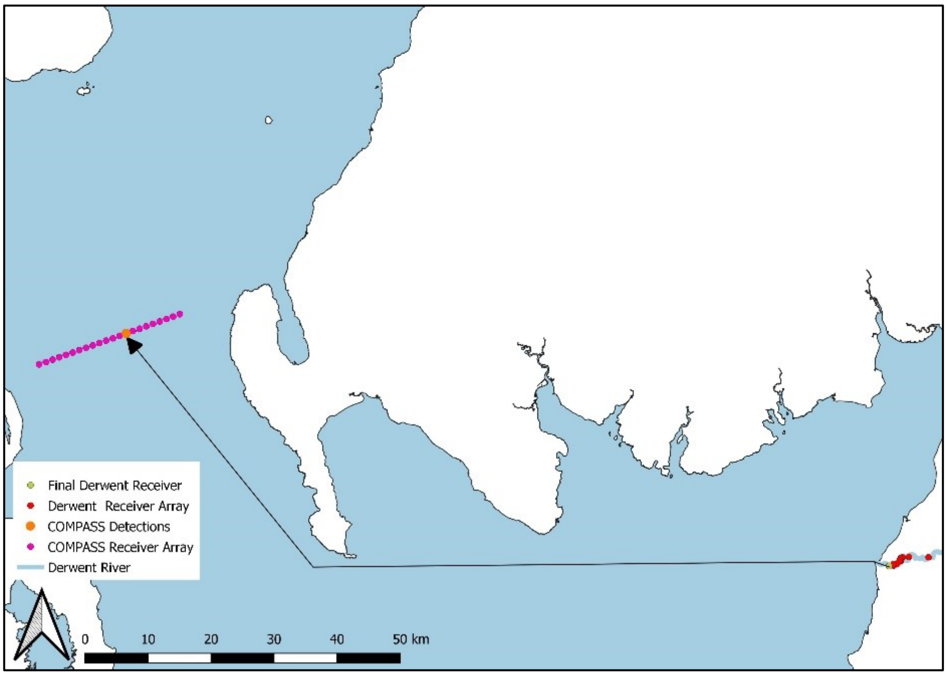



***Figure 5.3*** *Minimum theoretical distance travelled by fish (ID:34946), successfully migrating from the River Derwent's last river receiver to the COMPASS array in the Irish Sea.*

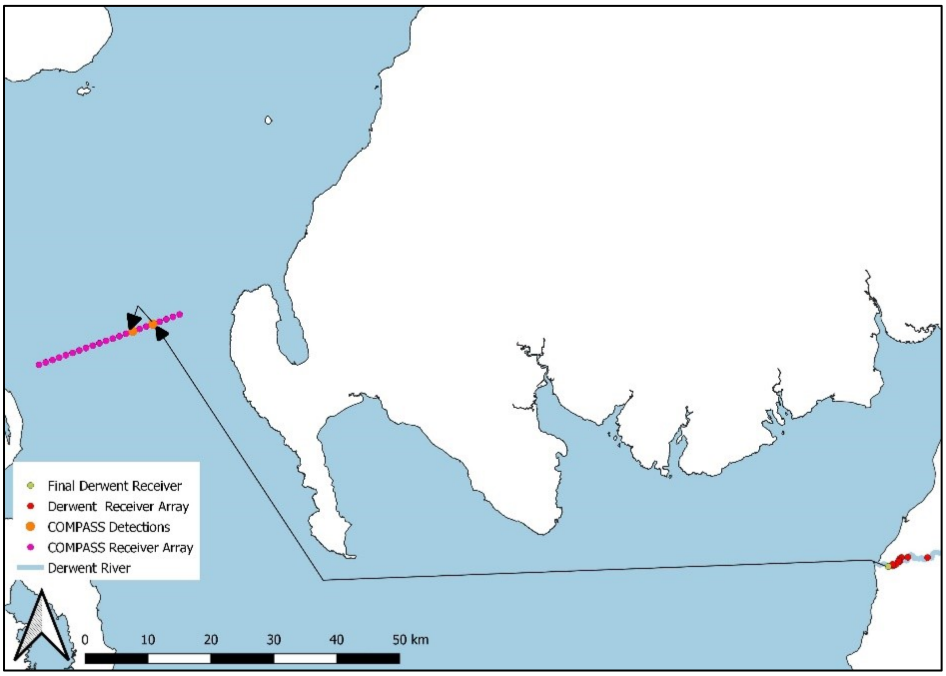



***Figure 5.4*** *Minimum theoretical distance travelled by fish (ID:34988), successfully migrating from the River Derwent's last river receiver to the COMPASS array in the Irish Sea.*

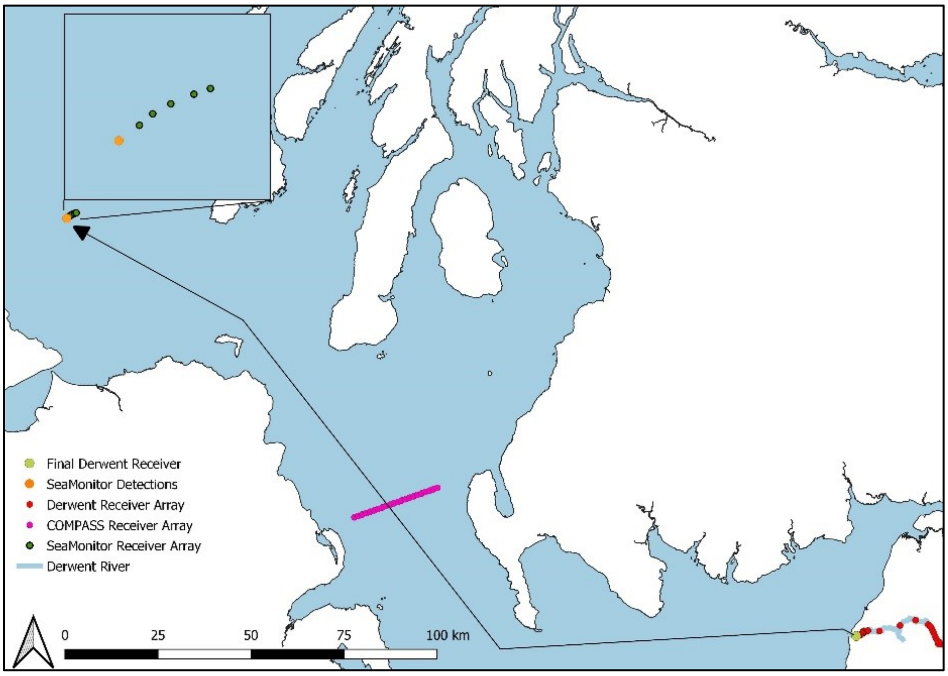



***Figure 5.5*** *Minimum theoretical distance travelled by fish (ID:34920), successfully migrating from the River Derwent's last river receiver to the sites of marine detection on both the COMPASS and SeaMonitor arrays in the Irish Sea.*

## 5.4 Discussion

The results presented here provide consistent evidence of northerly movements by smolts after entering the marine environment of the Irish Sea. Despite a small sample size, the three individuals detected had relatively similar migration speeds over varying distances. The average speed recorded for all three salmon smolts (0.23m.s$^{-1}$ or 21.5km.day$^{-1}$) is similar to the findings of Chaput *et al*. (2019) of 17–22km.day$^{-1}$ during Atlantic salmon smolt migration in the Gulf of St Lawrence (North America). However, the travel speeds found in the study reported here are considerably higher than those reported in the Barry *et al*. (2020) study, which indicated migration speeds of ca.7km.day$^{-1}$. In their study, Barry *et al*. (2020) tagged smolts in two rivers in Ireland, Castletown River (54°01'36.8"N 6°25'07.8"W) and the River Boyne (53°35'02.8"N 6°41'55.4"W), which is at the same latitude as the River Derwent. The three river systems which all flow into the Irish Sea, are separated by a channel of ca.200km, although the channel narrows to ca.35km further north creating a substantially narrower route for migration to the north. Due to a gradually narrowing channel, individuals are more likely to migrate through similar marine habitats and theoretically should experience similar environmental conditions. One explanation for the difference in the travel speeds noted above, is that migration progression rates are influenced by a combination of regional environmental differences and population specific features.

The Irish Sea is a semi-enclosed body of water characterised by concurrent action tides entering from both the north and the south (Dabrowski *et al*., 2010; Gaffney, 2001), creating semi-diurnal tides with areas of both high and low energy mixing (Howarth, 2015). However, intra-annual variability has been found there and it is known that current direction can change under specific environmental conditions such as wind, causing a greater southerly water flow (Barry *et al*., 2020; Dabrowski *et al*., 2010). SALSEA-Merge (2012) showed that post-smolt salmon use such currents during migration in marine environments and based on captures of smolts in northern Scotland, concluded that post-smolts moved northwards along with the shelf edge currents (Shelton *et al*., 1997). Previous modelling by Mork *et al*. (2012) indicated that the empirical data from the study by SALSEA-Merge (2012) is to be consistent with fish following water currents and actively swimming in the direction of those currents. Dabrowski *et al*. (2010) analysed seasonal circulation and flushing of the Irish Sea and found that net flow through the Irish Sea varied significantly throughout the year, but that annually average flow (2.50km$^3$/d) was northward, though southward flows were possible under certain meteorological conditions. The results of the study presented here and those of Barry *et al*. (2020) imply that migrating post-smolts may well be navigating with the predominant current in this area, however, these movements may well be considerably more complex and much more detailed study is required. In contrast however, Newton *et al*. (2021) used particle tracking to show that post-smolt Atlantic salmon were actively migrating in a direction that was not following the prevailing currents. The importance of using marine currents by migrating post-smolt Atlantic salmon thus requires further investigation.

Alternative possibilities for migratory pathway choice in post-smolts in marine environments could include that: i) post-smolts disperse in random directions once the open coast is reached; ii) post-smolts take the most direct migratory pathway to reach their feeding grounds in the northern hemisphere; and iii) post-smolts use coastlines as geographical markers during their migration to their northerly destination. None of the three alternative scenarios here can be resolved from the study presented here without marine current data, a higher receiver density of detections from more receivers located throughout the Irish Sea. For example, marine array in the southern Irish Sea would also be required to test if some fish exhibit a southerly migration trajectory or that there is random direction dispersal removing all assumptions that only a northern migration trajectory is chosen. Additionally, greater receiver density along the coastline and on existing marine arrays would be required to analyse if post-smolts are using coastlines as geographic markers for initial marine migration. This would provide increased detection efficiency and lead to greater accurate analysis and future understanding of post-smolt migrating behaviour.

Receiver detections not only provide timestamps for individual migration trajectories but may also indicate if predation of a tagged fish has occurred. Based on the detections in this study we have presumed that all River Derwent fish detected on the marine receivers were post-smolt Atlantic salmon and not a tag retained by a predator. Although this scenario cannot be completely ruled out, the assumption that detections are those of live post-smolts is supported by the similarity of the swimming speeds of detected smolts in this study, compared to other similar studies of Barry *et al*. (2020) and Chaput *et al*. (2019).

Currently literature on the coastal migration pathways of Atlantic salmon smolts is considerably limited. What information does exist particularly that from telemetry technology, is important to inform management strategy (Barry *et al*., 2020; Ounsley *et al*., 2020; Ohashi & Sheng, 2018) and could be used in conjunction with behavioural studies on current use and environmental pressures. Thus, this information can contribute to assessing overlap with potential threats, such as pelagic fisheries, and inform modelling, which can in turn predict future migration routes of a population during this important life stage. The findings from this study have also provided, along with the results from Barry *et al*. (2020), insight into future receiver array placements within the region, enabling future research on smolt migration pathways within the Irish Sea.

## 5.5 Conclusion

This paper provides the first empirical evidence that west coast England Atlantic salmon smolts, adapting to the new marine environment, utilise the broad existing hydrodynamic conditions and display a northern migration trajectory in the Irish Sea, up to 262km away from their natal river. Future work into understanding Irish Sea migration salmon pathways will require tracking a greater number of successful migrating individuals from rivers in both the east and west of the Irish Sea and a southern marine array is required to test for the potential of southern migration routes.

Gathering the results of this study has only been possible through cross jurisdictional and between research group collaboration. Meaningful and successful long distance migration telemetry studies are only possible when such collaborations are in place. The results of this study only emerged through the collaboration of three distinct jurisdictions and three separate research programmes: The Environment Agency/Natural England/University of Glasgow's River Derwent Tracking Project and the EU INTERREG Va funded COMPASS and SeaMonitor projects. Data sharing between projects has allowed a much greater insight into the northern migration of Atlantic salmon smolts through the Irish Sea from a river on the west coast of England. Further collaboration by the research community in this field is required to ensure marine migration trajectories are explored further.

# *Chapter 6:* Temporal variation in successful seaward migration of Atlantic salmon, *Salmo salar*, post-smolts from a UK tributary

**Data from this study is included (in part) in Lilly et al. (2023) Journal of Fish Biology 101(1) 265-283*


**Abstract**

Combining data from five transboundary acoustic telemetry studies to assess the temporal variation in the marine migration trajectories of River Derwent Atlantic salmon smolts (*Salmo salar,* Linnaeus 1758) through the Irish Sea. Data was collected from five organisations: 1) SeaMonitor; 2) COMPASS; 3) Atlantic Salmon Trust; 4) Marine Scotland; and 5) University of Glasgow from 2020 to 2022. This study has assisted in providing further evidence of west coast England Atlantic salmon post-smolts marine migration trajectories during the early marine phase of migration, displaying a northern trajectory through the Solway Firth and Irish Sea.



*Key Words: Post-smolt, Marine, Distance, Migration, Mortality*

## 6.1 Introduction

Migration is a common strategy in both aquatic and terrestrial species life cycles (Baker, 1978; Adams *et al*., 2022a; Limburg & Waldman, 2009; Lothian *et al*., 2018; Alerstam *et al*., 2003; Roff, 1988). The costs and benefits of migration strategies differ between species, but the benefits to migrating fish can include increased opportunities for foraging, leading to increased growth rate and improved likelihood of higher fecundity, (Hendry *et al*., 2004; Dingle & Drake, 2007; Lilly *et al*., 2022) which in turn may increase individual fitness. Migration is only maintained when the benefits are greater than the costs (Cresswell *et al*., 2011; Mangel & Satterhwaite, 2008; Adams *et al*., 2022a,b). These costs include increased energy expenditure, risk to novel diseases, parasites and anthropogenic pressures (Altizer *et al*., 2011; Holm *et al*., 2006; Shephard & Gargan, 2021; Crozier *et al*., 2004; Delgado & Ruzzante, 2020; Zydlewski *et al*., 2005).

Knowledge of the migration ecology of diadromous fish which migrate between marine and freshwater habitats remains incomplete (Gilbey *et al*., 2021). Evidence from the literature remains limited regarding the early marine migration phase of Atlantic salmon (*Salmo salar,* Linnaeus 1758). Anadromous Atlantic salmon face extreme challenges on their first migration from riverine systems to the vast marine environment and this migration is commonly thought to be characterised by increased mortality (Harvey *et al*., 2020). Migration from freshwater systems to marine habitats is a crucial life cycle phase and is seen as a strategy with adaptive value (Thorstad *et al*., 2008) allowing individuals to maximise fitness by exploiting a range of habitats (Lucas & Baras, 2001; Quinn & Myers, 2004; Harvey *et al*., 2020). Atlantic salmon undergo a series of behavioural, morphological, and physiological changes (Metcalfe *et al*., 1989; Crozier *et al*., 2004; Thorstad *et al*., 2012b; Delgado & Ruzzante, 2020;

Zydlewski *et al*., 2005) in a process called smolting, which pre-adapts individuals for high salinity environments, long distance migration, altered dietary requirements and novel predation pressures during their marine migration (Jonsson *et al*., 1991; Harvey *et al*., 2020).

The limited studies on Atlantic salmon post-smolt (the life stage on first migration to seawater) migration to-date, and trawling surveys conducted in north of Ireland indicate that fish emanating from southern tributaries in UK utilise currents along north European continental shelf (Ounsley *et al*., 2020; Shelton *et al*., 1997; Holst *et al*., 2000; SALSEA-Merge, 2012) to migrate north to the Norwegian Sea and/or to seas off West Greenland in the North-West Atlantic, to forage at marine feeding grounds (Klemetsen *et al*., 2003; Holm *et al*., 2000; Jacobsen *et al*., 2012; Mork *et al*., 2012; Ounsley *et al*., 2020; Dunbar & Thomson, 1979). Current knowledge of the early phase of post-smolt migration patterns throughout the northern hemisphere comes predominately from three separate approaches: i) capture at sea through targeted or opportunistic catches in commercial fishing or targeted trawling surveys (Ahlbeck-Bergendahl *et al*., 2019; Thorstad *et al*., 2012a; SALSEA-Merge, 2012; Green *et al*., 2022); ii) telemetry studies tracking fish through both freshwater and marine migration phases (Barry *et al*., 2020; Went, 1973; Klimley *et al*., 2013; Lothian *et al*., 2018; Chaput *et al*., 2019); and iii) hydrodynamic particle tracking modelling (Ounsley *et al*., 2020).

Telemetry when used to track migration in Atlantic salmon in marine environments is most commonly conducted using acoustic tracking technology. The most popular study approach uses the application of fixed position, continuous monitoring acoustic receivers and implanted acoustic transmitters to investigate migration (Green *et al*., 2022; Crossin *et al*., 2017; Heupel *et al*., 2010; Rowell *et al*., 2015). Such approaches can provide detailed spatial information and allow researchers to investigate potential environmental predictors of migration pathway choice and identify mortality sources during migration. Studies on the navigational cues used by Atlantic salmon post-smolts have shown that downstream migration behaviour is initiated by temperature, river water discharge and photoperiod (Riley *et al*., 2012; Gilbey *et al*., 2021; Lacroix *et al*., 2004a; Thorstad *et al*., 2012b). Despite this, our understanding of the cues used to determine offshore marine migration pathways, migration success or pathway choice is limited. Green *et al*. (2022) hypothesised that for fish migrating through the Irish Sea, the difference between successful and unsuccessful marine migrating individuals may be the result of regional environmental conditions and population specific features. This hypothesis was supported by evidence gathered by SALSEA-Merge (2012) and Shelton *et al*. (1997) suggesting that Atlantic salmon post-smolts migrating from the Irish Sea area took a northern trajectory using continental shelf edge currents to aid migration. Additionally, Mork *et al*. (2012) used modelling to suggest that post-smolts use water currents and passively swim with the prevailing current. Dabrowski *et al*. (2010) further indicated that, although there is variation in the Irish Sea currents, the predominant direction is northward, providing further indication that post-smolts migrate with the direction of the prevailing current. However, though acoustic telemetry has aided in providing answers regarding early marine trajectories of Atlantic salmon smolts, there are various draw backs to using this technological approach such as altering environment factors (i.e., currents, ambient noise) and unknown anthropogenic pressures and their influences on chosen migration pathways.

Additionally, Genetic approaches are a viable avenue to gain insights into the early marine trajectories of Atlantic salmon smolts. A significant portion of our knowledge, derived from published literature, originates from studies utilizing a capture-mark-recapture technique at sea. These investigations, employing genetic markers, enable the tracing of post-smolts back to their natal rivers (Harvey *et al*., 2019; Gilbey *et al*., 2021). While offering extensive spatial coverage, these studies are observational in nature, providing only a singular data point upon capture and lacking definitive information on pre-capture migration routes or speeds.

In this study, I used acoustic telemetry to investigate the migration pathways of Atlantic salmon post-smolts from the River Derwent over three separate years through the Irish sea. This study was only made possible through collaboration with five external organisations. There were three main objectives to: 1) Investigate the temporal variation in the choice of migration trajectory once fish reached the marine environment; 2) Compare the rate of movement between freshwater and marine habitats during the early migration phase; and 3) Compare the migration success of Atlantic salmon smolts in riverine systems with post-smolts in marine environments.

I tested five specific hypotheses related to early marine migration: i) There is no temporal variation in the characteristics of marine migration (migration pathways, duration of success rate) over three years; ii) Migration success rate is lower in the marine compared to riverine environment; iii) Larger individuals are more successful migrants in the marine environment; iv) Smolts travelling a shorter distance in the riverine environment will have higher migration success through the Irish Sea; and v) Smolts entering the marine environment early have higher migration success.

## 6.2 Methodology

### 6.2.1 Description of study site

The River Derwent in Cumbria, Northwest England has a total catchment area of 679km$^2$ and supports wild Atlantic salmon spawning and juvenile nursery areas. St Johns Beck is a tributary of the River Greta run west through the town of Keswick before intercepting the drainage water of Derwentwater Lake at which point becomes the River Derwent (54°36’07.1”N 3°09’10.1”W). The River Derwent flows north through Bassenthwaite Lake, which extends 7.15km in length, before flow further west through Cockermouth and Workington where the River Derwent drains into the Solway Firth (54°38’58.2”N 3°34’07.9”W) (Figure 6.1). The main stem riverine section is ca.50km in length.

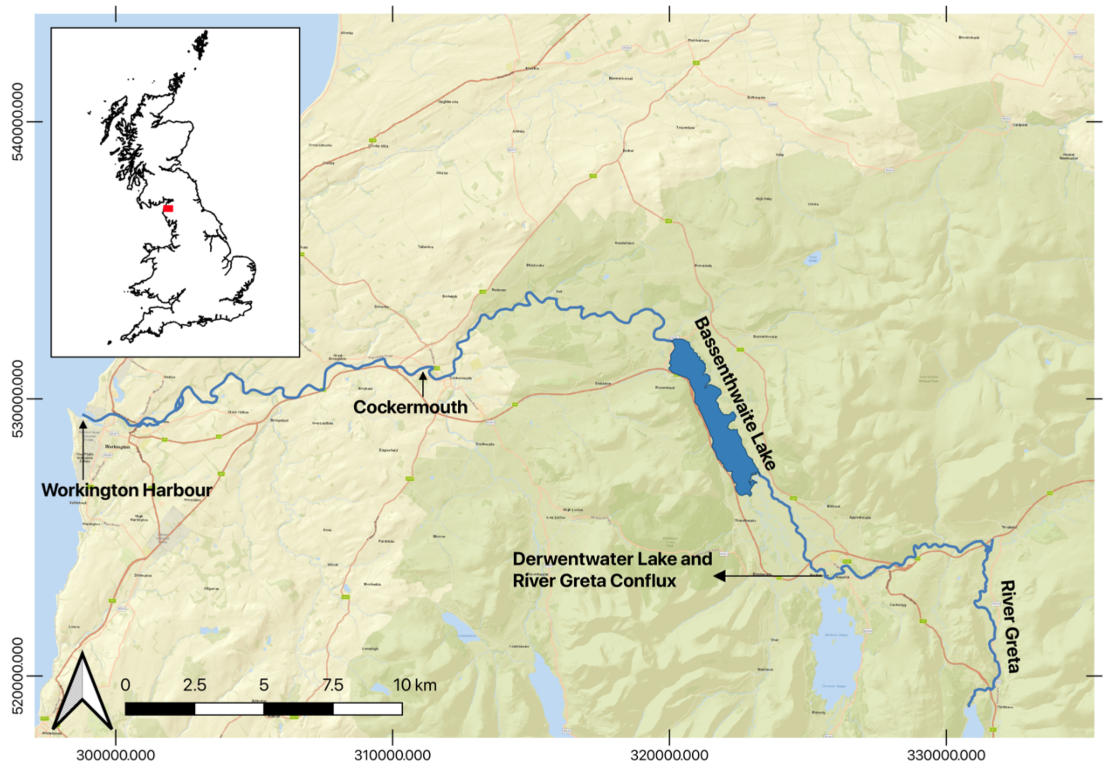



***Figure 6.1*** *River Derwent Catchment*

#### 6.2.2 Acoustic receiver deployment

##### 6.2.2.1 Riverine deployment

Fixed position acoustic receivers (69kHz; VR2W and VR2Txs (Innovasea Ltd., Nova Scotia, Canada)) were deployed throughout the River Derwent system in each of the three years between March 3rd and March 5th 2020 (*n=27*) (Figure 6.2), March 21st and 23rd 2021 (*n=44*) (Figure 6.3) and April 7th to 8th 2022 (*n=24*) (Figure 6.4). The VR2W receivers include a hydrophone and ID logger, whilst VR2Tx receivers allow for temperature to be registered at predetermined time intervals according to user settings. Receivers were attached to a mooring comprising a vertical steel rod welded on to a 20-40kg steel weight. All river receivers were attached by chain to the bank margins wherever suitable. In 2020 receivers in Bassenthwaite Lake were attached to a subsurface buoy, anchored by ca.40kg steel weight which had an additional surface buoy attached to aid in recovery. In 2021, all Bassenthwaite Lake receivers were attached to a vertical steel rod welded to a 40kg steel weight with a surface buoy attached for recovery. No receivers were deployed in Bassenthwaite Lake in 2022.

##### 6.2.2.2 Marine deployment

Five organisations and research projects deployed separate marine arrays. Here a receiver array comprises a linear curtain of receivers through which passing tagged fish can be detected. During the period of the study presented here these were: 1) Collaborative Oceanography and Monitoring for Protected Areas and Species Project (COMPASS); 2) SeaMonitor; 3) Atlantic Salmon Trust; 4) Marine Scotland; and 5) University of Glasgow (Figure 6.3-6.4). Each organisation deployed marine acoustic receiver arrays between 2020 and 2022 with varying receiver densities. During 2020, the COMPASS project deployed a receiver array over ca.24km across the Irish sea from Northern Ireland (54°53'18.6"N 5°39'24.1"W) to Scotland (54°58'12.0"N

5°18'54.2"W) (Figure 6.2-6.3). This array was redeployed in 2021, however there was no deployment in 2022. The SeaMonitor project deployed an array in the north channel (where the Irish Sea meets the North Atlantic) between Malin Head and Islay (55°22'33.0"N 7°19'43.3"W to 55°40'22.9"N 6°30'12.1"W) (Figure 6.2-6.4). In 2020, only ca.3km of the planned array was deployed (a consequence of COVID regulations) but this was extended to 64.5km in 2021 and 2022. In a separate project, the University of Glasgow deployed marine arrays in 2021 and 2022 which covered ca.8.1km, in northwest Arran/Outer Clyde region. The Atlantic Salmon Trust (AST) deployed a number of receiver arrays in the sea around the Hebrides and through the Minch. Their total receiver coverage stretched ca.137km. Finally, Marine Scotland deployed a single receiver on a coastal buoy off the west coast of the outer Hebrides (58°05'30.5"N 8°54'48.4"W) (Figure 6.3).

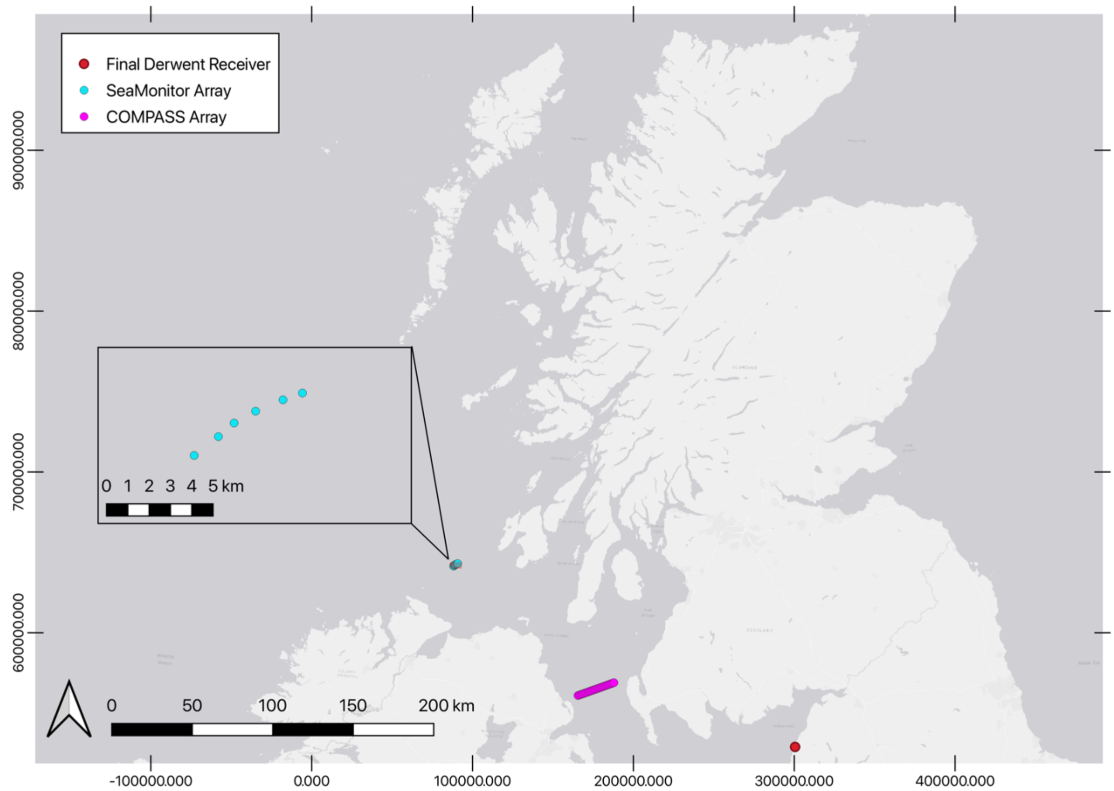



***Figure 6.2** Detailed map of marine receiver deployment of collaborating telemetry organisations during 2020.*

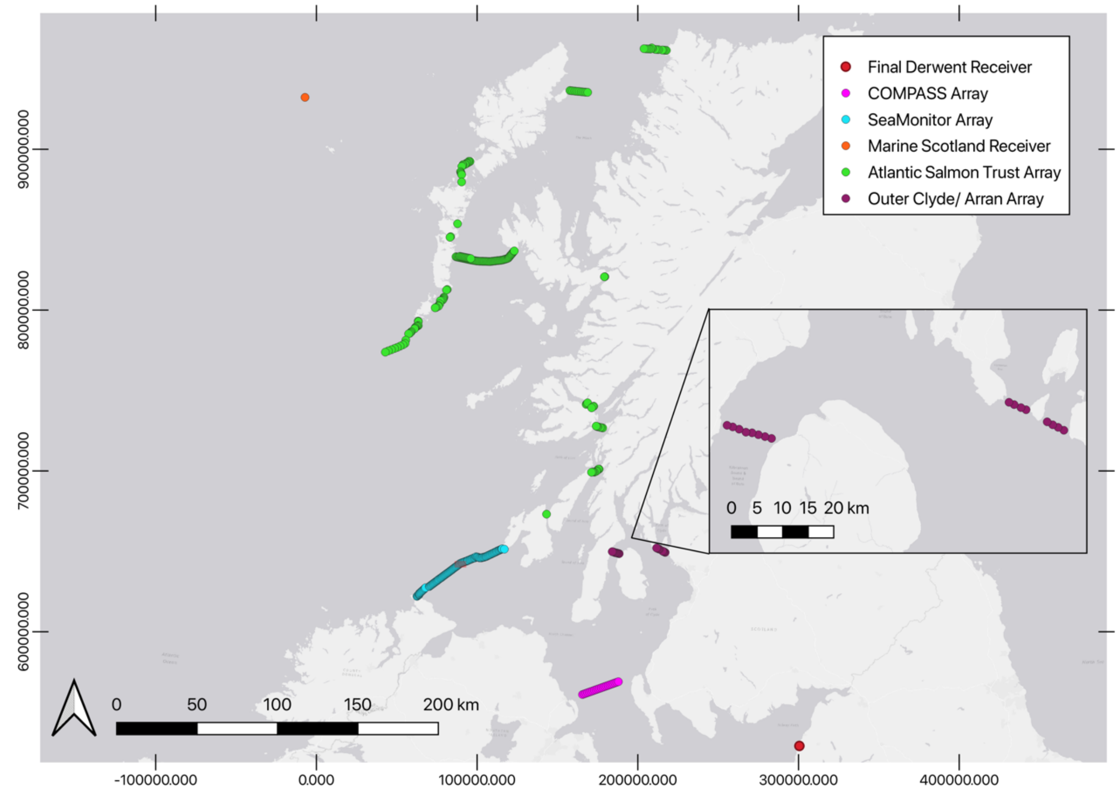



***Figure 6.3*** *Detailed map of marine receiver deployment of collaborating telemetry organisations during 2021.*

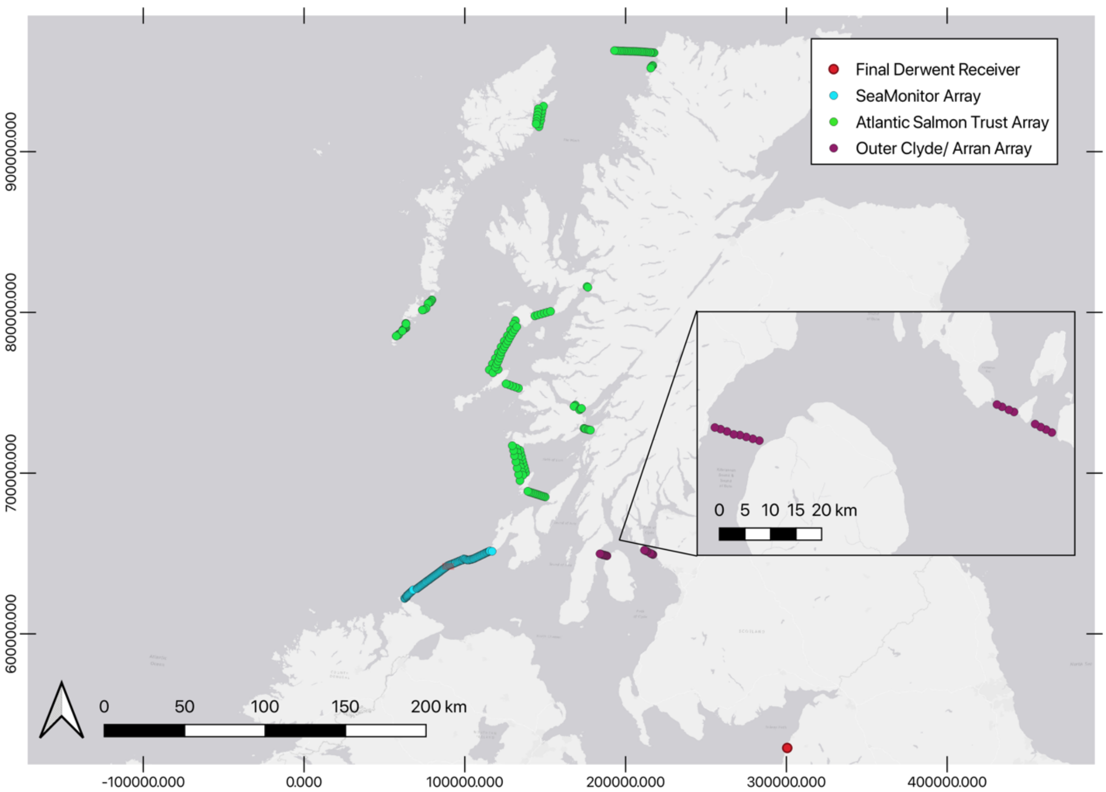



***Figure 6.4*** *Detailed map of marine receiver deployment of collaborating telemetry organisations during 2022.*

### 6.2.3 Smolt capture and acoustic tagging procedure

Atlantic salmon smolts migrating towards sea down the St John Beck were captured in a 1.2 m rotary screw trap between 1$^{st}$ and 5$^{th}$ May in 2020 (*n=100*), 14$^{th}$ April and 4$^{th}$ May in 2021 (*n=150*) and 5$^{th}$ May and 25$^{th}$ May in 2022 (*n=115*). In 2020 additional downstream fyke nets were deployed and subsequently additional netting side wings were added to the rotary screw trap in 2021 and 2022 to improve the capture of smolts at lower water levels. The trap was located ca.50km upstream from the discharge of the River Derwent into the Solway Firth at Workington harbour. The trap was checked and emptied daily to ensure that smolts did not remain in the trap for extended periods of time.

Fish captured were anaesthetized by immersing them in river water containing MS222 (Tricaine Methanesulfonate) and sodium bicarbonate solution (0.6g/6L river water). It took approximately three minutes for smolts to lose equilibrium (stage three of anaesthesia) which is required for the tagging procedure to be conducted. Fork length ($L_F$, mm) and weight (g) were recorded before those sufficiently large enough for tagging (>130mm/>20g) were placed onto a damp surgical sponge and scale samples were taken. All surgical equipment was disinfected using Reprodis/distilled water (1:20 ratio) and rinsed with distilled water. Fish were given low level anaesthesia (0.125g/2L) and river water was constantly applied across the gills to ensure fish remained sedated. A 10mm ventral incision was made anterior to the pelvic girdle. A V7-2L (69kHz) coded transmitter (VEMCO Ltd, 7mm diameter, 1.7g in air) was surgically placed inside the peritoneal cavity. The V7-2L tags had a nominal delay of 18–45 seconds and an estimated tag life of ca.75 days. The incision was closed by applying two interrupted surgeon knots with 4/0 Ethilon nylon sutures. Smolts were then placed into a recovery container on land for approximately 20 minutes to ensure normal swimming behaviour was exhibited (equilibrium restored). Fish were then placed into a river perforated container downstream from the rotary screw trap with good water flow throughout and given a further 40 minutes recovery.

6.2.3.1 Release group

Throughout the three-year study, there were two different release sites/groups. Fish were either released at the trapping site or at a site further downstream. This was to ensure that a large enough sample size of fish reached the lower catchment of the River Derwent and to increase the probability of ultimate river migration success, and thus a Trap and Transport experiment took place in 2021 and 2022.

In 2020 100% of tagged smolts were released immediately downstream of the trap at St Johns Beck. In 2021, 62% (*n=93*) of tagged individuals were released at St Johns Beck, the remaining 38% (*n=57*) were transported to be released in the river downstream of Bassenthwaite Lake. In 2022 100% of fish captured and tagged at St Johns Beck were transported downstream of Bassenthwaite Lake. All fish released at St Johns Beck are subsequently referred to as the St Johns Beck release group (SJB), smolts transported downstream of Bassenthwaite Lake are to be referred to as Trap and Transported release group (TT).

After 40+ minutes of recovery in St Johns Beck, all transported fish in 2021 (*n=57*) were placed into a large transport box with continuous aeration. In 2022, transported fish (*n=115*) were placed in large bags which were filled with oxygen and sealed before transportation. In both years smolts were transported ca.25km from St Johns Beck to a release site downstream of Bassenthwaite Lake (54°41'14.7"N 3°17'52.3"W). The journey took an average of 25 minutes. Smolts were transported in minimum groups of five to minimise predation risk once released. Fish were transported over six days in 2021 and eight days in 2022. All fish were checked at the release site for any signs of stress or poor swimming ability. Fish were placed into an in-river recovery container and given 30 minutes in flowing water to recover before final release.

### 6.2.4 Ethical statement

To ensure the ethical policies were followed, tagging was conducted by a personal licence holder (UK Home Office PIL 70/8794) using procedures which complied with the UK Home Office regulations and UK Home Office project licence number PP0483054. Replacement, reduction, and refinement was considered for this study. All fish were cared for and monitored throughout the procedure where stress and suffering were reduced at all times.

### 6.2.5 Statistical analysis

#### 6.2.5.1 False detection filtering

Analysis was conducted using R software version *4.0.2* (R Core Team, 2019). In order to ensure all detections being analysed are real detections, filtering for false detections was conducted using the R package *Glatos* (Holbrook *et al*., 2018; Pincock, 2012) which filtered for a short-interval detection criterion. Short interval criterion filters all single detections that occurred at one receiver station within a duration which is greater than 30 times the average signal delay of the tag (i.e., 840s) (Hayden *et al*., 2016; Kneebone *et al*., 2014; Lilly *et al*., 2021, 2022). Those above this duration period were deemed false detections. Additionally, signals detected during a period which was less than the tag's minimum signal delay (18s) were deemed false (Hanssen *et al*., 2022).

#### 6.2.5.2 Descriptive analysis

Descriptive data from across the 3-year study period were derived from the R package *Actel* (Flávio & Baktoft, 2020, 2021). Flávio & Baktoft (2020, 2021) state that *Actel* provides a systematic conditional pipeline to filter and analyse acoustic telemetry data in a reproducible fashion, for fish moving between receiver arrays. It also allows for detection efficiency estimations to be made for each receiver station. Additionally, *Actel* allows diel movement patterns to be observed by defining the arrival time recorded at each individual receiver.

#### 6.2.5.3 Loss estimates

To assess loss rates during freshwater migration, survival likelihood throughout the various riverine sections throughout the downstream migration route was calculated in *Actel* (Flávio & Baktoft, 2020, 2021). Those individuals that were detected at the last riverine receiver were deemed to be successful river migrants. However, the detection efficiency of river acoustic receivers is not always 100% due to ambient noise, fast water currents increasing smolt speed and potential submerged barriers such as logs and therefore, efficiency must be assessed when providing estimates of survival (Halfyard *et al*., 2013; Lilly *et al*., 2022). Efficiency is assessed by the number of smolts detected at a downstream receiver as a proportion of those not detected at the receiver upstream. In the River Derwent, there are a number of alternative river channels and thus alternative routes that could have allowed for downstream migration were taken into consideration when detection efficiency was calculated.

#### 6.2.5.4 Non-residency events

To establish the number of individual movements undertaken by each fish between receiver stations throughout the River Derwent, non-residency events were calculated using the R package *VTrack* (Campbell *et al*., 2012) RunresidenceExtraction function. This function provides timestamps for each receiver and is used to determine the duration of riverine migration.

#### 6.2.5.5 Migration pathways

Post-smolt detections in the Irish Sea 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 post-smolt density and individual detection points across various marine arrays were added to the map using the *stat_density_2d* function in the R package *ggplot2* (Wickham, 2011).

#### 6.2.5.6 Migration success

Total marine migration success of River Derwent post-smolts through the Irish Sea was defined as the number of post-smolts which were detected on any one of five organisation's marine arrays (COMPASS, SeaMonitor, Atlantic Salmon Trust, Marine Scotland, University of Glasgow) as a proportion of all of the post-smolts that left the riverine environment (i.e., successful river migrants). Marine migration success rate ($\%.km^{-1}$) was calculated as the proportion of fish which were successful in reaching the SeaMonitor array, divided by the direct minimum sea distance travelled (ca.260km) to reach the array (Figure 6.2-6.4). The minimum travel distance to the SeaMonitor array (Figure 6.2-6.4) is based on the minimum straight-line distance from the final River Derwent receiver to the first detection on the SeaMonitor array. Only migration through the Irish Sea in a northern direction was assessed using this method. Marine migration success estimates take no account of the possibility that post-smolts may have made a southern migration trajectory. Smolts detected on the Outer Clyde/ Arran array and then SeaMonitor array were discounted for migration success analysis and only overall duration was calculated for those smolts.

#### 6.2.5.7 Migration speed and duration

Mean migration duration and migration speed were calculated separately for the riverine migration phase and the early marine migration phase. This was calculated using the finale timestamp of an individual at either the release site (riverine migration calculation) or the final River Derwent receiver (early marine migration calculation) before reaching their final migration points in either the riverine environment (final receiver) or the marine migration (SeaMonitor array). The SeaMonitor array (Figure 6.2-6.4) was used to determine the early marine migration metrics because of the consistent annual deployment between 2020-2022. Mean rate of movement (ROM ($m.s^{-1}$) in kilometres per day ($km.day^{-1}$) was calculated for riverine and early marine migration by dividing the direct minimum distance travelled by the total duration (days) to migrate to the final destination point.

### 6.2.6 Statistical modelling

#### 6.2.6.1 Survival model

Generalised linear modelling (GLM) was undertaken to determine if factors such as fish fork length ($L_F$, mm), release group type (St Johns Beck or Trap and Transported) or year contributed to successful marine migration to the SeaMonitor array. The GLM was fitted with a binomial error structure and identity link function using the R Package *lme4* (Bates *et al*., 2014). Survival (the dependent variable) was coded as 1 for post-smolts detected on a receiver at the SeaMonitor array, and thus assumed to be successful migrants or 0 for an assumed unsuccessful for post-smolts migration.

*Initial model:*

*glm (survival ~* $L_F$ *+ Year +Release Group, , family = binomial(link = "identity"))*

6.2.6.2 Marine migration duration model

In order to determine if marine migration duration (days) was influenced by factors such as $L_F$ (mm), release group type or year, a general linear model (GLM) was produced using the R package *lme4* (Bates *et al*., 2014). Only smolts which were detected on the SeaMonitor array were included in the analysis.

*Initial model:*

*glm (Duration~* $L_F$ *+ Year + Release Group)*

Significant factors highlighted by the GLM where further investigated for significant categorical factors. The R package *multcomp* (Hothorn *et al*., 2016) was used post ANOVA testing with a Post Hoc Tukey HSD Test in order to compare potential differences within categorical data e.g., year.

## 6.1 Results

### 6.3.1 Tagging summary

In total, 365 Atlantic salmon smolts were tagged between 2020-2022. Fork length ($L_F$, mm), weight (g) and tag burden (%) averages are summarised in Table 6.1.

***Table 6.1*** *Summary data for River Derwent tagged Atlantic salmon smolts between 2020-2022. Summary of $L_F$ (mm), weight (g) and tag burden (%) for each year and release group: SJB- St Johns Beck release group, TT-Trap and Transport release group. Tag burden is calculated by dividing the weight of the tag in air (1.7g) by the weight of the individual* 100.*

| Year | $L_F$ (mm) ± SD (range) | Weight (g) ± SD (range) | Tag Burden (%) ± SD (range) |
|---|---|---|---|
| **2020 (SJB)** | 139.4 ± 0.65 (130-157) | 27.89 ± 0.42 (21.4-41.4) | 5.1 ± 0.07 (3.5-6.7) |
| **2021 (SJB)** | 141.9 ± 8.4 (130-164) | 29.4 ± 5.5 (21.5-44.5) | 4.9 ± 0.61 (3.6-6.1) |
| **2021 (TT)** | 141.0 ± 7.7 (130-164) | 29.8 ± 5.1 (21.5-44.5) | 4.8 ± 0.55 (3.6-6.1) |
| **2022 (TT)** | 138.7 ± 6.6 (130-161) | 27.4 ± 4.1 (21.2-40.4) | 5.1 ± 0.5 (3.9-6.2) |

### 6.3.2 Marine pathways

In this study, post-smolts migrating from the Workington Harbour through the Solway Firth across a three-year temporal scale displayed similar passage position on monitoring lines throughout their migration through the Irish Sea. In 2020, 25% of smolts (*n=2*) were detected on the COMPASS array, ca.135km from the River Derwent mouth and 12.5% (*n=1*) detected on SeaMonitor array (ca.260km; the year with limited SeaMonitor array deployment). In 2020, post-smolts were detected on the COMPASS array in the centre of the north channel and were also found on the central portion of the SeaMonitor array (Figure 6.5$^{A}$). However, in 2021 when the full SeaMonitor array was deployed post-smolts were detected nearer the coastline of Scotland (Figure 6.5$^{B}$). In addition, 9% (*n=4*) of post-smolts were detected migrating in the Outer Clyde off the northwest of Arran, although one post-smolt was found to migrate out of the area to be later detected in the SeaMonitor array. Across the SeaMonitor array, post-smolts were found to cluster either near the coastline of Scotland or within the centre of the array at a similar position to the single detection in 2020. In 2022 post-smolts transition from the Irish Sea to the North Atlantic were not evenly distributed across the SeaMonitor Array as previously seen in previous years (Figure 6.5$^{C}$), with no post-smolts throughout the three-year study period being detected travelling through the Minch.

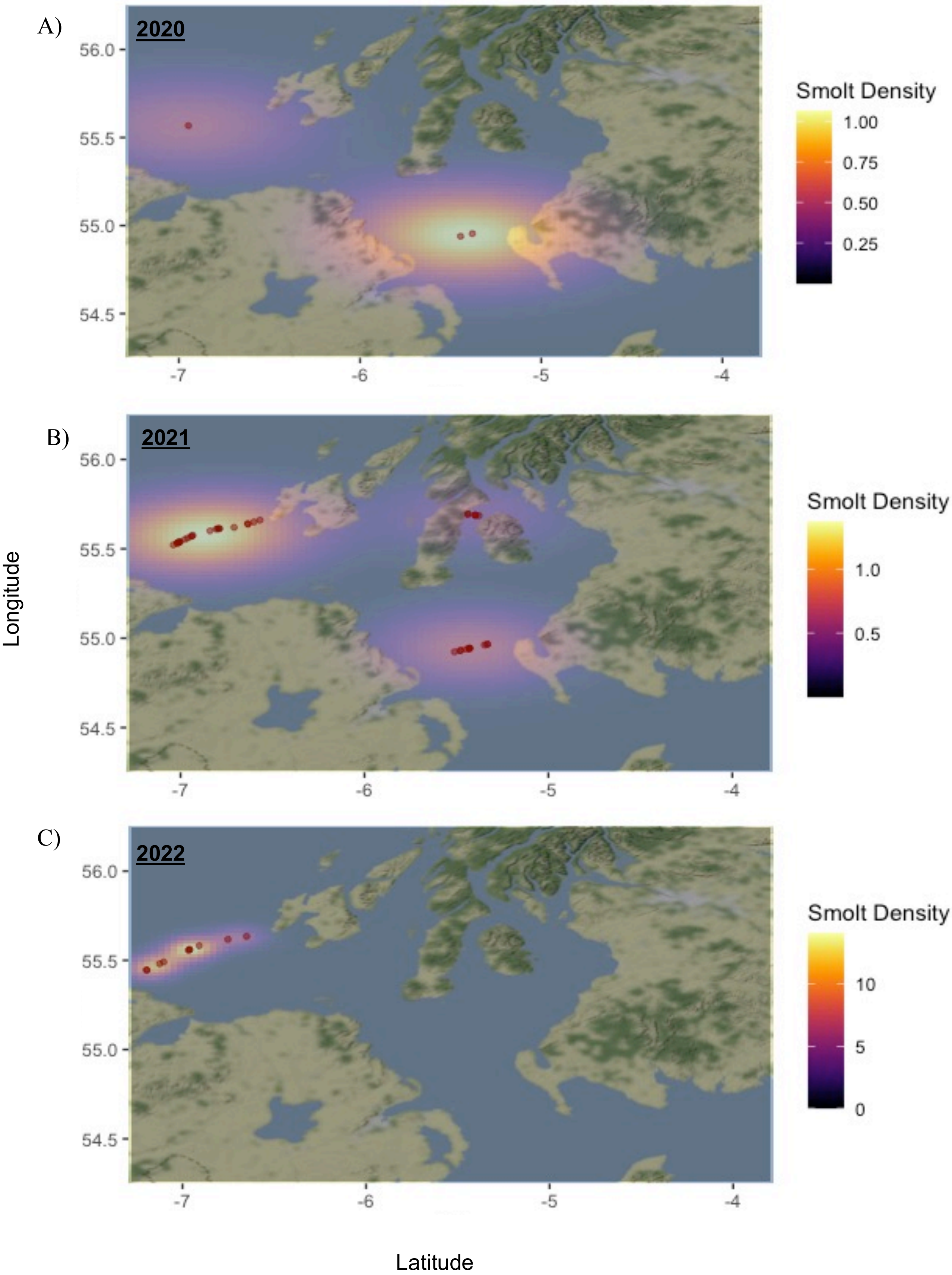



***Figure 6.5*** *Heatmaps displaying the density of River Derwent Atlantic salmon post-smolt at COMPASS, Arran/ Outer Clyde and SeaMonitor marine monitoring lines during the period of this study. A) in 2020; COMPASS n=2, SeaMonitor n=1. B) in 2021; Compass n=11, Outer Clyde/ Arran n=4, SeaMonitor n=12, Marine Scotland n=1. C) In 2022; SeaMonitor n=9.*

### 6.3.3 Migration success

Across the three-year study period, approximately 26.5% (*n=97*) of all River Derwent tagged post-smolts (*n=365*) were found to have entered the Solway Firth at Workington harbour. However, approximately only 6% (*n=22*) of all post-smolts tagged and released in the river were detected on the SeaMonitor array, having made a successful early marine migration over the ca.260km from the final River Derwent receiver to their first detection on the SeaMonitor array. In 2020 only 8% fish (*n=8*) were deemed successful within the riverine environment and 37.5% (*n=3*) of these were later detected marine arrays, two were detected on COMPASS and one post-smolt being detected on SeaMonitor. Thus, the migration success rate of post-smolts in 2020 was 0.77%.$km^{-1}$ within the marine environments studied here.

In 2021 River Derwent post-smolts were found to have greater riverine success with 28% (*n=40*) of post-smolts being deemed successful in the riverine environment (42.5% (*n=17*) St Johns Beck release group; 57.5% (*n=23*) Trap and Transported release group). Out of the *40* that entered the Solway Firth, 30% (*n=12*) individuals were later detected on the SeaMonitor array. The success rate of post-smolts in 2021 was 0.73%.$km^{-1}$. In 2022, 42% (*n=48*) of individuals, all Trap and Transport released fish were deemed successful within the riverine environment and were assumed to migrate into the Solway Firth. 18.7 % (*n=9*) of individuals were successfully detected on the SeaMonitor array, giving 2022 a migration success rate of 0.69%.$km^{-1}$.

Early marine migration success was not predicted by year of the study ($p$=0.87), $L_F$ ($p$=0.38) or the release group ($p$=0.36) of the post-smolts from the River Derwent.

6.3.4 Migration duration and speed

Median entry date into the marine environment and mean migration duration differed between years. The median entry (days) of post-smolts entry into the Solway Firth for 2020 was May 22$^{nd}$ ± 7.11 (± IQR; range: May 14$^{th}$- June 4$^{th}$), in 2021 it was May 5$^{th}$ ± 4.5 (± IQR; range: April 27$^{th}$-May 12$^{th}$) and in 2022 it was May 18$^{th}$ ± 9.48 (± IQR; range: May 10$^{th}$- June 9$^{th}$). In order to reach the SeaMonitor array from the final River Derwent Receiver, in 2020 a single post-smolt took ca.10 days to travel ca.260km (26.2km.day$^{-1}$) at a minimum speed of 1.97 body lengths per second (BL.s$^{-1}$) in the marine environment. However, in 2021 it took post-smolts on average 32.2 days ± 9.73 (± SD, range: 10.64-46.39) to travel the minimum early marine travel distance of ca.260km, giving an average speed of 9.37km.day$^{-1}$ (range: 5.6-24.4), with one post-smolt being later detected on the Marine Scotland receiver (ca.558km from the final Derwent river receiver) ca.16 days after entering the Solway Firth, giving a speed of 34.87km.day$^{-1}$. Although in 2022, post-smolts were found to have a faster average speed compared to 2021 of 17.97km.day$^{-1}$ (range: 9.95–17.9), taking post-smolts on average 19.33 days ± 11.78 (± SD, range: 7.18-45.84) to reach the SeaMonitor array.

Modelling (GLM) migration duration of successful smolts through the Solway Firth/Irish Sea showed that year was a significant variable ($p$=0.007). The Post Hoc Tukey HSD test compared the differences between the years, finding that in 2021 post-smolts were found to have a significantly longer marine migration duration ($q$=1.88, $\alpha$=0.01, $p$=0.005) compared to 2020 and 2022 to reach the SeaMonitor array. Additionally, duration in 2022 was significantly faster in comparison to 2021 ($q$=1.46, $\alpha$=0.05, $p$=0.04). $L_F$ was also found to be a significant determinant of migration duration in the Irish Sea ($p$=0.038). Larger post-smolts ($L_F$:140-153mm) taking longer (mean: 32.6 days ± 10.69km.day$^{-1}$) during marine migration in comparison with smaller ($L_F$: 130-139mm) post-smolts (average: 21.24 days ± 16.48km.day$^{-1}$). The release group of post-smolts (St Johns Beck or Trap and Transport) ($p$=0.14) did not significantly improve the model.

## 6.4 Discussion

Our understanding of early marine migration of post-smolts is still limited with regards to potential trajectories, speed and survival rates (Barry *et al.*, 2020; Green *et al.*, 2022; Chaput *et al*., 2019; Furey *et al*., 2015). Information from acoustic studies and from = behavioural studies on environmental cues is important to inform future local and national Atlantic salmon management strategies (Barry *et al*., 2020; Ounsley *et al*., 2020; Ohashi & Sheng, 2018; Green *et al*., 2022). The majority of studies investigating early marine migration have been conducted using small sample sizes. Although, these investigations provide valuable insight into early marine migration trajectories, our study highlights the temporal variation in early marine migration from a single UK river. This work also provides further evidence for a northerly movement through the Irish Sea are occurring for Irish Sea smolts, although at differing rates across a temporal scale. The results of this study contribute to assessing overlap with potential anthropogenic conflicts, inform modelling of early marine migration which will allow for potential predictions of future migration routes of both regional and national Atlantic salmon populations during the early marine migration phase (Flye *et al*., 2021; Lilly *et al*., 2023).

### 6.4.1 Marine migration speed

The speeds recorded differed across the three-year study period, 2021 mean speed (9.73km.day$^{-1}$) was consistent with Barry *et al*. (2020) which indicated migration speeds of ca.7km.day$^{-1}$, although in 2020 and 2022 findings were similar to those recorded by Chaput *et al*. (2019) where speeds in our study were found to be ca.17-20km.day$^{-1}$ through the Irish Sea. It has been suggested that migration speed is potentially influenced by tributary location and the environment conditions in which smolts migrate through rivers and the marine environment (Green *et al*., 2022). However, there seems to be significant inter-annual variation for fish leaving from the same location.

### 6.4.2 Migration loss rate

The early marine migration is thought to incur additional costs in comparison to riverine migration (Thorstad *et al*., 2012b), where post-smolts experience increased salinity, novel predation pressures and new food sources (Klemetsen *et al*., 2003; Thorstad *et al*., 2011). The rate of unsuccessful migration of River Derwent post-smolts within the Irish Sea was relatively low in comparison with Barry *et al*. (2020) and Thorstad *et al*. (2011), ranging from 0.27-0.33%.km$^{-1}$. Thorstad *et al*. (2012b) found that post-smolt mortality increased with distance from their natal tributary. However, telemetry studies can overestimate mortality rates, through the potential of capture/handling/post-tagging effects and limited receiver layout reducing detection levels at sea. Increased unsuccessful migration rates of Atlantic salmon post-smolts is associated with predation. High abundance of predators such as harbour seals (*Phoca vitulinai, Linnaeus 1758*), bottlenose dolphins (*Delphinus truncates, Montagu 1821*) and a variety of piscivorous bird species were present within and surrounding river mouths during key migration periods when salmonids are in high abundance, suggesting that they may utilise them as a prey source (Allegue *et al*., 2020; Arso Civil *et al*., 2019; Carter *et al*., 2001; Kennedy & Crozier, 2010; Thorstad, *et al*., 2012a,b; Wilson *et al*., 1997; Lilly *et al*., 2023), although species distribution and impact on migrating smolts remains unknown during early post-smolt marine migration (Brown *et al*., 2012; Flávio *et al*., 2020; Kennedy & Crozier, 2010; Kierly *et al*., 2000; Mackey *et al*., 2004; Righton *et al*., 2001; Lilly *et al*., 2023). Nonetheless, we are unable to determine with certainty if detections in this study are of a true post-smolt or those of a predator (Lilly *et al*., 2023). Research has found that acoustic tags are able to continue to signal from the predator's stomach, if a predator remains in the water, and could remain within the predator's stomach for up to 47 days (average 29 days) (Thorstad *et al*., 2012a). Yet, it has been found that some predators, particularly fish show movements that are similar to those expected by post-smolts, however, depth of movement was significantly different. Future studies should utilise predation/depth sensor tags to provide a more accurate depiction of true smolt and post-smolt behaviour compared to their predators (Thorstad *et al*., 2012a; Gibson *et al*., 2015; Hanssen *et al*., 2022; Lennox *et al*., 2021; Nash *et al*., 2022). We assume that detections are those of a post-smolt based on swimming speeds and chosen marine trajectories which is comparable with other early migration studies within the Irish Sea (Barry *et al*., 2020; Green *et al*., 2022; Lilly *et al*., 2023).

Mortality during early marine migration by post-smolts may also be due to anthropogenic impacts, such as diseases and parasites from fish farms and climate change (Forseth *et al*., 2017). Due to the potential low detection efficiency across the marine arrays we can assume a likely higher survival rate exists in River Derwent post-smolts during early marine migration.

### 6.4.3 Migration pathways

The results presented here provide consistent evidence of a generally northern trajectory of movement by post-smolts after entering the Solway Firth during the early marine migration phase from the River Derwent. The Irish Sea is a semi-enclosed body of water characterised by concurrent action tides entering from both the north and south (Dabrowski *et al*., 2010; Gaffney, 2001; Green *et al*., 2022), this in turn creates semi-diurnal currents, allowing for both high and low energy mixing to occur (Howarth, 2015). Conversely, specific environmental conditions allow for inter-annual variability regarding current direction to alter within the Irish sea. Post-smolts have been found to use such currents during early marine migration (SALSEA-Merge, 2012). Through the recapture of post-smolts in northern Scotland and marine migration modelling conducted by Mork *et al*. (2012), movements of post-smolts were found to be occurring with the continental shelf edge currents (Shelton *et al*., 1997) and they found active swimming to occur towards the direction of these currents. The River Derwent post-smolt early marine migration analysis implies that post-smolts are likely navigating with the predominant current in the Solway Firth and move through the Irish sea in a northerly direction. However, post-smolt movements within the early marine phase have been detailed as more complex and a study with greater spatial detail is required to differentiate current influence on post-smolt trajectory choice. Newton *et al*. (2021) found with the use of particle tracking, post-smolts actively migrated by swimming in a direction that did not follow the prevailing currents. Therefore, there is potential of alternative migration strategy at a population specific level occurring and more detailed investigations are required (Green *et al*., 2022).

Green *et al*. (2022) states there are potential alternative possibilities for post-smolt migration choice within the early marine migration phase which include: i) post-smolts disperse in random directions once the open coast is reached; ii) post-smolts take the most direct migratory pathway to reach their feeding grounds in the northern hemisphere; and iii) post-smolts use coastlines as geographical markers during their migration to their northerly destination. However, without hydrographic data on marine currents and greater acoustic receiver density within the Solway Firth and Irish Sea, it is impossible to resolve any of these potential hypotheses. Due to lack of a southern array we can only assume that all smolts which entered the Solway Firth chose a northern trajectory. Increased receiver density across a broader range will help resolve the assumptions of a general northern trajectory route or if random dispersal of post-smolts exists.

## 6.5 Conclusion

In conclusion, this study has assisted in providing further evidence of west coast England Atlantic salmon post-smolts marine migration trajectories during the early marine phase of migration, displaying a northern trajectory through the Solway Firth and Irish Sea. We show pathways up to ca.558km from their natal river. Here we have provided substantial baseline data for survival (%.km$^{-1}$) and smolt speed/duration showing inter annual variation of early marine migrating post-smolts from the River Derwent. Further investigation into understanding Irish sea migration pathways of post-smolts will require a greater density of post-smolt detections from more tributaries throughout the Irish Sea, with greater southernly receiver densities to test for potential southern migration pathway choice. Data gathered within this study has only been possible through cross jurisdictional, and between research group, collaboration between the Environment Agency, Natural England, University of Glasgow, COMPASS, SeaMonitor, Atlantic Salmon Trust and Marine Scotland projects. Data sharing between these projects has allowed detailed mapping and analysis of post-smolt early marine migration trajectories from a west coast England tributary. Further collaborative efforts will allow for greater insight into trajectory choice of Atlantic salmon and help inform potential future management strategies.

# *Chapter 7:* General Discussion

## 7.1 Thesis Justification

The River Derwent is a site of European Importance, classified as a principal salmon river, with a Special Area of Conservation (SAC) designation detailing Annex II species Atlantic salmon (*Salmo salar*, Linnaeus 1758) as a qualifying features. Atlantic salmon are well studied due to their economical, ecological, and cultural importance across Europe, Scandinavia, and North America (Hansen *et al*., 1993; Thorstad *et al*., 2012b; Havn *et al*., 2020). In recent decades there has been a significant decline in the populations of anadromous Atlantic salmon, and various studies have indicated population abundances may be at historic lows where a ~30-50% decline has been recorded across UK populations since 2006 (Dadswell *et al*., 2022; ICES, 2023, 2021; Chaput, 2012; Jutila *et al.,* 2003; Mills 1991; Parrish *et al*., 1998; Aas *et al*., 2010), resulting in recent reassessment by the IUCN Red List of Threatened Species, where Atlantic salmon have been reclassified from 'Least Concern' to 'Endangered' in the UK. Previously, declines were frequently linked to distinct natural and anthropogenic conflicts such as: i) habitat fragmentation as a result of hydropower dams, canal construction and low-head weirs; ii) pollution run off from industrial and agricultural means; and iii) both commercial and recreational overfishing activities (Duncan and Lockwood, 2001; Fenkes *et al*., 2016; Belliard *et al*., 2018; Brink *et al*., 2018). However, due to the complexity of the Atlantic salmon life cycle, migrating through both freshwater and saltwater environments, governmental bodies such as Environment Agency, Natural England and CEFAS, have sustained ongoing management challenges, as not only are there threats associated with riverine environments but also marine.

Due to the River Derwent's importance in supporting a UK Atlantic salmon population, the central focus of this thesis was to emphasize how riverine systems, such as the River Derwent, have the ability to affect migrating Atlantic salmon smolts and the potential costs associated with migration. In addition, this thesis analyses the natural and anthropogenic bottleneck zones such as standing waters and low-head weirs which are present throughout the River Derwent, which have been identified throughout literature as some of the leading causes of Atlantic salmon populations declines, causing costly delays and increasing the likelihood of predation (Gauld *et al*., 2013; Thorstad *et al*., 2012b; Larinier, 2001, 2000; Marschall *et al*., 2011 Newton *et al*., 2018; Moore *et al*., 2013). Whist we have a decent grasp of the challenges smolts face during migration, there is limited knowledge regarding the interannual and spatial variations in these challenges.

Furthermore, less emphasis has been put on investigating the success of the early marine migration of post-smolts, particularly from English rivers. Due to the lack of clarity in literature regarding marine impacts on migrating Atlantic salmon, influencing the future use and management of the marine environment is challenging. By gathering baseline data for English Atlantic salmon populations and undertaking analysis to improve our understanding of the impacts potential obstacles have on Atlantic salmon it might allow for future management and mitigation to be implemented to improve the survival of post-smolts at sea.

## 7.2 Current management and approaches

In recent decades, freshwater environmental management of rivers has predominately centred around the elimination of structural impediments to migrating species, enhancing water quality parameters and decreasing the levels of exploitation on these fragile systems (Kemp, 2015; Thorstad *et al*., 2012b, 2021; Cantonati *et al*., 2020). Throughout England and Wales alone, 97% of riverine systems are fragmented, with approximately 66,381 river spanning obstacles such as weirs and dams currently established (Jones *et al*., 2019). Current management has sought to either remove current and unused structures or implement mitigation measures which allow for fish passage. Legislation for both current and new structures to ensure fish passes are included in line with the EU Water Framework Directive (Directive 2000/60/EC), and EU Eel Regulation (EC No. 1100/2007) (Newton *et al*., 2018) to aid in passage of various migrating species (Fjeldstad *et al*., 2012; Holbrook *et al*., 2011). As a designated special area of conservation (River Derwent and Bassenthwaite Lake SAC) these are also objectives to maintain and improve the status of the site to bring it into 'Favourable Condition'.

The expansion of industrial, agricultural and urban development in the 19$^{th}$ and 20$^{th}$ centuries led to the extinction of Atlantic salmon across numerous UK rivers (Mawle & Milner, 2003). Mawle & Milner (2003) have shown that over the past four decades, there has been a growing trend of stringent regulations governing discharges from industrial, agricultural and sewage systems coupled with substantial investments in water treatment, which together has brought about significant enhancements in water quality throughout the UK. This has led to Atlantic salmon populations expanding their ranges within English river systems (Dodd & Adams, 2014; Evans *et al*., 2001).

Lastly, overfishing has undeniably posed a historical challenge for diadromous salmonids, where recreational fishing provides economic opportunities (Aprahamian *et al*., 2010). Although recreational overfishing has been significantly mitigated through proactive measures, such as the reduction in net fisheries in freshwater systems. However, it is important to note that rules and regulations regarding recreational net fishing vary widely depending on country, region and county.

Additionally the practice of catch-and-release as a proactive measure which has long been adopted by coarse anglers throughout the UK has been found to reduce the risk of local populations falling below their conservational limits (Winfield, 2016; ICES, 2017, 2018, 2021; White *et al*., 2023). Catch and release practices have gained increasing popularity throughout the commercial fishing community, predominantly driven by growing awareness of conservation issues surrounding salmonid species (Gargan *et al*., 2012). Copeland *et al*. (2017) indicated that anglers now display a keen interest in habitat management, with their primary motivation surrounding the key desire to "give something back" to the environment rather than catching for self-gain. However, anglers still remain misinformed regarding the best catch and release practices promoted by local fisheries trusts, such as air exposure times, type of hook avoidance, handling practices and induced stress and the associated fish behaviours (Cooke & Suski, 2005; Pelletier *et al*., 2007), subjecting targeted fish to the negative consequences of incorrect practices (i.e., injury or death). Therefore, it is prevalent to encourage and continuing to increase the active involvement of anglers in conservation practices, habitat management and sustain effective communication between anglers and governing bodies is crucial to conserve an already vulnerable species.

## 7.3 The need for river spanning small scale infrastructure

Global river modification is not uncommon, there is a long history of weir and dam developments occurring in developed countries (Gauld *et al.,* 2013; Dynesius & Nilsson, 1994; Nilsson *et al*., 2005). The modification of rivers has played a crucial role in accommodating human population expansion through mitigation of flood control, hydroelectric power production and farming in floodplain areas (Havn *et al*., 2020; Nilsson *et al*., 2005; Poff & Hart, 2002; Gauld *et al*., 2013). However, the role that small-scale river-spanning barriers, such as low-head weirs have on increased habitat fragmentation of riverine ecosystems has been well documented (Fullerton *et al*., 2010; Gauld *et al*., 2013; Jungwirth, 1998; Kemp & O'Hanley, 2010). These structures have been shown to hinder complex migration strategies, limit dispersal and alter the downstream movement of water, sediment and nutrient movement (Antonio *et al*., 2007; Branco *et al*., 2012; Gauld *et al*., 2013).

Whilst planning and legislative requirements have driven the implementation and construction of new and/or improved fish pass facilities to be present, larger rivers are typically targeted for remedial action before the smaller connected tributaries, which often facilitate the key nursery habitats compared to the main river stem (Ovidio & Philippart, 2002). These small tributaries are extremely vulnerable to low head weir pressures, they exhibit rapid responses to excessive rainfall events, leading to the displacement of fish and limited movement between habitats (Stock & Schlosser, 1991). However, the impacts of small structures, which could contribute greatly to river habitat fragmentation, have not received appropriate attention (Marmulla & Ingendahl, 1996; Croze *et al*., 2000). Information regarding the impacts on overall fish community structure and migration strategies still remains limited, which is required to develop effective restoration plans for rivers networks impacted by artificial habitat fragmentation as outlined by the Water Framework Directive (Maia, 2017).

It has been debated whether, when a small-scale structure is determined to be a complete, partial, or temporary obstruction to migrating fish and riverine movement. The foremost priority should be the complete removal of the respective barrier, rather than opting for modifications (Kemp & O'Hanley, 2010; King & O'Hanley, 2016), which is seen as a more viable approach for effective watershed management (O'Hanley 2011; Bednarek, 2001). Chapter 4 of this thesis details the extent to which low-head weirs present along the River Derwent are impacting on Atlantic salmon migration potential and if active swimming is undertaken. The main outcome was that smolt migration failure increased significantly at a weir compared to migration failure during open river migration, although the losses were structure specific. Considering the evidence, although weir migration failure was structure specific, in general low-head weirs have a negative impact on migrating Atlantic salmon smolts. Although there is a pressing requirement for additional research of small-scale barriers, the impact they have on migrating species and the potential for new development with minimal ecological impact. Numerous questions still remain unanswered regarding the future implications and consequences of weir retention or removal on the local ecology structure, species adaptability to new flow regimes if removal is permitted.

## 7.4 Further understanding required

Like many research endeavours, numerous questions arise in tandem with those that are resolved. This thesis presents five studies aimed at bridging the knowledge gaps in existing literature concerning interannual spatial variation in Atlantic salmon migration in riverine and early-marine environments and to provided evidence to support management undertaken by the Environment Agency and Natural England regarding small scale barriers present on the River Derwent and their impacts on the local Atlantic salmon population. Atlantic salmon have been subject to extensive research, although emphasis on migration strategies, the costs associated and the pathway choices within the riverine and early marine phases is limited.

To tackle these knowledge gaps in fisheries research, the utilization of acoustic telemetry has proven to be an effective method for studying migrating fish within freshwater and deep marine environments (Welch *et al*., 2008; Klimley *et al*., 2013; Klinard *et al.*, 2019; Rechisky *et al.,* 2013; Abecasis *et al.*, 2018; Hays *et al*., 2019; Lennox *et al*., 2017; Matley *et al*., 2022). This technique was employed in the current study on the River Derwent. The advancement of acoustic telemetry technologies has facilitated the growth in fish and fisheries research in recent years, offering valuable scientific insights into the life history strategies, behavioural and movement ecology of numerous aquatic species which were previously difficult to study.

Atlantic salmon undertake long distance migrations between freshwater and saltwater habitats and particular attention has been paid to the smolt migration stage due to the high migration failure rates associated with this life stage. We know through previous research that smolt migration failure in rivers varies significantly but it is typically regarded as high (Thorstad *et al*., 2004, 2012b; Hedger *et al*., 2008; Bonte *et al*., 2012; Adams *et al*., 2022b). Understanding the spatial and temporal variation in migration failure rates throughout a river system has received less attention. Chapter 2 aimed to distinguish the interannual spatial variation in migration failure rates throughout the riverine system by analysing the River Derwent in sections across a three year study period. Lothian *et al*. (2018) suggested the rate of migration success of Atlantic salmon depleted throughout the river system (0.41%.km$^{-1}$ success rate). Though evidence to suggest this was universal or site specific remained limited. Chapter 2 results revealed migration failure rates through the River Derwent differed both between sections and across years, with the most upper reach sections having a profound impact on migration success of Atlantic salmon smolts during 2020 and 2021.

As migration failure rate was extremely high during the 2020 baseline study, a low sample size reached the lower areas of the River Derwent (i.e., Coops Weir and Yearl Weir), thus, reducing the ability to assess the costs associated with migration in the lower river reaches. In order to address the issues regarding high migration failure rates within the upper reaches of the River Derwent, a Trap and Transport experiment was included to increase the volume of data available for assessing smolt survival in section 3 of the River Derwent (refer to Chapter 2 for section analysis). Previous studies which have incorporated Trap and Transport of smolts have commonly used hatchery fish (Carey & McCormick, 1998; Sigourney *et al*., 2015), although trapping of wild migrating smolts and transporting them around high migration failure zones (bottleneck zones) has been a mitigation strategy for pacific salmonids in certain rivers since 1970's (Chapman *et al*., 1997). In the present study (Chapter 2), two particular bottleneck zones, which emphasised the high migration failure rates of migrating Atlantic salmon smolts along the River Derwent during the three year study period, were the natural standing waters of Bassenthwaite Lake and two low-head weirs (Coops Weir and Yearl Weir) in the lower river section at Workington, Cumbria.

Research into Atlantic salmon smolt migration through natural standing waters has received little attention across the decades, although the few studies analysing standing water impacts indicate smolts migrating through display non-unidirectional movements (Hanssen *et al*., 2022; Honkanen *et al*., 2018, 2021; Lilly *et al*., 2021) though small scale movement analysis was limited within these studies due to receiver densities. Chapter 3 aimed to expand on previous research by analysing the small scale movements of smolts within Bassenthwaite Lake with a greater receiver density, identifying factors that could increase lake migration success likelihood. Additionally, Lilly *et al*. (2021) analysed smolt migration through Loch Lomond and found that a zone approximately 1.75km from the loch outtake provided navigation cues that were "just right" to aid in successful smolt exit in an area near the lake outflow which is referred to as the "Goldilocks" theory". In Chapter 3 I aimed to assess if the Goldilocks Zone was universal and applicable to Bassenthwaite Lake or site-specific. Chapter 3 had four main hypotheses: 1) migration failure rate in Bassenthwaite Lake is consistent in magnitude with other standing water studies in the UK (~60%); 2) larger smolts have higher migration success through Bassenthwaite Lake than smaller smolts; 3) both successful and unsuccessful migrating smolts exhibit indirect migration trajectories in Bassenthwaite Lake; and 4) smolts which enter the Goldilocks Zone are more likely to orientate towards Bassenthwaite Lake outlet.

Despite testing various morphological, behavioural and environmental traits, I was unable to pinpoint distinctive features exclusive to successful lake migrants. Chapter 3 indicated the applicability of the Goldilocks Zone to Bassenthwaite Lake, although it remains uncertain whether this concept extends to all standing waters and natural lakes or is geographically specific. Furthermore, previous research incorporating environmental variables such as wind direction which could influence migration trajectories of Atlantic salmon through standing waters are limited. Migration through standing waters is thought to be partially dependents on wind driven surface currents (Thorpe *et al*., 1981). However, the results from Chapter 3 suggest that surface wind currents throughout Bassenthwaite Lake many to be strong enough to provide navigational cues and space utilisation was declared as random. Behavioural changes in lake migrants from random migration trajectories to purposeful movements to the lake outlet is most likely due to shifts in flow discharge at the exit point (Lilly *et al*., 2021). In light of the substantial migration failure rates observed in the 2021 study, it is imperative to conduct further investigations to examine whether movement out natural standing waters is influenced by flow discharge rates.

Once smolts successfully migrate out of Bassenthwaite Lake, or have been transported around the lake system, smolts were faced with two low-head weirs (Coops Weir and Yearl Weir) ca.25km downstream at Workington. The trap and transportation of smolts around Bassenthwaite Lake provided evidence in allowing for the assumption that the reduction in km to migrate faced by smolts is associated with increased migration success rates found along the River Derwent.

However, low-head weirs have not received appropriate attention and the impact they may have through increase habitat fragmentation on Atlantic salmon smolt downstream migration still remains unclear. In Chapter 4 of this thesis I looked to assess: 1) the inter-annual variability in migration failure rate across three years; 2) whether the prolonged duration spent above weirs resulted in route choice; and 3) assess the potential biotic and environmental factors which are associated with weir migration success. The results indicated that small-scale river spanning infrastructure such as low-head weirs are having an impact on River Derwent migration success rates, although given the option smolts have the ability to choose their preferred migration route and actively swim away from the main river stem (Honkanen *et al*., 2021; Lacroix *et al*., 2004a, b; Svendsen *et al*. 2007; Davidsen *et al*., 2009; Fängstam 1993; Lilly *et al*., 2021). Previous research has alluded to the potential accumulative affects that multiple river barriers could have on migrating smolt migration failure rates through increased injury, delays and predation (Havn *et al*., 2020; Larinier, 2008; Norrgård *et al*., 2013; Newton *et al*., 2018). Results from Chapter 4 concluded that migration success across Coops Weir declined, though the Yearl Weir was found to incur a greater cost and migration failure rate was high. However, due to poor receiver density surrounding the weirs and ambient noise influences, we cannot entirely conclude smolts missed are actual migration failures or have been simply missed. It is imperative future work on small scale weir impacts utilise different tag options such as radio tags (Newton *et al*., 2018; Lothian & Lucas, 2021) or undertake active tracking methods (Chavarie *et al*., 2022) to assess if failure rates are accurate.

A limiting factor to undertaking any fish telemetry study, is the size of the targeted species relative to the size of the acoustic tag used (McCleave & Stred 1975; Ross & McCormick, 1981; Lefrançois *et al*., 2001; Newton *et al*., 2016). Currently in telemetry smolt migration research there is bias as large smolts are often utilised (e.g., Lefèvre *et al*., 2012) which reduces tag mass to body mass ratios (Newton *et al*., 2016) and falsely represents the true behaviour of population as a whole (Gingerich *et al*., 2012, Deng *et al*., 2015). Although ping rate of the signal, transmitter and battery size must all be considered, the main factor in the selection process is the transmitter size in relation to the size of the fish the study is targeting. Winter (1996) proposed the '2% rule' which, according to guidelines, the weight of the transmitter in air (1.7g) should not exceed "2%" of a fish's body weight in air. The purpose of this is to remove the risk of potential behavioural alterations such as alter swimming ability and induced stress (Brown *et al*., 1999) or increased migration failure associated with tagging (tag burden effect) (McCleave & Stred, 1975; Ross & McCormick, 1981; Adams *et al*., 1998; Honkanen *et al*., 2018; Lothian *et al*., 2018). A significant underlying assumption in telemetry studies is that fish bearing tags exhibit similar behavioural responses as their untagged counterparts (Zale *et al*., 2005; Drenner *et al*., 2012; Newton *et al*., 2016). However, testing of this assumption in the natural environment in unfeasible, as we are unable to track untagged and therefore "tagless" fish with the same frequency or accuracy. The '2% rule' has however been challenged, with suggestions that the ratio of tag mass to body mass could be extended to approximately 6%-12% (Brown *et al*., 2011, Rechisky & Welch, 2010; Newton *et al*., 2016; Chaput *et al*., 2019). In Chapter 2, we provide evidence to suggest it is possible to have a greater tag burden (>2%) without the reduction in altering migration behaviours or increase migration failure likelihood. Thus, by moving away from the '2% rule' to a more pragmatic and species-specific standard and tag smaller smolts, which in turn provides a more representative measure of a population.

While acoustic telemetry has provided significant insight into river migration and has also been instrumental in tracking aquatic species worldwide (Lennox *et al*., 2017; Matley *et al*., 2022). Previous research has established that Atlantic salmon both post-smolts face elevated migration failure rates in the early marine environment, primarily as a result of exposure to novel natural and anthropogenic stressors (Altizer *et al*., 2011; Holm *et al*., 2006; Shephard & Gargan, 2021; Crozier *et al*., 2004; Delgado & Ruzzante, 2020; Zydlewski *et al*., 2005).

Once smolts navigate out of the River Derwent into the Solway Firth, many are assumed to migrate north through the Irish Sea to reach the continental shelf edge currents (Shelton *et al*., 1997) located along the western coast of the Outer Hebrides in order to head towards key feeding grounds in the Norwegian Sea, Greenland coast and west of the Vøring Plateau escarpment (Klemetsen *et al*., 2003; Holm *et al*., 2000; Jacobsen *et al*., 2012; Mork *et al*., 2012; Ounsley *et al*., 2020; Dunbar & Thomson, 1979; Gilbey *et al*., 2021). However, prior to the research described in Chapter 5 and 6 of this thesis, the migration trajectories of migrating Derwent post-smolts remained unknown. Information regarding migration trajectories of post-smolts within the Irish

Sea was limited to particle tracking studies conducted by Ounsley *et al*. (2020) and a limited amount of tracking data provided by Barry *et al*. (2020) who analysed smolt migration from a small number of Irish tributaries. Chapters 5 and 6 were achieved because of transboundary collaboration efforts across five different organisations. Working together, various deep sea acoustic telemetry arrays were deployed in order to establish baseline data around the migration trajectories taken by River Derwent smolts. In 2020 we were able to conclude that smolts were indeed taking a northern trajectory by detecting three smolts as they made long distance migrations (ca.250km) within the Irish Sea.

In Chapter 6, which combined data from all three study years (2020-2022), a large number of tagged post-smolts were detected across multiple sea arrays throughout the Irish Sea, concluding that they moved in a northern trajectory. However, the absence of a southern array during the study means that we cannot conclude, with certainty, that fish only moved in a northern direction.

An analysis of previous literature by Thorstad *et al*. (2012b) inferred that migration failure rates are higher in the early marine phase due to additional costs incurred in comparison to riverine migration, where salinity levels, novel predation pressures and new food sources pose significant risks (Klemetsen *et al*., 2003; Thorstad *et al*., 2011). However, this simply is not the case for River Derwent smolts where migration failure rates still remains higher in rivers compared to marine environments. It still remains unclear if overestimate of migration failure rates in the early marine environment is due the potential of capture/handling/post-tagging effects and insufficient or sub-optimal receiver layout allowing for post-smolts to be missed. Nonetheless, Chapters 5 and 6 highlight the importance and future requirement for transboundary collaboration to improve the number of detections over a wide geographical area. The data obtained should lead to the development of more effective monitoring and management strategies.

## 7.5 Limitations of the study

Like most field studies, the planning and the outcome of my study were very different, particularly in 2020. Originally, I planned for tagging to commence and take place over a set number of weeks, however, due to the restraints faced during the COVID-19 pandemic we were constrained for time. Thus, tagging of smolts was conducted across a much-shorter window (days) than originally anticipated. Due to the limited number of possible tagging days, unfortunately tagging and release was conducted during a severe draught period which we would have had an opportunity to avoid pre COVID-19.

Whilst we were able to obtain baseline information regarding smolt survival, timing and basic drivers throughout the riverine system, complete repeatability of the study is extremely difficult as we are unlikely to ever face a situation like COVID-19 where there was limited interaction between humans and both the River Derwent and Bassenthwaite Lake.

During 2021 tagging, we experienced an excessive amount of rainfall across a two day period which resulted in a large proportion of smolts being captured during a 24 hour period (~900 smolts and parr). This resulted in a higher number of smolts being released in a single day rather than across the planned migration window.

The high rainfall experienced in 2021 may have resulted in an assumed knock on effect in capture rates in 2022, though poor recruitment could be a contributing factor. The proportion of smolts I planned to tag was unachievable and I hypothesised the high rainfall was an attributing factor to the reduction in 2022 capture rates and juvenile salmon (0+ and 1++ ages) were likely flushed downstream of the original tagging location. This resulted in only 115 smolts captured out of the planned 175 smolts required for 2022 tagging. Fish monitoring concluded 2022 was one of the lowest fish recording periods seen on the River Derwent in recent years (refer to Figure 1.8) .

The study on the early marine migration of Atlantic salmon smolts (presented in Chapter 5 and 6) was restricted during 2020 (COVID-19) whereby collaborative partners from the SeaMonitor-project only managed to get fraction of their intended marine array out, and thus smolts could have easily migrated north through the planned array stretch but were missed due to receivers not being in place. Additionally, during 2020 Atlantic Salmon Trust, Marine Scotland and University of Glasgow were unable to deploy any marine arrays, which again meant that any River Derwent fish moving in these areas were not detected.

Prior and during any acoustic telemetry study adequate range testing of the acoustic telemetry equipment is required as a variety of environmental factors unique to each riverine system such as rain, wind direction/speed, temperature and salinity can impede the detection ranges of the deployed receivers (Kessel *et al*., 2014) and the result provided are used to guide receiver placement. The range testing requires deploying an acoustic tag at a fixed location and depth and deploying additional acoustic receivers across various spatial distances from the set tag (e.g., 50m) and testing the range in which the tag is detected.

In order to improve the methodology, I would look to increase receiver density throughout the river system (Chapter 2 and 4) particularly in areas where migration failure rates were high in the 2020 and where detection efficiency was poor due to potential ambient noise influence and in areas where water currents were fast, this would be an advantage particularly within the weir sections. Overall by increasing receiver density it would greatly improve overall accuracy of salmonid migration within the River Derwent.

## 7.6 Concluding statement

The results presented in this thesis offer valuable baseline insights into the costs of migration, the selected migratory routes, and the impacts barriers have on River Derwent smolts and post-smolts. Prior to this study, our understanding of River Derwent Atlantic salmon populations and the interannual spatial variations in migration failure rates and migration behaviours was limited. With growing concerns about the rapid decline in Atlantic salmon populations and increased exposure to anthropogenic stressors such as flood control structures and renewable energy development, there is a pressing need for further research (Waldman & Quinn, 2022).

Building on the findings in this thesis, future research should leverage this evidence to investigate the factors contributing to spatial variations in river migration failure rates. Additionally, we must look to assess the consequences of removing artificial river-spanning infrastructure not only on Atlantic salmon populations but also on aquatic ecosystems as a whole. This research can provide valuable insights to regulatory bodies, enabling them to implement effective river management practices and mitigation measures to address anthropogenic barriers as they can help strike a balance between the preservation of salmon populations and the development of river systems (Tallis & Polasky, 2009).

# Appendix A: Supplementary Information for all Chapters

The following supplementary information provides tagging dates for all three-year tagging events, receiver deployments for all river and lake receivers.

***Table A.1*** *Summary of mean tagging dates, number of smolts tagged per event, mean ±SD of fork length ($L_F$, mm), weight (g) and tag burden (%). Tag burden is calculated by dividing the weight of the tag in air (1.7g) by the weight of the individual *100. Release group: SJB= St Johns Beck release group, TT, Trap and Transport release group.*

| **Tagged Date** | ***n* =** | **Release Group** | **$F_L$ (mm) ± SD (range)** | **Weight (g) ± SD (range)** | **Tag Burden (%) ± SD (range)** |
|---|---|---|---|---|---|
| **01/05/2020** | 24 | SJB | 141.7 ± 5.55 (132 - 154) | 30.2 ± 4.24 (24.6 - 41.4) | 5.05 ± 0.67 (3.6 - 6.1) |
| **02/05/2020** | 35 | SJB | 138.3 ± 5.76 (130 - 157) | 27.1 ± 3.68 (21.0 - 40.1) | 5.60 ± 0.69 (3.7 - 7.1) |
| **03/05/2020** | 41 | SJB | 138.7 ± 7.32 (130 - 157) | 27.1 ± 4.28 (21.4. - 39.4) | 5.65 ± 0.77 (3.8 - 7.0) |
| **2020 Total** | 100 | | 139.3 ± 6.49 (130 - 157) | 27.8 ± 4.24 (21.0 - 41.4) | 5.49 ± 0.76 (3.6 - 7.1) |
| **14/04/2021** | 1 | SJB | 153 | 35.6 | 4.2 |
| **16/04/2021** | 6 | SJB | 149.3 ± 11.75 (136 - 164) | 33.6 ± 8.73 (22.4 - 42.2) | 4.74 ± 1.30 (3.5 - 6.6) |
| **18/04/2021** | 6 | SJB | 144.5 ± 5.16 (140 - 153) | 30.6 ± 4.19 (26.0 - 38.1) | 4.97 ± 0.62 (3.9 - 5.7) |
| **20/04/2021** | 10 | TT | 143.6 ± 7.08 (134 - 157) | 31.0 ± 4.99 (24.8 - 39.8) | 4.94 ± 0.78 (3.7 - 6.0) |
| **21/04/2021** | 6 | TT | 138.3 ± 5.35 (133 - 148) | 28.2 ± 4.25 (23.9 - 35.6) | 5.41 ± 0.76 (4.2 - 6.2) |
| **22/04/2021** | 8 | TT | 136.8 ± 5.89 (130 - 146) | 27.6 ± 3.05 (23.1 - 32.7) | 5.49 ± 0.60 (4.5 - 6.4) |
| **24/04/2021** | 8 | SJB | 139.3 ± 10.9 (132 - 161) | 28.4 ± 6.99 (22.2 - 42.7) | 5.51 ± 1.13 (3.5 - 6.7) |
| **25/04/2021** | 6 | SJB | 139.8 ± 6.86 (134 - 152) | 28.1 ± 4.65 (23.4 - 35.4) | 5.45 ± 0.82 (4.2 - 6.4) |
| **27/04/2021** | 17 | SJB / TT | 140.7 ± 7.73 (130 - 157) | 29.2 ± 5.37 (21.3 - 40.7) | 5.28 ± 0.91 (3.6 - 7.0) |
| **29/04/2021** | 10 | SJB / TT | 139.8 ± 8.96 (134 - 159) | 28.9 ± 6.54 (22.3 - 44.5) | 5.37 ± 0.95 (3.3 - 6.7) |
| **03/05/2021** | 34 | SJB | 142.5 ± 7.69 (131 - 158) | 29.8 ± 5.25 (21.5 - 40.3) | 5.18 ± 0.89 (3.7 - 6.9) |
| **04/05/2021** | 29 | SJB / TT | 141.4 ± 8.97 (131 - 164) | 29.5 ± 5.72 (22.3 - 43.5) | 5.25 ± 0.94 (3.4 - 6.7) |
| **05/05/2021** | 9 | SJB | 141.8 ± 4.62 (134 - 146) | 28.8 ± 3.14 (24.5 - 32.6) | 5.25 ± 0.59 (4.6 - 6.1) |
| **2021 Total** | 150 | | 141.6 ± 8.09 (130 - 164) | 29.5 ± 5.37 (21.3 - 44.5) | 5.23 ± 0.88 (3.3 - 7.0) |
| **05/05/2022** | 29 | TT | 139.0 ± 0.04 (130 - 154) | 27.5 ± 6.21 (21.2 - 37.9) | 5.58 ± 4.17 (4.0 - 7.1) |
| **06/05/2022** | 10 | TT | 138.8 ± 0.01 (131 - 147) | 27.9 ± 5.35 (24.2 - 35.4) | 5.46 ± 0.69 (4.2 - 6.2) |
| **07/05/2022** | 16 | TT | 139.9 ± 7.47 (131 - 157) | 28.5 ± 4.76 (21.7 - 39.5) | 5.40 ± 0.86 (3.8 - 6.9) |
| **08/05/2022** | 13 | TT | 137.5 ± 5.06 (131 - 146) | 26.1 ± 3.14 (21.9 - 31.5) | 5.81 ± 0.67 (4.8 - 6.8) |
| **09/05/2022** | 13 | TT | 140.8 ± 6.34 (133 - 158) | 28.8 ± 4.24 (23.8 - 40.4) | 5.41 ± 0.66 (3.7 - 6.3) |
| **11/05/2022** | 20 | TT | 138.9 ± 9.20 (131 - 161) | 27.9 ± 5.09 (21.7 - 40.2) | 5.51 ± 0.86 (3.7 - 6.9) |
| **12/05/2022** | 6 | TT | 135.2 ± 3.19 (132 - 141) | 24.9 ± 1.47 (23.4 - 27.5) | 6.04 ± 0.34 (5.5 - 6.4) |
| **25/05/2022** | 8 | TT | 135.4 ± 4.60 (130 - 143) | 25.6 ± 2.11 (23.2 - 29.4) | 5.89 ± 0.47 (5.1 - 6.5) |
| **2022 Total** | 115 | | 138.7 ± 6.65 (130 - 161) | 27.4 ± 4.14 (21.2 - 40.4) | 5.58 ± 0.75 (3.7 - 7.1) |

# Appendix B: Supplementary Information for Chapter 2.

(Temporal patterns of spatial variation in migration success of Atlantic salmon in a riverine environment)

The following supplementary information provides a summary of receiver deployment throughout the River Derwent during 2020-2022, illustrating receiver deployment through the sections.

***Table B.1*** *Receiver deployment and detection efficiency (%) throughout the River Derwent in 2020.*

| Type | ID | Latitude | Longitude | Section | Days Deployed | Detection Efficiency (%) |
|---|---|---|---|---|---|---|
| **River** | VR2W - 135755 | 54.614253 | -3.066358 | 1 | 124 | 85 |
| **River** | VR2W - 135758 | 54.603804 | -3.156726 | 1 | 124 | 63.3 |
| **River** | VR2W - 131692 | 54.631183 | -3.185222 | 1 | 140 | 97 |
| **Lake** | VR2Tx - 484127 | 54.631 | -3.19965 | 2 | 170 | - |
| **Lake** | VR2Tx - 484132 | 54.63624 | -3.19685 | 2 | 170 | 71.9 |
| **Lake** | VR2Tx - 484131 | 54.64032 | -3.20462 | 2 | 170 | 81.2 |
| **Lake** | VR2Tx - 484126 | 54.64524 | -3.21021 | 2 | 170 | 74.2 |
| **Lake** | VR2Tx - 484129 | 54.65089 | -3.2147 | 2 | 170 | 83.3 |
| **Lake** | VR2Tx - 484128 | 54.65688 | -3.2198 | 2 | 170 | 93.1 |
| **Lake** | VR2Tx - 484130 | 54.66289 | -3.22435 | 2 | 170 | 89.3 |
| **Lake** | VR2Tx - 484133 | 54.66846 | -3.22904 | 2 | 170 | 100 |
| **Lake** | VR2Tx - 484134 | 54.67368 | -3.23457 | 2 | 170 | 100 |
| **River** | VR2W - 126852 | 54.677578 | -3.244023 | 3 | 124 | 100 |
| **River** | VR2W - 135761 | 54.68775 | -3.2968 | 3 | 125 | 90.9 |
| **River** | VR2Tx - 484136 | 54.674407 | -3.361235 | 3 | 139 | 40 |
| **River** | VR2Tx - 484137 | 54.660141 | -3.446216 | 3 | 124 | 90 |
| **River** | VR2W - 135752 | 54.660059 | -3.494656 | 3 | 124 | - |
| **River** | VR2W - 135759 | 54.659476 | -3.510356 | 3 | 124 | - |
| **River** | VR2W - 135763 | 54.65398 | -3.514249 | 3 | 139 | - |
| **River** | VR2W - 126850 | 54.65531 | -3.51643 | 3 | 139 | 100 |
| **River** | VR2W - 135762 | 54.653565 | -3.515852 | 3 | 139 | 75 |
| **River** | VR2W - 135753 | 54.65387 | -3.51774 | 3 | 139 | 12.5 |
| **River** | VR2W - 135756 | 54.649443 | -3.523675 | 3 | 139 | - |
| **River** | VR2W - 135765 | 54.64715 | -3.53169 | 3 | 125 | 100 |

***Table B.2*** *Receiver deployment and detection efficiency (%) throughout the River Derwent in 2021.*

| Type | ID | Latitude | Longitude | Section | Days Deployed | Detection Efficiency (%) |
|---|---|---|---|---|---|---|
| **River** | VR2W - 126852 | 54.60899 | -3.06230 | 1 | 121 | 13.6 |
| **River** | VR2Tx - 484133 | 54.61422 | -3.06639 | 1 | 121 | 4.8 |
| **River** | VR2W - 103996 | 54.60887 | -3.10508 | 1 | 120 | 4.8 |
| **River** | VR2W - 108496 | 54.59908 | -3.15426 | 1 | 120 | - |
| **River** | VR2W - 135753 | 54.60401 | -3.15645 | 1 | 120 | 8.1 |
| **River** | VR2W - 131692 | 54.62387 | -3.17333 | 1 | 120 | 91.9 |
| **Lake** | VR2W - 135760 | 54.63084 | -3.18482 | 2 | 113 | 96.8 |
| **Lake** | VR2Tx - 486174 | 54.63580 | -3.19565 | 2 | 113 | 82.3 |
| **Lake** | VR2Tx - 486177 | 54.63428 | -3.20012 | 2 | 113 | 84.5 |
| **Lake** | VR2Tx - 486172 | 54.64900 | -3.21358 | 2 | 113 | 80.7 |
| **Lake** | VR2Tx - 486169 | 54.65575 | -3.21872 | 2 | 113 | 82.1 |
| **Lake** | VR2Tx - 486180 | 54.66362 | -3.22743 | 2 | 113 | 8.9 |
| **Lake** | VR2Tx - 486173 | 54.66527 | -3.22473 | 2 | 113 | 8.9 |
| **Lake** | VR2Tx - 486175 | 54.66523 | -3.23017 | 2 | 113 | 87 |
| **Lake** | VR2Tx - 484132 | 54.66685 | -3.22762 | 2 | 113 | 13 |
| **Lake** | VR2Tx - 486179 | 54.66853 | -3.22470 | 2 | 113 | 27.8 |
| **Lake** | VR2Tx - 486178 | 54.66842 | -3.23038 | 2 | 113 | 25.9 |
| **Lake** | VR2Tx - 486181 | 54.66997 | -3.22797 | 2 | 113 | 5.6 |
| **Lake** | VR2Tx - 484136 | 54.66825 | -3.23583 | 2 | 113 | 20.4 |
| **Lake** | VR2Tx - 486167 | 54.67002 | -3.23387 | 2 | 113 | 3.7 |
| **Lake** | VR2Tx - 486171 | 54.67160 | -3.23053 | 2 | 113 | 40.7 |
| **Lake** | VR2Tx - 486170 | 54.67318 | -3.22825 | 2 | 113 | 18.5 |
| **Lake** | VR2Tx - 484135 | 54.67162 | -3.23417 | 2 | 113 | 1.9 |
| **Lake** | VR2Tx - 484137 | 54.67317 | -3.23340 | 2 | 113 | 33.3 |
| **Lake** | VR2Tx - 484129 | 54.67483 | -3.23082 | 2 | 113 | 53.7 |
| **Lake** | VR2Tx - 484127 | 54.67477 | -3.23625 | 2 | 113 | 18.5 |
| **Lake** | VR2Tx - 486176 | 54.67797 | -3.23862 | 2 | 113 | 42.6 |
| **Lake** | VR2Tx - 486168 | 54.67802 | -3.23630 | 2 | 113 | - |
| **Lake** | VR2W - 135765 | 54.67753 | -3.24358 | 2 | 120 | 95.2 |
| **River** | VR2W - 135758 | 54.68786 | -3.29339 | 3 | 120 | 94.7 |
| **River** | VR2W - 135752 | 54.68688 | -3.30222 | 3 | 120 | 16.3 |
| **River** | VR2W - 135762 | 54.67545 | -3.36124 | 3 | 120 | 19.3 |
| **River** | VR2W - 135754 | 54.66002 | -3.44642 | 3 | 120 | 100 |
| **River** | VR2Tx - 484134 | 54.65931 | -3.50982 | 3 | 121 | 22.2 |
| **River** | VR2W - 126850 | 54.65789 | -3.51445 | 3 | 121 | 63.5 |
| **River** | VR2Tx - 484126 | 54.65405 | -3.51411 | 3 | 121 | 100 |
| **River** | VR2W - 105520 | 54.65520 | -3.51660 | 3 | 121 | 5.1 |
| **River** | VR2W - 135757 | 54.65344 | -3.51584 | 3 | 121 | 10.2 |
| **River** | VR2W - 135756 | 54.65371 | -3.51781 | 3 | 121 | 5.1 |
| **River** | VR2W - 135761 | 54.64947 | -3.52366 | 3 | 121 | 5.1 |
| **River** | VR2Tx - 484131 | 54.64916 | -3.53263 | 3 | 121 | 100 |

| | | | | | | |
|---|---|---|---|---|---|---|
| **River** | VR2Tx - 484128 | 54.64728 | -3.53188 | 3 | 121 | 38.2 |
| **River** | VR2W - 135755 | 54.64649 | -3.54242 | 3 | 121 | 12.1 |

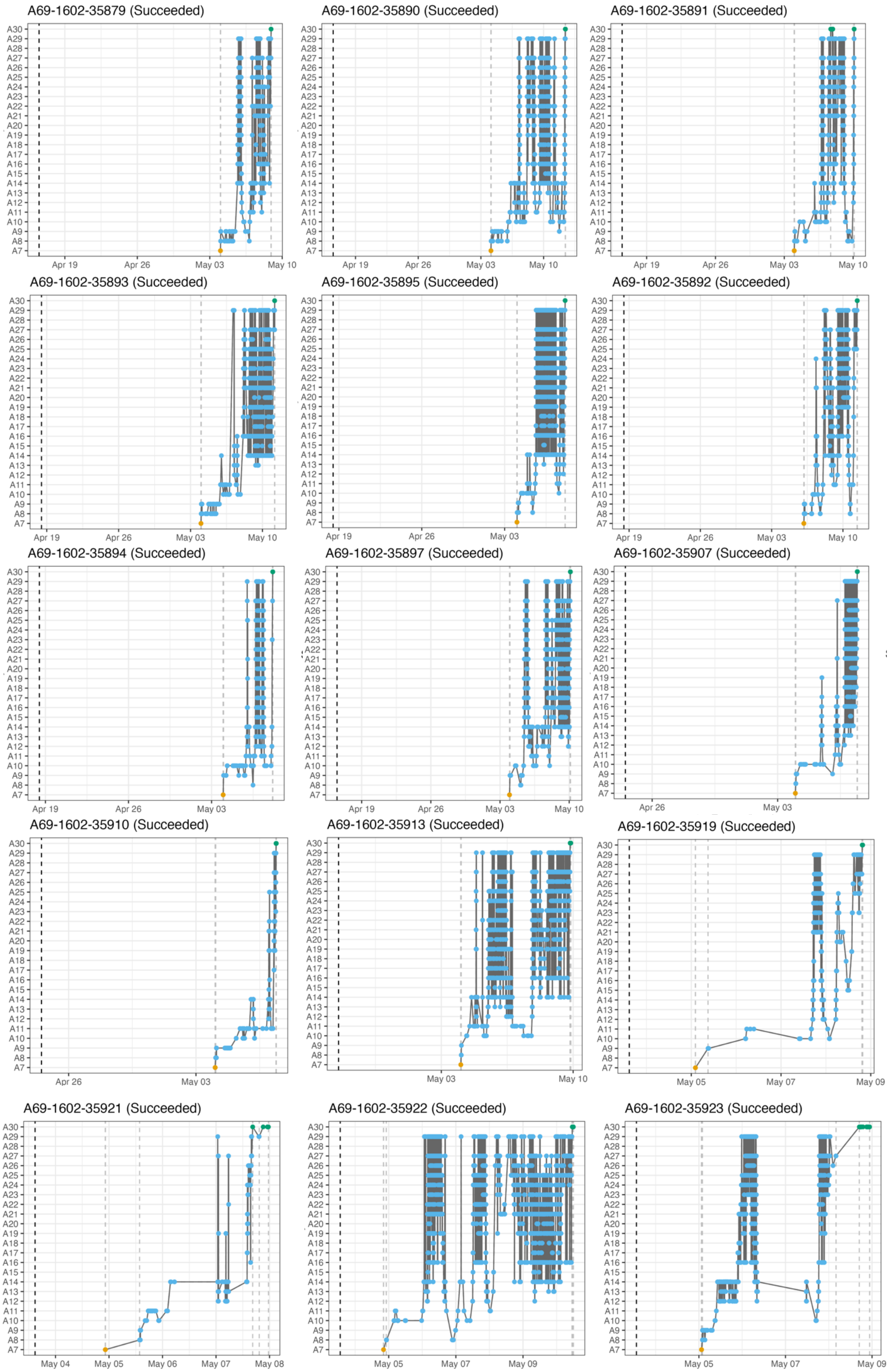
*Table B.3* Receiver deployment and detection efficiency (%) throughout the River Derwent in 2022.

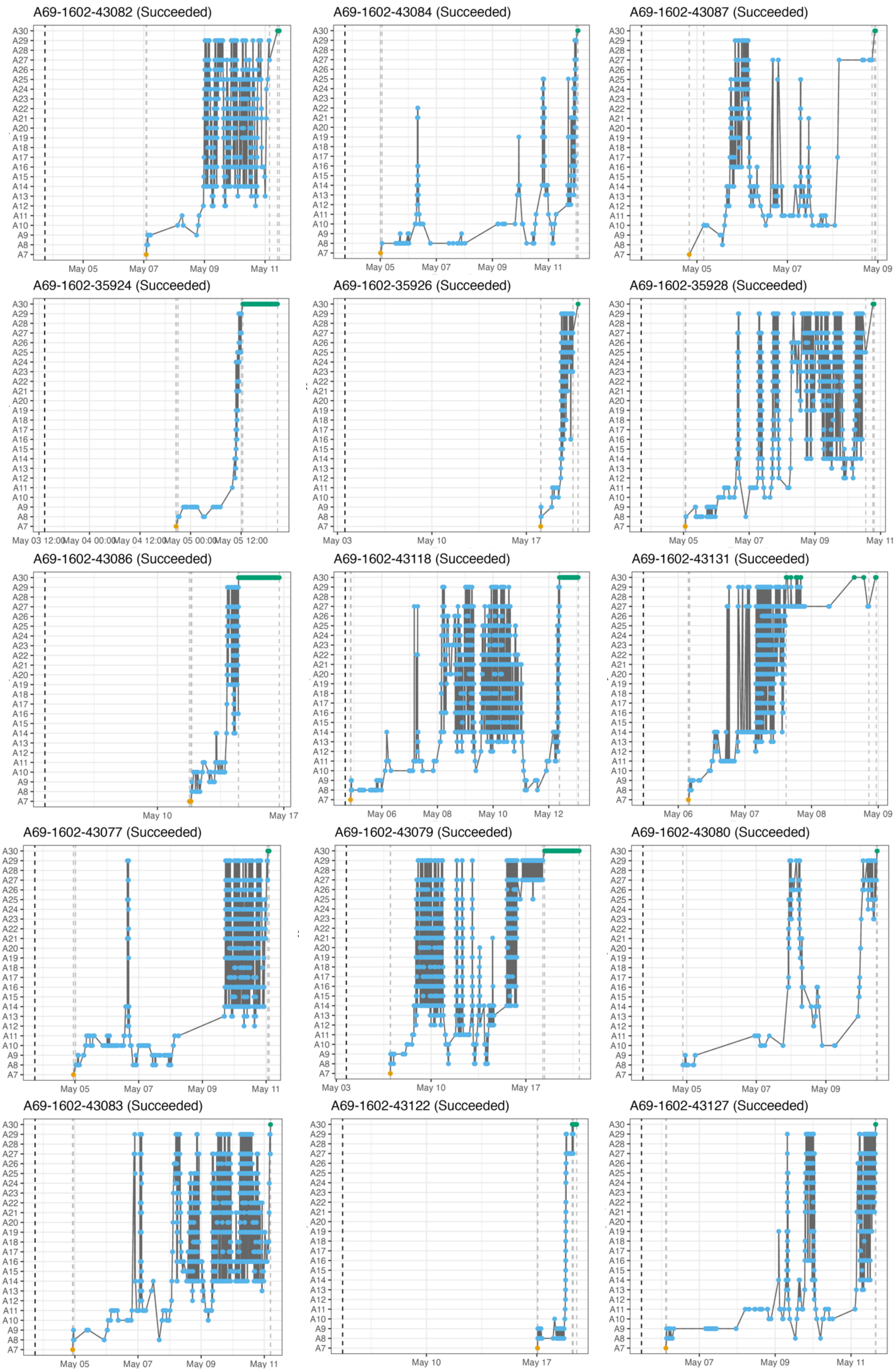
| Type | ID | Latitude | Longitude | Section | Days Deployed | Detection Efficiency (%) |
|---|---|---|---|---|---|---|
| **River** | VR2Tx - 480410 | 54.687067 | -3.259025 | 3 | 117 | 25.7 |
| **River** | VR2Tx - 486175 | 54.687814 | -3.294135 | 3 | 117 | 89 |
| **River** | VR2Tx - 486170 | 54.687100 | -3.303152 | 3 | 117 | 84.1 |
| **River** | VR2Tx - 486171 | 54.687903 | -3.305247 | 3 | 117 | 87.8 |
| **River** | VR2Tx - 484127 | 54.686985 | -3.334159 | 3 | 117 | 97.6 |
| **River** | VR2Tx - 484133 | 54.674626 | -3.361275 | 3 | 117 | 98.6 |
| **River** | VR2Tx - 486179 | 54.671285 | -3.359235 | 3 | 117 | 88.9 |
| **River** | VR2Tx - 484126 | 54.666754 | -3.382345 | 3 | 117 | 17.5 |
| **River** | VR2Tx - 484135 | 54.668371 | -3.426363 | 3 | 117 | 20.6 |
| **River** | VR2Tx - 486167 | 54.660023 | -3.44642 | 3 | 117 | 98.4 |
| **River** | VR2Tx - 486177 | 54.659557 | -3.495688 | 3 | 117 | 98.3 |
| **River** | VR2Tx - 484136 | 54.658603 | -3.513464 | 3 | 118 | 5 |
| **River** | VR2Tx - 486176 | 54.658015 | -3.514325 | 3 | 118 | 20 |
| **River** | VR2Tx - 484128 | 54.655016 | -3.513884 | 3 | 118 | - |
| **River** | VR2Tx - 486180 | 54.654103 | -3.514076 | 3 | 118 | - |
| **River** | VR2Tx - 484132 | 54.655388 | -3.516561 | 3 | 118 | - |
| **River** | VR2Tx - 486172 | 54.65344 | -3.515840 | 3 | 118 | 96.7 |
| **River** | VR2Tx - 486173 | 54.653886 | -3.517737 | 3 | 118 | 71.7 |
| **River** | VR2Tx - 484137 | 54.650037 | -3.522877 | 3 | 118 | - |
| **River** | VR2Tx - 484134 | 54.649454 | -3.523680 | 3 | 118 | 100 |
| **River** | VR2Tx - 486169 | 54.649118 | -3.531626 | 3 | 118 | - |
| **River** | VR2Tx - 486178 | 54.647551 | -3.526661 | 3 | 118 | - |
| **River** | VR2Tx - 486181 | 54.647275 | -3.531879 | 3 | 118 | -- |
| **River** | VR2Tx - 484131 | 54.646430 | -3.542710 | 3 | 118 | 100 |

# Appendix C: Supplementary Information for Chapter 3.

(Investigating the migration patterns and characteristics of Atlantic salmon smolts through Bassenthwaite Lake)

The following supplementary information provides examples of the migratory trajectories of acoustically tagged Atlantic salmon smolts (successful versus unsuccessful migrants) migrating through Bassenthwaite Lake in 2021 using *Actel*.


A69-1602-35879 (Succeeded)
Apr 19 Apr 26 May 03 May 10
A69-1602-35890 (Succeeded)
Apr 19 Apr 26 May 03 May 10
A69-1602-35891 (Succeeded)
Apr 19 Apr 26 May 03 May 10
A69-1602-35893 (Succeeded)
Apr 19 Apr 26 May 03 May 10
A69-1602-35895 (Succeeded)
Apr 19 Apr 26 May 03
A69-1602-35892 (Succeeded)
Apr 19 Apr 26 May 03 May 10
A69-1602-35894 (Succeeded)
Apr 19 Apr 26 May 03
A69-1602-35897 (Succeeded)
Apr 19 Apr 26 May 03 May 10
A69-1602-35907 (Succeeded)
Apr 26 May 03
A69-1602-35910 (Succeeded)
Apr 26 May 03
A69-1602-35913 (Succeeded)
May 03 May 10
A69-1602-35919 (Succeeded)
May 05 May 07 May 09
A69-1602-35921 (Succeeded)
May 04 May 05 May 06 May 07 May 08
A69-1602-35922 (Succeeded)
May 05 May 07 May 09
A69-1602-35923 (Succeeded)
May 05 May 07 May 09


A69-1602-43082 (Succeeded)
A69-1602-43084 (Succeeded)
A69-1602-43087 (Succeeded)
A69-1602-35924 (Succeeded)
A69-1602-35926 (Succeeded)
A69-1602-35928 (Succeeded)
A69-1602-43086 (Succeeded)
A69-1602-43118 (Succeeded)
A69-1602-43131 (Succeeded)
A69-1602-43077 (Succeeded)
A69-1602-43079 (Succeeded)
A69-1602-43080 (Succeeded)
A69-1602-43083 (Succeeded)
A69-1602-43122 (Succeeded)
A69-1602-43127 (Succeeded)

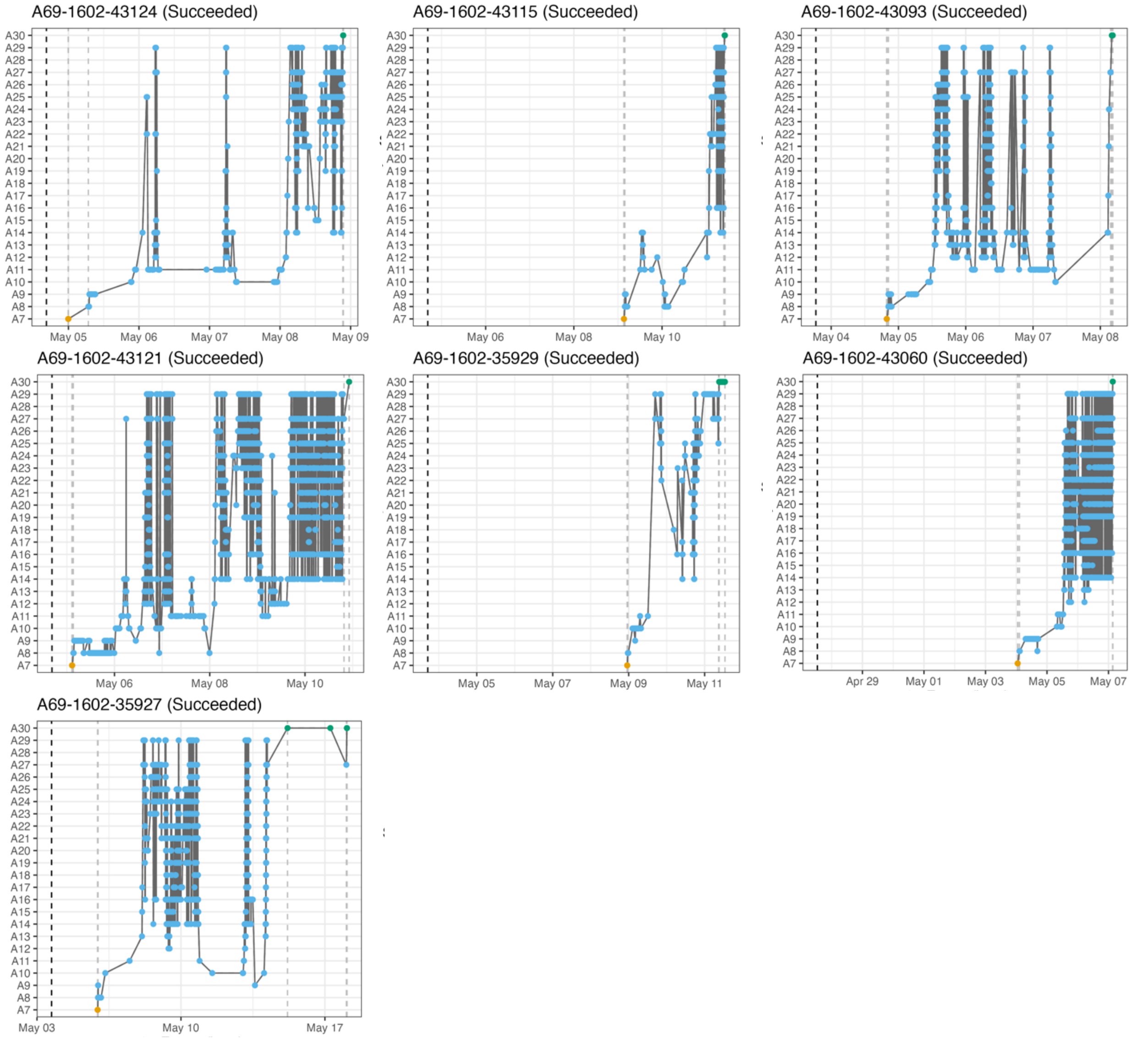
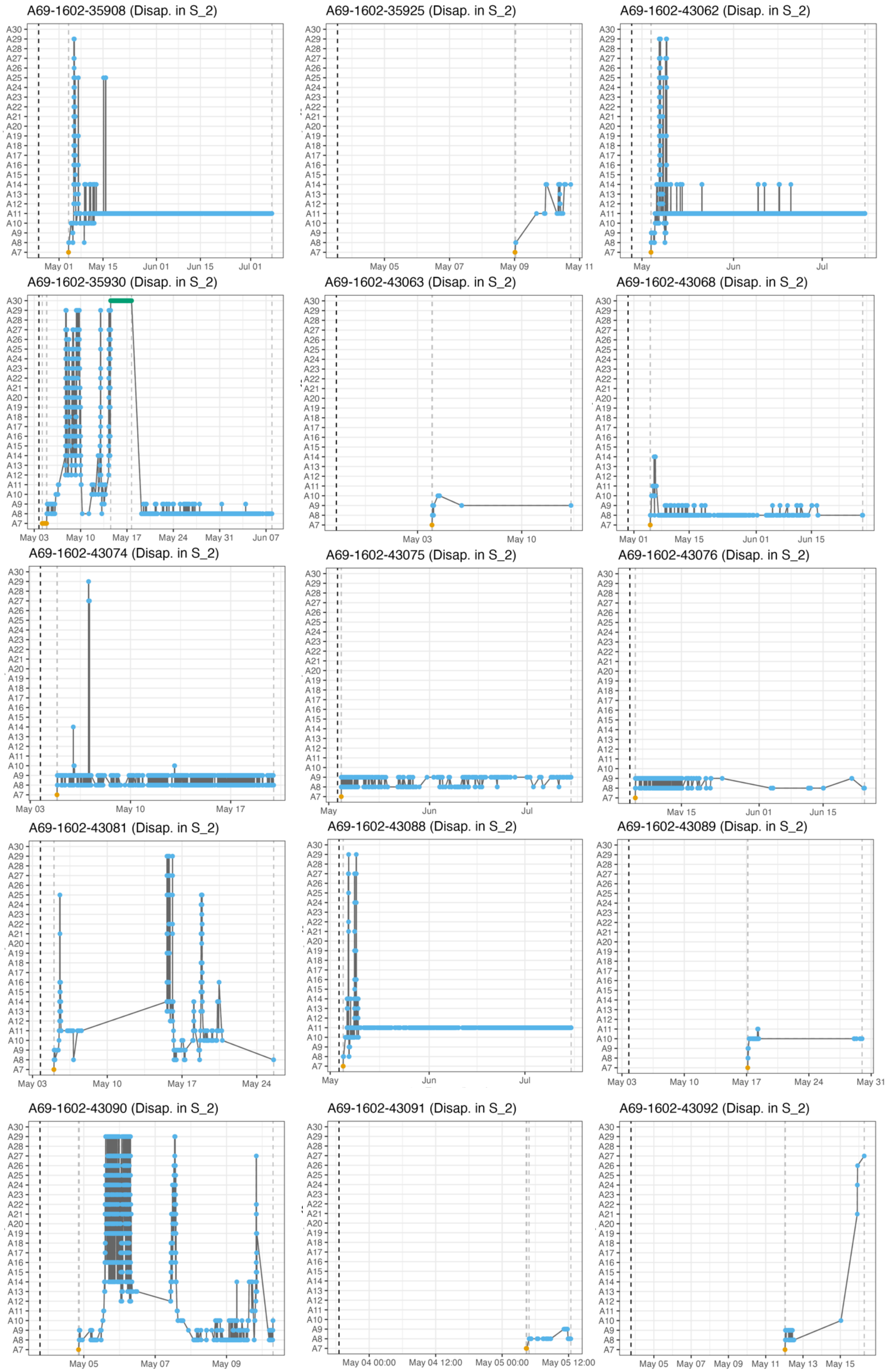



***Figure C.1*** *Migration plots of each successful lake migrant in Bassenthwaite Lake in 2021 (Chapter 3). Orange = lake entrance, Blue = migration through the lake, Green = lake exit. Receivers were given a name prior to analysis which is displayed on the y axis. Each plot represents an individual's migration with date of migration displayed on the x axis.*


A69-1602-35908 (Disap. in S_2)
A69-1602-35925 (Disap. in S_2)
A69-1602-43062 (Disap. in S_2)
A69-1602-35930 (Disap. in S_2)
A69-1602-43063 (Disap. in S_2)
A69-1602-43068 (Disap. in S_2)
A69-1602-43074 (Disap. in S_2)
A69-1602-43075 (Disap. in S_2)
A69-1602-43076 (Disap. in S_2)
A69-1602-43081 (Disap. in S_2)
A69-1602-43088 (Disap. in S_2)
A69-1602-43089 (Disap. in S_2)
A69-1602-43090 (Disap. in S_2)
A69-1602-43091 (Disap. in S_2)
A69-1602-43092 (Disap. in S_2)

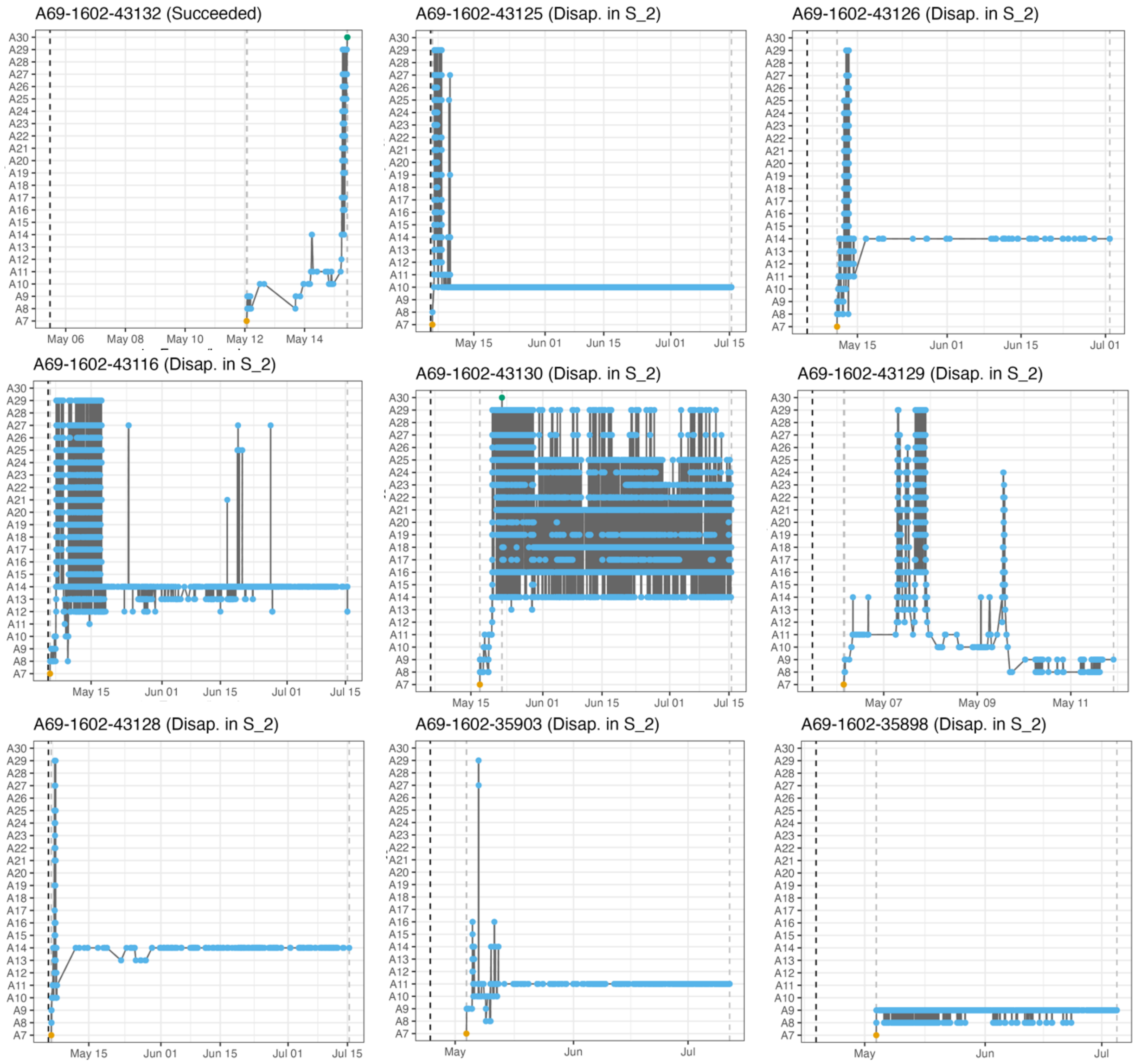



***Figure C.2*** *Migration plots of each unsuccessful lake migrant in Bassenthwaite Lake in 2021 (Chapter 3). Orange = lake entrance, Blue = migration through the lake, Green = lake exit. Receivers were given a name prior to analysis which is displayed on the y axis. Each plot represents an individual's migration with date of migration displayed on the x axis.*

## References


Aarestrup, K. and Koed, A. (2003). Survival of migrating sea trout (*Salmo trutta*) and Atlantic salmon (*Salmo salar*) smolts negotiating weirs in small Danish rivers. *Ecology of Freshwater Fish*, **12**(3), 169-176.

Aarestrup, K., Jepsen, N., Rasmussen, G. and Okland, F. (1999). Movements of two strains of radio tagged Altlantic salmon, *Salmo salar* L., smolts through a reservoir. *Fisheries Management and Ecology*, **6**(2), 97-107.

Aas, Ø., Klemetsen, A., Einum, S. and Skurdal, J. eds. (2010). *Atlantic salmon ecology*. John Wiley and Sons.

Abecasis, D., Steckenreuter, A., Reubens, J., Aarestrup, K., Alós, J., Badalamenti, F., Bajona, L., Boylan, P., Deneudt, K., Greenberg, L. and Brevé, N. (2018). A review of acoustic telemetry in Europe and the need for a regional aquatic telemetry network. *Animal Biotelemetry*, **6**, 1-7.

Adams, C.E., Chavarie, L., Rodger, J.R., Honkanen, H.M., Thambithurai, D. and Newton, M.P. (2022a). An opinion piece: the evolutionary and ecological consequences of changing selection pressures on marine migration in Atlantic salmon. *Journal of Fish Biology*, **100**(4), 860-867.

Adams, C.E., Honkanen, H.M., Bryson, E., Moore, I.E., MacCormick, M. and Dodd, J.A. (2022b). A comparison of trends in population size and life history features of Atlantic salmon (*Salmo salar*) and anadromous and non-anadromous Brown trout (*Salmo trutta*) in a single catchment over 116 years. *Hydrobiologia*, **849**(4), 945-965.

Adams, N.S., Rondorf, D.W., Evans, S.D., Kelly, J.E. and Perry, R.W. (1998). Effects of surgically and gastrically implanted radio transmitters on swimming performance and predator avoidance of juvenile chinook salmon (*Oncorhynchus tshawytscha*). *Canadian Journal of Fisheries and Aquatic Sciences*, **55**(4), 781-787.

Agostinelli, C. and Lund, U. (2022). R package 'circular': Circular Statistics (version 0.4-95). URL https://r-forge.r-project.org/projects/circular/

Ahlbeck-Bergendahl, I., April, J., Bardarson, H., Bolstad, G.H., Bradbury, I., Buoro, M., Chaput, G., Dauphin, G., Ensing, D., Erkinaro, J. and Fiske, P. (2019). *Working group on North Atlantic salmon (WGNAS)* (Doctoral dissertation, Inconnu).

Alerstam, T., Hedenström, A. and Åkesson, S. (2003). Long-distance migration: evolution and determinants. *Oikos*, **103**(2), 247-260.

Alexander, G., Sweeting, R. and McKeown, B. (1994). The shift in visual pigment dominance in the retinae of juvenile coho salmon (*Oncorhynchus kisutch*): an indicator of smolt status. *The Journal of Experimental biology*, **195**(1), 185-197.

Allegue, H., Thomas, A.C., Liu, Y. and Trites, A.W. (2020). Harbour seals responded differently to pulses of out-migrating coho and Chinook smolts. *Marine Ecology Progress Series*, **647**, 211-227.

Altizer, S., Bartel, R. and Han, B.A. (2011). Animal migration and infectious disease risk. *science*, **331**(6015), 296-302.

Antonio, R.R., Agostinho, A.A., Pelicice, F.M., Bailly, D., Okada, E.K. and Dias, J.H.P. (2007). Blockage of migration routes by dam construction: can migratory fish find alternative routes?. *Neotropical Ichthyology*, **5**(2), 177-184.

Antonsson, T., Heidarsson, T. and Snorrason, S.S. (2010). Smolt emigration and survival to adulthood in two Icelandic stocks of Atlantic salmon. *Transactions of the American Fisheries Society*, **139**(6), 1688-1698.

Aprahamian, M.W., Hickley, P., Shields, B.A. and Mawle, G.W. (2010). Examining changes in participation in recreational fisheries in England and Wales. *Fisheries Management and Ecology*, **17**(2), 93-105.

Armstrong, J.D., McKelvey, S., Smith, G.W., Rycroft, P. and Fryer, R.J. (2018). Effects of individual variation in length, condition and run-time on return rates of wild-reared Atlantic salmon *Salmo salar* smolts. *Journal of Fish Biology*, **92**(3), 569-578.

Arnold, G. and Dewar, H. (2001). Electronic tags in marine fisheries research: a 30-year perspective. In *Electronic Tagging and Tracking in Marine Fisheries: Proceedings of the Symposium on Tagging and Tracking Marine Fish with Electronic Devices, February 7–11, 2000, East-West Center, University of Hawaii* ( 7-64). Springer Netherlands.

Arnold, G.P., Webb, P.W. and Holford, B.H. (1991). The role of the pectoral fins in station-holding of Atlantic salmon parr (*Salmo salar* L.). *Journal of Experimental Biology*, *156*(1), 625-629.

Arso Civil, M., Quick, N.J., Cheney, B., Pirotta, E., Thompson, P.M. and Hammond, P.S. (2019). Changing distribution of the east coast of Scotland bottlenose dolphin population and the challenges of area-based management. *Aquatic Conservation: Marine and Freshwater Ecosystems*, **29**, 178-196.

Atkinson, G. and Moore, D. (1999). The case for releasing grilse. *Atlantic Salmon Journal*, **48**(3), 68-72.

Avgar, T., Street, G. and Fryxell, J.M. (2014). On the adaptive benefits of mammal migration. *Canadian Journal of Zoology*, **92**(6), 481-490.

Baguette, M., Blanchet, S., Legrand, D., Stevens, V.M. and Turlure, C. (2013). Individual dispersal, landscape connectivity and ecological networks. *Biological Reviews*, **88**(2), 310-326.

Bailey, H., Mate, B.R., Palacios, D.M., Irvine, L., Bograd, S.J. and Costa, D.P. (2009). Behavioural estimation of blue whale movements in the Northeast Pacific from state-space model analysis of satellite tracks. *Endangered Species Research*, **10**, 93-106.

Baisez, A., Bach, J.M., Leon, C., Parouty, T., Terrade, R., Hoffmann, M. and Laffaille, P. (2011). Migration delays and mortality of adult Atlantic salmon *Salmo salar* en route to spawning grounds on the River Allier, France. *Endangered species research*, **15**(3), 265-270.

Baker, R. (1978). *Evolutionary Ecology of Animal Migration*. Holmes and Meier Publishers.

Baras, E., Lambert, H. and Philippart, J.C. (1994). A comprehensive assessment of the failure of *Barbus barbus* spawning migrations through a fish pass in the canalized River Meuse (Belgium). *Aquatic Living Resources*, **7**(3), 181-189.

Bardonnet, A. and Baglinière, J.L.(2000). Freshwater habitat of Atlantic salmon (*Salmo salar*). *Canadian Journal of Fisheries and Aquatic Sciences*, **57**(2), 497-506.

Barry, J., Fitzgerald, C., Callaghan, J.O., Kennedy, R., Rosell, R. and Roche, W. (2024). Interannual variation in survival of wild Atlantic salmon smolts through a dynamic estuarine habitat. *Fisheries Management and Ecology*, p.e12685.

Barry, J., Kennedy, R.J., Rosell, R. and Roche, W.K. (2020). Atlantic salmon smolts in the Irish Sea: first evidence of a northerly migration trajectory. *Fisheries Management and Ecology*, **27**(5), 517-522.

Barry, J., Whelan, K., Llewelyn, I., Campbell, R. (2017). *From Headwater to Headland: Improving smolt survival in rivers and estuaries* 1–40. https://doi.org/10.13140/RG.2.2.30229.01766

Bates, D., Mächler, M., Bolker, B. and Walker, S. (2014). Fitting linear mixed-effects models using lme4. *arXiv preprint arXiv:1406.5823.*

Beaugrand, G., Reid, P.C., Ibanez, F., Lindley, J.A. and Edwards, M. (2002). Reorganization of North Atlantic marine copepod biodiversity and climate. *Science*, **296**(5573), 1692-1694.

Bednarek, A.T. (2001). Undamming rivers: a review of the ecological impacts of dam removal. *Environmental management*, **27**, 803-814.

Belliard, J., Beslagic, S., Delaigue, O. and Tales, E. (2018). Reconstructing long-term trajectories of fish assemblages using historical data: the Seine River basin (France) during the last two centuries. *Environmental Science and Pollution Research*, **25**(24), 23430-23450.

Berry, J. (1934). British mammals and birds as enemies of the Atlantic salmon (*Salmo salar*). *Reports of the Avon Biological Research*, **35**, 31-64.

Birnie-Gauvin, K., Tummers, J.S., Lucas, M.C. and Aarestrup, K. (2017b). Adaptive management in the context of barriers in European freshwater ecosystems. *Journal of Environmental Management*, **204**, 436-441.

Birnie-Gauvin, K., Aarestrup, K., Riis, T.M., Jepsen, N. and Koed, A. (2017a). Shining a light on the loss of rheophilic fish habitat in lowland rivers as a forgotten consequence of barriers, and its implications for management. *Aquatic Conservation: Marine and Freshwater Ecosystems*, **27**(6), 1345-1349.

Björnsson, B.T., Stefansson, S.O. and Hansen, T. (1995). Photoperiod regulation of plasma growth hormone levels during parr-smolt transformation of Atlantic salmon: implications for hypoosmoregulatory ability and growth. *General and Comparative Endocrinology*, **100**(1), 73-82.

Björnsson, B.T., Stefansson, S.O. and McCormick, S.D. (2011). Environmental endocrinology of salmon smoltification. *General and comparative endocrinology*, **170**(2), 290-298.

Bleeker, P. (1859). *Enumeratio specierum piscium hucusque in Archipelago indico observatarum, adjectis habitationibus citationibusque, ubi descriptiones earum recentiores reperiuntur, nec non speciebus Musei Bleekeriani Bengalensibus, Japonicis, Capensibus Tasmanicisque*. Lange and Company.

Bonte, D., Van Dyck, H., Bullock, J.M., Coulon, A., Delgado, M., Gibbs, M., Lehouck, V., Matthysen, E., Mustin, K., Saastamoinen, M. and Schtickzelle, N. (2012). Costs of dispersal. *Biological Reviews*, **87**(2), 290-312.

Bordeleau, X., Pardo, S.A., Chaput, G., April, J., Dempson, B., Robertson, M., Levy, A., Jones, R., Hutchings, J.A., Whoriskey, F.G. and Crossin, G.T. (2020). Spatio-temporal trends in the importance of iteroparity across Atlantic salmon populations of the northwest Atlantic. *ICES Journal of Marine Science*, **77**(1), 326-344.

Boström, M. (2013). Fish predation by the great cormorant (*Phalacrocorax carbo sinensis*). *Aqua licentiate theses*, (2013: 1).

Bourgeois, C.E. and O'Connell, M.F. (1988). Observations on the seaward migration of Atlantic salmon (*Salmo salar* L.) smolts through a large lake as determined by radiotelemetry and Carlin tagging studies. *Canadian Journal of Zoology*, **66**(3), 685-691.

Branco, P., Segurado, P., Santos, J.M., Pinheiro, P. and Ferreira, M.T. (2012). Does longitudinal connectivity loss affect the distribution of freshwater fish?. *Ecological Engineering*, **48**, 70-78.

Brink, K., Gough, P., Royte, J., Schollema, P.P. and Wanningen, H. (2018). From sea to source 2.0. *World fish migration foundation, Groningen*.

Brown, R.S., Cooke, S.J., Anderson, W.G. and McKinley, R.S. (1999). Evidence to challenge the "2% rule" for biotelemetry. *North American Journal of Fisheries Management*, **19**(3), 867-871.

Brown, R.S., Eppard, M.B., Murchie, K.J., Nielsen, J.L. and Cooke, S.J. (2011). An introduction to the practical and ethical perspectives on the need to advance and standardize the intracoelomic surgical implantation of electronic tags in fish. *Reviews in Fish Biology and Fisheries*, **21**, 1-9.

Brown, S.L., Bearhop, S., Harrod, C. and McDonald, R.A. (2012). A review of spatial and temporal variation in grey and common seal diet in the United Kingdom and Ireland. *Journal of the Marine Biological Association of the United Kingdom*, **92**(8), 1711-1722.

Bujold, V., Cunjak, R.A., Dietrich, J.P. and Courtemanche, D.A. (2004). Drifters versus residents: assessing size and age differences in Atlantic salmon (*Salmo salar*) fry. *Canadian Journal of Fisheries and Aquatic Sciences*, **61**(2), 273-282.

Bunt, C.M., Castro-Santos, T. and Haro, A. (2012). Performance of fish passage structures at upstream barriers to migration. *River Research and Applications*, **28**(4), 457-478.

Buren, A.D., Koen-Alonso, M., Pepin, P., Mowbray, F., Nakashima, B., Stenson, G., Ollerhead, N. and Montevecchi, W.A. (2014). Bottom-up regulation of capelin, a keystone forage species. *PLoS One*, **9**(2), p.e87589.

Campbell, H.A., Watts, M.E., Dwyer, R.G. and Franklin, C.E. (2012). V-Track: software for analysing and visualising animal movement from acoustic telemetry detections. *Marine and Freshwater Research*, **63**(9), 815-820.

Cantonati, M., Poikane, S., Pringle, C.M., Stevens, L.E., Turak, E., Heino, J., Richardson, J.S., Bolpagni, R., Borrini, A., Cid, N. and Čtvrtlíková, M. (2020). Characteristics, main impacts, and stewardship of natural and artificial freshwater environments: consequences for biodiversity conservation. *Water*, **12**(1), 260.

Carey, J.B. and McCormick, S.D. (1998). Atlantic salmon smolts are more responsive to an acute handling and confinement stress than parr. *Aquaculture*, **168**(1-4), 237-253.

Carss, D.N., Kruuk, H. and Conroy, J.W.H. (1990). Predation on adult Atlantic salmon, *Salmo salar* L., by otters, *Lutra lutra* (L.), within the River Dee system, Aberdeenshire, Scotland. *Journal of Fish Biology*, **37**(6), 935-944.

Carter, T.J., Pierce, G.J., Hislop, J.R.G., Houseman, J.A. and Boyle, P.R. (2001). Predation by seals on salmonids in two Scottish estuaries. *Fisheries Management and Ecology*, **8**(3), 207-225.

Caudill, C.C., Daigle, W.R., Keefer, M.L., Boggs, C.T., Jepson, M.A., Burke, B.J., Zabel, R.W., Bjornn, T.C. and Peery, C.A. (2007). Slow dam passage in adult Columbia River salmonids associated with unsuccessful migration: delayed negative effects of passage obstacles or condition-dependent mortality?. *Canadian Journal of Fisheries and Aquatic Sciences*, **64**(7), 979-995.

Ceballos, G. and Ehrlich, P.R. (2002). Mammal population losses and the extinction crisis. *Science*, **296**(5569), 904-907.

Chanseau, M., Croze, O. and Larinier, M. (1999). The impact of obstacles on the Pau River (France) on the upstream migration of returning adult Atlantic salmon (*Salmo salar* L.). *Bulletin Francais de la Peche et de la Pisciculture*, **353**.

Chapman, D., Carlson, C., Weitkamp, D., Matthews, G., Stevenson, J. and Miller, M. (1997). Homing in sockeye and chinook salmon transported around part of their smolt migration route in the Columbia River. *North American Journal of Fisheries Management*, **17**(1), 101-113.

Chaput, G. (2012). Overview of the status of Atlantic salmon (*Salmo salar*) in the North Atlantic and trends in marine mortality. *ICES Journal of Marine Science*, **69**(9), 1538-1548.

Chaput, G., Carr, J., Daniels, J., Tinker, S., Jonsen, I. and Whoriskey, F. (2019). Atlantic salmon (*Salmo salar*) smolt and early post-smolt migration and survival inferred from multi-year and multi-stock acoustic telemetry studies in the Gulf of St. Lawrence, northwest Atlantic. *ICES Journal of Marine Science*, **76**(4), 1107-1121.

Chavarie, L., Honkanen, H.M., Newton, M., Lilly, J.M., Greetham, H.R. and Adams, C.E. (2022). The benefits of merging passive and active tracking approaches: New insights into riverine migration by salmonid smolts. *Ecosphere*, **13**(5), p.e4045.

Cherry (2016) *Atlantic salmon (Salmo salar)*, *Nature Table*. Available at: https://animalcaseprofile.wordpress.com/2016/05/01/atlantic-salmon-salmo-salar/ (Accessed: 18 June 2023).

Clements, S., Jepsen, D., Karnowski, M. and Schreck, C.B. (2005). Optimization of an acoustic telemetry array for detecting transmitter-implanted fish. *North American Journal of Fisheries Management*, **25**(2), 429-436.

Condron, A., DeConto, R., Bradley, R.S. and Juanes, F. (2005). Multidecadal North Atlantic climate variability and its effect on North American salmon abundance. *Geophysical Research Letters*, **32**(23).

Cooke, S.J. and Suski, C.D. (2005). Do we need species-specific guidelines for catch-and-release recreational angling to effectively conserve diverse fishery resources?. *Biodiversity and Conservation*, **14**, 1195-1209.

Cooke, S.J., Donaldson, M.R., O'connor, C.M., Raby, G.D., Arlinghaus, R., Danylchuk, A.J., Hanson, K.C., Hinch, S.G., Clark, T.D., Patterson, D.A. and Suski, C.D. (2013). The physiological consequences of catch-and-release angling: perspectives on experimental design, interpretation, extrapolation and relevance to stakeholders. *Fisheries Management and Ecology*, **20**(2-3), 268-287.

Cooke, S.J., Woodley, C.M., Brad Eppard, M., Brown, R.S. and Nielsen, J.L. (2011). Advancing the surgical implantation of electronic tags in fish: a gap analysis and research agenda based on a review of trends in intracoelomic tagging effects studies. *Reviews in Fish Biology and Fisheries*, **21**, 127-151.

Copeland, C., Baker, E., Koehn, J.D., Morris, S.G. and Cowx, I.G. (2017). Motivations of recreational fishers involved in fish habitat management. *Fisheries Management and Ecology*, **24**(1), 82-92.

Cote, D., Kehler, D.G., Bourne, C. and Wiersma, Y.F. (2009). A new measure of longitudinal connectivity for stream networks. *Landscape Ecology*, **24**, 101-113.

Coutant, C.C. (2001). Turbulent attraction flows for guiding juvenile salmonids at dams. In *Behavioral technologies for fish guidance: American Fisheries Society Symposium* (p. 57).

Cresswell, K.A., Satterthwaite, W.H. and Sword, G.A. (2011). Understanding the evolution of migration through empirical examples. *Animal migration: a synthesis*, p7-16.

Crisp, D.T. and Hurley, M.A. (1991). Stream channel experiments on downstream movement of recently emerged trout*, Salmo trutta* L. and salmon, *S. salar* L.—I. Effect of four different water velocity treatments upon dispersal rate. *Journal of Fish Biology*, **39**(3), 347-361.

Crisp, D.T. (1988). Prediction, from temperature, of eyeing, hatching and 'swim-up'times for salmonid embryos. *Freshwater biology*, **19**(1), 41-48.

Crossin, G.T., Heupel, M.R., Holbrook, C.M., Hussey, N.E., Lowerre-Barbieri, S.K., Nguyen, V.M., Raby, G.D. and Cooke, S.J. (2017). Acoustic telemetry and fisheries management. *Ecological Applications*, **27**(4), 1031-1049.

Croze, O., Salaun, B., Chanseau, M. and Larinier, M. (2000). Study of the efficiency of two fish pass installations for Atlantic salmon smolts (*Salmo salar* L.) at the hydroelectric power stations of Guilhot and Las Mijanes (Ariège-09).

Crozier, W.W., Schön, P.J., Chaput, G., Potter, E.C.E., Maoileidigh, N.O. and MacLean, J.C. (2004). Managing Atlantic salmon (*Salmo salar* L.) in the mixed stock environment: challenges and considerations. *ICES Journal of Marine Science*, **61**(8), 1344-1358.

Cuvier, G. (1816). Le règne animal distribué d'après son organisation, pour servir de base à l'histoire naturelle des animaux et d'introduction à l'anatomie comparée. Vol. 1. Les mammifères et les oiseaux. A. Belin, Paris, xxxvii, 540

Dabrowski, T., Hartnett, M. and Olbert, A.I., 2010. Influence of seasonal circulation on flushing of the Irish Sea. *Marine Pollution Bulletin*, *60*(5), 748-758.

Dadswell, M., Spares, A., Reader, J., McLean, M., McDermott, T., Samways, K. and Lilly, J. (2022). The decline and impending collapse of the Atlantic Salmon (*Salmo salar*) population in the North Atlantic Ocean: a review of possible causes. *Reviews in Fisheries Science & Aquaculture*, **30**(2), 215-258.

Daley, R.K., Williams, A., Green, M., Barker, B. and Brodie, P. (2015). Can marine reserves conserve vulnerable sharks in the deep sea? A case study of *Centrophorus zeehaani* (Centrophoridae), examined with acoustic telemetry. *Deep Sea Research Part II: Topical Studies in Oceanography*, **115**, 127-136.

Davidsen, J., Svenning, M.A., Orell, P., Yoccoz, N., Dempson, J.B., Niemelä, E., Klemetsen, A., Lamberg, A. and Erkinaro, J. (2005). Spatial and temporal migration of wild Atlantic salmon smolts determined from a video camera array in the sub-Arctic River Tana. *Fisheries Research*, **74**(1-3), 210-222.

Davidsen, J.G., Plantalech Manel-la, N., Økland, F., Diserud, O.H., Thorstad, E.B., Finstad, B., Sivertsgård, R., McKinley, R.S. and Rikardsen, A.H. (2008). Changes in swimming depths of Atlantic salmon *Salmo salar* post-smolts relative to light intensity. *Journal of Fish Biology*, **73**(4), 1065-1074.

Davidsen, J.G., Rikardsen, A.H., Halttunen, E., Thorstad, E.B., Økland, F., Letcher, B.H., Skarðhamar, J. and Næsje, T.F. (2009). Migratory behaviour and survival rates of wild northern Atlantic salmon *Salmo salar* post-smolts: effects of environmental factors. *Journal of Fish Biology*, **75**(7), 1700-1718.

Deinet, S., Scott-Gatty, K., Rotton, H., Twardek, W.M., Marconi, V., McRae, L., Baumgartner, L.J., Brink, K., Claussen, J.E., Cooke, S.J. and Darwall, W. (2020). The Living Planet Index (lpi) for Migratory Freshwater Fish: Technical Report.

Delgado, M.L. and Ruzzante, D.E. (2020). Investigating diadromy in fishes and its loss in an-omics era. *Iscience*, **23**(12), 101837.

Deng, Z.D., Carlson, T.J., Li, H., Xiao, J., Myjak, M.J., Lu, J., Martinez, J.J., Woodley, C.M., Weiland, M.A. and Eppard, M.B. (2015). An injectable acoustic transmitter for juvenile salmon. *Scientific Reports*, **5**(1), 8111.

Dieperink, C., Bak, B.D., Pedersen, L.F., Pedersen, M.I. and Pedersen, S. (2002). Predation on Atlantic salmon and sea trout during their first days as postsmolts. *Journal of Fish Biology*, **61**(3), 848-852.

Dingle, H. and Drake, V.A. (2007). What is migration?. *Bioscience*, **57**(2), 113-121.

Dodd, J.A. and Adams, C.E. (2014). Clyde re-built: when will river invertebrate communities return to a pre-industrial condition?. *Glasgow Naturalist*, **26**(Part 1), 55-62.

Dodd, J.R., Cowx, I.G. and Bolland, J.D. (2018). Win, win, win: low cost baffle fish pass provides improved passage efficiency, reduced passage time and broadened passage flows over a low-head weir. *Ecological Engineering*, **120**, 68-75.

Drenner, S.M., Clark, T.D., Whitney, C.K., Martins, E.G., Cooke, S.J. and Hinch, S.G. (2012). A synthesis of tagging studies examining the behaviour and survival of anadromous salmonids in marine environments. *PloS one*, **7**(3), p.e31311.

Ducharme, L.J.A. (1969). Atlantic salmon returning for their fifth and sixth consecutive spawning trips. *Journal of the Fisheries Board of Canada*, **26**(6), 1661-1664.

Dunbar, M.J. and Thomson, D.H. (1979). West Greenland salmon and climatic change [Atlantic salmon, *Salmo salar* L.]. *Meddelelser om Groenland (Denmark)*.

Duncan, J.R. and Lockwood, J.L. (2001). Extinction in a field of bullets: a search for causes in the decline of the world's freshwater fishes. *Biological Conservation*, **102**(1), 97-105.

Dynesius, M. and Nilsson, C. (1994). Fragmentation and flow regulation of river systems in the northern third of the world. *Science*, **266**(5186), 753-762.

Espinoza, M., Lédée, E.J., Simpfendorfer, C.A., Tobin, A.J. and Heupel, M.R. (2015). Contrasting movements and connectivity of reef-associated sharks using acoustic telemetry: Implications for management. *Ecological Applications*, **25**(8), 2101-2118.

Evans, C.D., Cullen, J.M., Alewell, C., Kopácek, J., Marchetto, A., Moldan, F., Prechtel, A., Rogora, M., Veselý, J. and Wright, R. (2001). Recovery from acidification in European surface waters. *Hydrology and Earth System Sciences*, **5**(3), 283-298.

Evropeizeva, N.W. (1959). Experimental analysis of the young salmon (*Salmo salar* L.) in the stage of transition to life in the sea. *Ra PV Randn. Cons. Int. Explor. Mer*, **148**, 29-39.

Fängstam, H. (1993). Individual downstream swimming speed during the natural smolting period among young of Baltic salmon (*Salmo salar*). *Canadian Journal of Zoology*, **71**(9), 1782-1786.

Fenkes, M., Shiels, H.A., Fitzpatrick, J.L. and Nudds, R.L. (2016). The potential impacts of migratory difficulty, including warmer waters and altered flow conditions, on the reproductive success of salmonid fishes. *Comparative Biochemistry and Physiology Part A: Molecular and Integrative Physiology*, **193**, 11-21.

Ferguson, J.W. (2005). *The behavior and ecology of downstream migrating Atlantic Salmon (Salmo salar L.) and Brown Trout (Salmo trutta L.) in regulated rivers in northern Sweden*. Vattenbruksinstitutionen, Sveriges lantbruksuniversitet.

Ferguson, J.W., Absolon, R.F., Carlson, T.J. and Sandford, B.P. (2006). Evidence of delayed mortality on juvenile Pacific salmon passing through turbines at Columbia River dams. *Transactions of the American Fisheries Society*, **135**(1), 139-150.

Fernandes, W.P., Ibbotson, A.T., Griffiths, S.W., Maxwell, D.L., Davison, P.I. and Riley, W.D. (2015). Does relatedness influence migratory timing and behaviour in Atlantic salmon smolts?. *Animal Behaviour*, **106**, 191-199.

Finstad, B., Økland, F., Thorstad, E.B., Bjørn, P.A. and McKinley, R.S. (2005). Migration of hatchery-reared Atlantic salmon and wild anadromous brown trout post-smolts in a Norwegian fjord system. *Journal of Fish Biology*, **66**(1), 86-96.

Fjeldstad, H.P., Barlaup, B.T., Stickler, M., Gabrielsen, S.E. and Alfredsen, K. (2012). Removal of weirs and the influence on physical habitat for salmonids in a Norwegian river. *River Research and Applications*, **28**(6), 753-763.

Flávio, H. and Baktoft, H. (2021). Actel: Standardised analysis of acoustic telemetry data from animals moving through receiver arrays. *Methods in Ecology and Evolution*, **12**(1), 196-203.

Flávio, H., Aarestrup, K., Jepsen, N. and Koed, A. (2019). Naturalised Atlantic salmon smolts are more likely to reach the sea than wild smolts in a lowland fjord. *River Research and Applications*, **35**(3), 216-223.

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

Fleming, I. A., and Einum, S. (2011). Reproductive ecology: A tale of two sexes. In Ø. Aas, S. Einum, A. Klemesten, and J. Skurdal (Eds.), *Atlantic Salmon Ecology* (33-65). Wiley. https://doi.org/10.1002/9781444327755.ch2

Fleming, I.A. (1996). Reproductive strategies of Atlantic salmon: ecology and evolution. *Reviews in Fish Biology and Fisheries*, **6**, 379-416.

Fleming, I.A. (1998). Pattern and variability in the breeding system of Atlantic salmon (*Salmo salar*), with comparisons to other salmonids. *Canadian Journal of Fisheries and Aquatic Sciences*, **55**(S1), 59-76.

Flye, M.E., Sponarski, C.C., Zydlewski, J.D. and McGreavy, B. (2021). Understanding collaborative governance from a communication network perspective: A case study of the Atlantic Salmon recovery framework. *Environmental Science and Policy*, **115**, 79-90.

Forseth, T., Barlaup, B.T., Finstad, B., Fiske, P., Gjøsæter, H., Falkegård, M., Hindar, A., Mo, T.A., Rikardsen, A.H., Thorstad, E.B. and Vøllestad, L.A. (2017). The major threats to Atlantic salmon in Norway. *ICES Journal of Marine Science*, **74**(6), 1496-1513.

Frank, H.J., Mather, M.E., Smith, J.M., Muth, R.M., Finn, J.T. and McCormick, S.D. (2009). What is “fallback”?: metrics needed to assess telemetry tag effects on anadromous fish behavior. *Hydrobiologia*, **635**, 237-249.

Fraser, D., Palmer, S., Stewart-Russon, I. (2015). Cumulative effects of hydropower schemes on fish migration and populations. Environment Agency Science Report SC120078, Environment Agency, Bristol, UK.

Frechette, D.M., Dugdale, S.J., Dodson, J.J. and Bergeron, N.E. (2018). Understanding summertime thermal refuge use by adult Atlantic salmon using remote sensing, river temperature monitoring, and acoustic telemetry. *Canadian Journal of Fisheries and Aquatic Sciences*, **75**(11), 1999-2010.

Friedland, K.D., Hansen, L.P., Dunkley, D.A. and MacLean, J.C. (2000). Linkage between ocean climate, post-smolt growth, and survival of Atlantic salmon (*Salmo salar* L.) in the North Sea area. *ICES Journal of Marine science*, **57**(2), 419-429.

Friedland, K.D., Reddin, D.G. and Castonguay, M. (2003). Ocean thermal conditions in the post-smolt nursery of North American Atlantic salmon. *ICES Journal of Marine Science*, **60**(2), 343-355.

Fujihara, M.P. and Hungate, F.P. (1971). Chondrococcus columnaris disease of fishes: influence of Columbia River fish ladders. *Journal of the Fisheries Board of Canada*, **28**(4), 533-536.

Fullerton, A.H., Burnett, K.M., Steel, E.A., Flitcroft, R.L., Pess, G.R., Feist, B.E., Torgersen, C.E., Miller, D.J. and Sanderson, B.L. (2010). Hydrological connectivity for riverine fish: measurement challenges and research opportunities. *Freshwater Biology*, **55**(11), 2215-2237.

Furey, N.B., Vincent, S.P., Hinch, S.G. and Welch, D.W. (2015). Variability in migration routes influences early marine survival of juvenile salmon smolts. *PLoS One*, **10**(10), p.e0139269.

Gaffney, S.P. (2001). *Use of satellite imagery to essess trends in water clarity in the Irish Sea* (Doctoral dissertation, Ph. D. Thesis, National University of Ireland Galway, Galway).

García-Vazquez, E., Moran, P., Martinez, J.L., Perez, J., De Gaudemar, B. and Beall, E. (2001). Alternative mating strategies in Atlantic salmon and brown trout. *Journal of Heredity*, *92*(2), 146-149.

Garcia de Leaniz, C. (2008). Weir removal in salmonid streams: implications, challenges and practicalities. *Hydrobiologia*, **609(**1), 83-96.

Gargan, P.G., Forde, G., Hazon, N., Russell, D.J.F. and Todd, C.D. (2012). Evidence for sea lice-induced marine mortality of Atlantic salmon (*Salmo salar*) in western Ireland from experimental releases of ranched smolts treated with emamectin benzoate. *Canadian Journal of Fisheries and Aquatic Sciences*, **69**(2), 343-353.

Gauld, N.R., Campbell, R.N.B. and Lucas, M.C. (2013). Reduced flow impacts salmonid smolt emigration in a river with low-head weirs. *Science of the Total Environment*, **458**, 435-443.

Gazit, T., Apostle, R. and Branton, R. (2013). Deployment, tracking, and data management: technology and science for a global ocean tracking network. *Journal of International Wildlife Law and Policy*, **16**(2-3), 112-127.

Gibson, A.J.F., Halfyard, E.A., Bradford, R.G., Stokesbury, M.J. and Redden, A.M. (2015). Effects of predation on telemetry-based survival estimates: insights from a study on endangered Atlantic salmon smolts. *Canadian Journal of Fisheries and Aquatic Sciences*, **72**(5), 728-741.

Gilbey, J., Utne, K.R., Wennevik, V., Beck, A.C., Kausrud, K., Hindar, K., Garcia de Leaniz, C., Cherbonnel, C., Coughlan, J., Cross, T.F. and Dillane, E. (2021). The early marine distribution of Atlantic salmon in the North-east Atlantic: A genetically informed stock-specific synthesis. *Fish and Fisheries*, **22**(6), 1274-1306.

Gingerich, A.J., Bellgraph, B.J., Brown, R.S., Tavan, N.T., Deng, Z.D. and Brown, J.R. (2012). Quantifying reception strength and omnidirectionality of underwater radio telemetry antennas: Advances and applications for fisheries research. *Fisheries Research*, **121**, 1-8.

Goulette, G.S., Hawkes, J.P., Kocik, J.F., Manning, J.P., Music, P.A., Wallinga, J.P. and Zydlewski, G.B. (2014). Opportunistic acoustic telemetry platforms: benefits of collaboration in the Gulf of Maine. *Fisheries*, **39**(10), 441-450.

CEFAS. (2019). CEFAS, Environment Agency and Natural Resources Wales; Assessment of salmon stocks and fisheries in England and Wales [Internet]. Available from: https://assets.publishing.service.gov.uk/government/uploads/system/uploads/attachment_data/file/919701/SalmonReport-2018-background_final.pdf

Gowans, A.R.D., Armstrong, J.D., Priede, I.G. and Mckelvey, S. (2003). Movements of Atlantic salmon migrating upstream through a fish-pass complex in Scotland. *Ecology of Freshwater Fish*, **12**(3), 177-189.

Grant, J.W., Steingrímsson, S.Ó., Keeley, E.R. and Cunjak, R.A. (1998). Implications of territory size for the measurement and prediction of salmonid abundance in streams. *Canadian Journal of Fisheries and Aquatic Sciences*, **55**(S1), 181-190.

Gray, R.H. and Haynes, J.M. (1977). Depth distribution of adult chinook salmon (*Oncorhynchus tshawytscha*) in relation to season and gas-supersaturated water. *Transactions of the American Fisheries Society*, **106**(6), 617-620.

Green, A., Honkanen, H.M., Ramsden, P., Shields, B., del Villar-Guerra, D., Fletcher, M., Walton, S., Kennedy, R., Rosell, R., O'Maoiléidigh, N. and Barry, J. (2022). Evidence of long-distance coastal sea migration of Atlantic salmon, *Salmo salar*, smolts from northwest England (River Derwent). *Animal Biotelemetry*, **10**(1), p.3.

Greene, C.H., Block, B.A., Welch, D., Jackson, G., Lawson, G.L. and Rechisky, E.L. (2009). Advances in conservation oceanography: new tagging and tracking technologies and their potential for transforming the science underlying fisheries management. *Oceanography*, **22**(1), 210-223.

Gregory, S.D., Gillson, J.P., Whitlock, K., Barry, J., Gough, P., Hillman, R.J., Mee, D., Peirson, G., Shields, B.A., Talks, L. and Toms, S. (2023). Estimation of returning Atlantic salmon stock from rod exploitation rate for principal salmon rivers in England & Wales. *ICES Journal of Marine Science*, **80**(10), 2504-2519.

Gross, M.R. (1987). The evolution of diadromy in fishes. 14–25. In *Common Strategies of Anadromous and Catadromous Fishes. American Fisheries Society Symposium* (Vol. 1).

Guiny, E., Ervine, D.A. and Armstrong, J.D. (2005). Hydraulic and biological aspects of fish passes for Atlantic salmon. *Journal of Hydraulic Engineering*, **131**(7), 542-553.

Gustafson-Marjanen, K.I. and Dowse, H.B. (1983). Seasonal and diel patterns of emergence from the redd of Atlantic salmon (*Salmo salar*) fry. *Canadian Journal of Fisheries and Aquatic Sciences*, **40**(6), 813-817.

Halfyard, E.A., Gibson, A.J.F., Ruzzante, D.E., Stokesbury, M.J.W. and Whoriskey, F.G. (2012). Estuarine survival and migratory behaviour of Atlantic salmon *Salmo salar* smolts. *Journal of Fish Biology*, **81**(5), 1626-1645.

Halfyard, E.A., Gibson, A.J.F., Stokesbury, M.J., Ruzzante, D.E. and Whoriskey, F.G. (2013). Correlates of estuarine survival of Atlantic salmon postsmolts from the Southern Upland, Nova Scotia, Canada. *Canadian Journal of Fisheries and Aquatic Sciences*, **70**(3), 452-460.

Halvorsen, M. and Jørgensen, L. (1996). Lake-use by juvenile Atlantic salmon (*Salmo salar* L.) and other salmonids in northern Norway. *Ecology of Freshwater Fish*, **5**(1), 28-36.

Handeland, S.O., Berge, Å., Björnsson, B.T. and Stefansson, S.O. (1998). Effects of temperature and salinity on osmoregulation and growth of Atlantic salmon (*Salmo salar* L.) smolts in seawater. *Aquaculture*, **168**(1-4), 289-302.

Handeland, S.O., Järvi, T., Fernö, A. and Stefansson, S.O. (1996). Osmotic stress, antipredatory behaviour, and mortality of Atlantic salmon (*Salmo salar*) smolts. *Canadian Journal of Fisheries and Aquatic Sciences*, **53**(12), 2673-2680.

Hansen, L.P. and Jonsson, B. (1985). Downstream migration of hatchery-reared smolts of Atlantic salmon (*Salmo salar* L.) in the River Imsa, Norway. *Aquaculture*, **45**(1-4), 237-248.

Hansen, L.P. and Quinn, T.P. (1998). The marine phase of the Atlantic salmon (*Salmo salar*) life cycle, with comparisons to Pacific salmon. *Canadian Journal of Fisheries and Aquatic Sciences*, **55**(S1), 104-118.

Hansen, L.P., Jonsson, N. and Jonsson, B. (1993). Oceanic migration in homing Atlantic salmon. *Animal behaviour*, **45**(5), 927-941.

Hanssen, E.M., Vollset, K.W., Salvanes, A.G.V., Barlaup, B., Whoriskey, K., Isaksen, T.E., Normann, E.S., Hulbak, M. and Lennox, R.J. (2022). Acoustic telemetry predation sensors reveal the tribulations of Atlantic salmon (*Salmo salar*) smolts migrating through lakes. *Ecology of Freshwater Fish*, **31**(2), 424-437.

Haraldstad, T., Kroglund, F., Kristensen, T., Jonsson, B. and Haugen, T.O. (2017). Diel migration pattern of Atlantic salmon (*Salmo salar*) and sea trout (*Salmo trutta*) smolts: an assessment of environmental cues. *Ecology of Freshwater Fish*, **26**(4), 541-551.

Harris, A. (2012). astroFns: astronomy: time and position functions, misc. utilities. *R package version*, 4-1.

Hartman, W.L. (1973). *Effects of exploitation, environmental changes, and new species on the fish habitats and resources of Lake Erie* (No. 22). Technical report.

Harvey, A.C., Glover, K.A., Wennevik, V. and Skaala, Ø. (2020). Atlantic salmon and sea trout display synchronised smolt migration relative to linked environmental cues. *Scientific reports*, **10**(1), p1-13.

Havn, T.B., Sæther, S.A., Thorstad, E.B., Teichert, M.A.K., Heermann, L., Diserud, O.H., Borcherding, J., Tambets, M. and Økland, F. (2017). Downstream migration of Atlantic salmon smolts past a low head hydropower station equippped with Archimedes screw and Francis turbines. *Ecological Engineering*, **105**, 262-275.

Havn, T.B., Thorstad, E.B., Borcherding, J., Heermann, L., Teichert, M.A., Ingendahl, D., Tambets, M., Sæther, S.A. and Økland, F. (2020). Impacts of a weir and power station on downstream migrating Atlantic salmon smolts in a German river. *River Research and Applications*, **36**(5), 784-796.

Hawkes, J.P., Saunders, R., Vashon, A.D. and Cooperman, M.S. (2013). Assessing efficacy of non-lethal harassment of double-crested cormorants to improve Atlantic salmon smolt survival. *Northeastern Naturalist*, **20**(1), 1-18.

Hayden, T.A., Holbrook, C.M., Binder, T.R., Dettmers, J.M., Cooke, S.J., Vandergoot, C.S. and Krueger, C.C. (2016). Probability of acoustic transmitter detections by receiver lines in Lake Huron: results of multi-year field tests and simulations. *Animal Biotelemetry*, **4**, 1-14.

Hays, G. C., Bailey, H., Bograd, S. J., Bowen, W. D., Campagna, C., Carmichael, Casale, P., Chiaradia, A., Costa, D.P., Cuevas, E., Nico de Bruyn, P.J., Dias, M.P., Duarte, C.M., Dunn, D.C., Dutton, P.H., Esteban, N., Friedlaender, A., Goetz, K.T., Godley, B.J., Halpin, P.N., and Sequeira, A.M.M. (2019). Translating marine animal tracking data into conservation policy and management, *CellPress*, **34***(*5), 459-473. https://doi.org/10.1016/j.tree.2019.01.009

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

Hedger, R.D., Sundt-Hansen, L.E., Forseth, T., Diserud, O.H., Ugedal, O. and Finstad, A.G. (2013). Modelling the complete life-cycle of Atlantic salmon (*Salmo salar* L.) using a spatially explicit individual-based approach. *Ecological Modelling*, **248**, 119-129.

Hedger, R.D., Uglem, I., Thorstad, E.B., Finstad, B., Chittenden, C.M., Arechavala-Lopez, P., Jensen, A.J., Nilsen, R. and Økland, F. (2011). Behaviour of Atlantic cod, a marine fish predator, during Atlantic salmon post-smolt migration. *ICES Journal of Marine Science*, **68**(10), 2152-2162.

Heggenes, J. and Borgstrøm, R. (1988). Effect of mink, *Mustela vison Schreber*, predation on cohorts of juvenile Atlantic salmon, *Salmo salar* L., and brown trout, *S. trutta* L., in three small streams. *Journal of Fish Biology*, **33**(6), 885-894.

Heinimaa, S. and Heinimaa, P. (2004). Effect of the female size on egg quality and fecundity of the wild Atlantic salmon in the sub-arctic River Teno. *Boreal Environment Research*, **9**(1), 55.

Hendry, A.P., Morbey, Y.E., Berg, O.K. and Wenburg, J.K. (2004). Adaptive variation in senescence: reproductive lifespan in a wild salmon population. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, **271**(1536), 259-266.

Hendry, K. and Cragg-Hine, D. (2003). Ecology of the Atlantic salmon. Conserving natura 2000 rivers ecology series no. **7**. *English Nature, Peterborough*, p.36.

Heupel, M.R., Simpfendorfer, C.A. and Fitzpatrick, R. (2010). Large–scale movement and reef fidelity of grey reef sharks. *PloS one*, **5**(3), p.e9650.

Hill, N.L., Trueman, J.R., Prévost, A.D., Fraser, D.J., Ardren, W.R. and Grant, J.W. (2019). Effect of dam removal on habitat use by spawning Atlantic salmon. *Journal of Great Lakes Research*, **45**(2), 394-399.

Hindar, K., Gallaugher, P. and Wood, L. (2004). Wild Atlantic salmon in Europe: status and perspectives. *The World Summit on Salmon*, 47-52.

Hitt, S., Pittman, S.J. and Nemeth, R.S. (2011). Diel movements of fishes linked to benthic seascape structure in a Caribbean coral reef ecosystem. *Marine Ecology Progress Series*, **427**, 275-291.

Hoar, W.S. (1976). Smolt transformation: evolution, behavior, and physiology. *Journal of the Fisheries Board of Canada*, **33**(5), 1233-1252.

Hockersmith, E.E., Muir, W.D., Smith, S.G., Sandford, B.P., Perry, R.W., Adams, N.S. and Rondorf, D.W. (2003). Comparison of migration rate and survival between radio-tagged and PIT-tagged migrant yearling Chinook salmon in the Snake and Columbia rivers. *North American Journal of Fisheries Management*, **23**(2), 404-413.

Holbrook, C., Hayden, T., Binder, T., Pye, J. and Nunes, A. (2018). Glatos: A package for the Great Lakes Acoustic Telemetry Observation System. R package version 0.2. 7.9000.

Holbrook, C.M., Kinnison, M.T. and Zydlewski, J. (2011). Survival of migrating Atlantic salmon smolts through the Penobscot River, Maine: a prerestoration assessment. *Transactions of the American Fisheries Society*, **140**(5), 1255-1268.

Holm, M., Holst, J.C. and Hansen, L.P. (2000). Spatial and temporal distribution of post-smolts of Atlantic salmon (*Salmo salar* L.) in the Norwegian Sea and adjacent areas. *ICES Journal of Marine Science*, **57**(4), 955-964.

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

Honkanen, H.M., Orrell, D.L., Newton, M., McKelvey, S., Stephen, A., Duguid, R.A. and Adams, C.E. (2021). The downstream migration success of Atlantic salmon (*Salmo salar*) smolts through natural and impounded standing waters. *Ecological Engineering*, **161**, p.106161.

Honkanen, H.M., Rodger, J.R., Stephen, A., Adams, K., Freeman, J. and Adams, C.E. (2018). Counterintuitive migration patterns by Atlantic salmon *Salmo salar* smolts in a large lake. *Journal of Fish Biology*, **93**(1), 159-162.

Horton, T.W., Block, B.A., Drumm, A., Hawkes, L.A., O'Cuaig, M., Maoiléidigh, N.Ó., O'Neill, R., Schallert, R.J., Stokesbury, M.J. and Witt, M.J. (2020). Tracking Atlantic bluefin tuna from foraging grounds off the west coast of Ireland. *ICES Journal of Marine Science*, **77**(6), 2066-2077.

Hothorn, T., Bretz, F., Westfall, P., Heiberger, R.M., Schuetzenmeister, A., Scheibe, S. and Hothorn, M.T. (2016). Package 'multcomp'. *Simultaneous inference in general parametric models. Project for Statistical Computing, Vienna, Austria*.

Howarth, M.J. (2015). *SEA6 Technical Report* . rep. UK Department of Trade and Industry's offshore energy Strategic Environmental Assessment programme. Available at: https://assets.publishing.service.gov.uk/government/uploads/system/uploads/attachment_data/file/197294/SEA6_Hydrography_POL.pdf (Accessed: 10 December 2021).

Hussey, N.E., Kessel, S.T., Aarestrup, K., Cooke, S.J., Cowley, P.D., Fisk, A.T., Harcourt, R.G., Holland, K.N., Iverson, S.J., Kocik, J.F. and Mills Flemming, J.E. (2015). Aquatic animal telemetry: a panoramic window into the underwater world. *Science*, **348**(6240), p.1255642

Hutchings, J.A., Ardren, W.R., Barlaup, B.T., Bergman, E., Clarke, K.D., Greenberg, L.A., Lake, C., Piironen, J., Sirois, P., Sundt-Hansen, L.E. and Fraser, D.J. (2019). Life-history variability and conservation status of landlocked Atlantic salmon: an overview. *Canadian Journal of Fisheries and Aquatic Sciences*, **76**(10), 1697-1708.

Hvidsten, N.A. and Johnsen, B.O. (1997). Screening of Descending Atlantic Salmon (*Salmo salar* L) Smolts from a Hydro Power Intake in The River Orkla, Norway. *Nordic Journal of Freshwater Research*, **73**, 44-49.

Hvidsten, N.A. and Møkkelgjerd, P.I. (1987). Predation on salmon smolts, *Salmo salar* L., in the estuary of the River Surna, Norway. *Journal of Fish Biology*, **30**(3), 273-280.

Hvidsten, N.A., Jensen, A.J. and VivDs, H., Bakke q., Heggberget TG. (1995). Downstream migration of Atlantic salmon smolts in relation to water flow, water temperature, moon phase and social interaction–Nord. *J. Freshw. Res*, **70**, 38-48.

Ibbotson, A.T., Beaumont, W.R. and Pinder, A.C. (2011). A size-dependent migration strategy in Atlantic salmon smolts: Small smolts favour nocturnal migration. *Environmental Biology of Fishes*, **92**(2), 151-157.

Ibbotson, A.T., Beaumont, W.R.C., Pinder, A., Welton, S. and Ladle, M. (2006). Diel migration patterns of Atlantic salmon smolts with particular reference to the absence of crepuscular migration. *Ecology of Freshwater Fish*, **15**(4), 544-551.

ICES. (2021). Report of the Working group on North Atlantic Salmon (WGNAS). *ICES Scientific Reports*, **3**(29), 1-407.

ICES. (2017). *Report of the working group on north Atlantic Salmon (WGNAS)*, 29 March–7 April 2017, Copenhagen, Denmark. ICES CM 2017/ACOM:20. 296

ICES. (2018). *ICES Advice basis*. https://doi.org/ 10.17895/ices.pub.4503

ICOLD. (2018). World register of dams. Paris: International commission on large dams. https://www.icoldcigb.org/GB/world_register/general_synthesis.asp [Accessed: May 24, 2023].

International Energy Agency, (2012). Technology Roadmap: Hydropower. Paris, France: IEA.

Jacobsen, J.A. and Hansen, L.P. (2001). Feeding habits of wild and escaped farmed Atlantic salmon, *Salmo salar* L., in the Northeast Atlantic. *ICES Journal of Marine Science*, **58**(4), 916-933.

Jacobsen, J.A., Hansen, L.P., Bakkestuen, V., Halvorsen, R., Reddin, D.G., White, J., Ó Maoiléidigh, N., Russell, I.C., Potter, E.C.E., Fowler, M. and Smith, G.W. (2012). Distribution by origin and sea age of Atlantic salmon (*Salmo salar*) in the sea around the Faroe Islands based on analysis of historical tag recoveries. *ICES Journal of Marine Science*, **69**(9), 1598-1608.

Jager, H.I., Chandler, J.A., Lepla, K.B. and Van Winkle, W. (2001). A theoretical study of river fragmentation by dams and its effects on white sturgeon populations. *Environmental Biology of Fishes*, **60**, 347-361.

Jammalamadaka, S.R. and SenGupta, A. (2001). *Topics in circular statistics* (Vol. 5). world scientific.

Järvi, T. (1989). Synergistic effect on mortality in Atlantic salmon, *Salmo sala*r, smolt caused by osmotic stress and presence of predators. *Environmental Biology of Fishes*, **26**, 149-152.

Jepsen, N., Aarestrup, K., Økland, F. and Rasmussen, G. (1988). Survival of radiotagged Atlantic salmon (*Salmo salar* L.)–and trout (*Salmo trutta* L.) smolts passing a reservoir during seaward migration. *Hydrobiologia*, **371**(0), 347-353.

Jepsen, N., Holthe, E. and Økland, F. (2006). Observations of predation on salmon and trout smolts in a river mouth. *Fisheries Management and Ecology*, **13**(5), 341-343.

Jepsen, N., Klenke, R., Sonnesen, P. and Bregnballe, T. (2010). The use of coded wire tags to estimate cormorant predation on fish stocks in an estuary. *Marine and Freshwater Research*, **61**(3), 320-329.

Jepsen, N., Pedersen, S. and Thorstad, E. (2000). Behavioural interactions between prey (trout smolts) and predators (pike and pikeperch) in an impounded river. *Regulated Rivers: Research and Management: An International Journal Devoted to River Research and Management*, **16**(2), 189-198.

Johansen, M., Erkinaro, J. and Amundsen, P.A. (2011). The when, what and where of freshwater feeding. *Atlantic Aalmon Ecology*, (4), 67-87.

Jones, J., Börger, L., Tummers, J., Jones, P., Lucas, M., Kerr, J., Kemp, P., Bizzi, S., Consuegra, S., Marcello, L. and Vowles, A. (2019). A comprehensive assessment of stream fragmentation in Great Britain. *Science of The Total Environment*, **673**, 756-762.

Jones, M.W. and Hutchings, J.A. (2001). The influence of male parr body size and mate competition on fertilization success and effective population size in Atlantic salmon. *Heredity*, **86**(6), 675-684.

Jones, M.W. and Hutchings, J.A. (2002). Individual variation in Atlantic salmon fertilization success: implications for effective population size. *Ecological applications*, **12**(1), 184-193.

Jonsson, B. and Jonsson, N. (2009). A review of the likely effects of climate change on anadromous Atlantic salmon *Salmo salar* and brown trout *Salmo trutta*, with particular reference to water temperature and flow. *Journal of Fish Biology*, **75**(10), 2381-2447.

Jonsson, B. and Jonsson, N. (2011). Population enhancement and population restoration. *Ecology of Atlantic Salmon and Brown Trout: Habitat As A Template for Life Histories*, 567-632.

Jonsson, B., Jonsson, N. and Hansen, L.P. (1991). Differences in life history and migratory behaviour between wild and hatchery-reared Atlantic salmon in nature. *Aquaculture*, **98**(1-3), 69-78.

Jonsson, N. and Jonsson, B. (2003). Energy allocation among developmental stages, age groups, and types of Atlantic salmon (Salmo salar) spawners. *Canadian Journal of Fisheries and Aquatic Sciences*, **60**(5), 506-516.

Jungwirth, M. (1998). River continuum and fish migration–going beyond the longitudinal river corridor in understanding ecological integrity. *Fish Migration and Fish Bypasses*, 19-32.

Jutila, E. and Jokikokko, E. (2008). Seasonal differences in smolt traits and post-smolt survival of wild Atlantic salmon, *Salmo salar*, migrating from a northern boreal river. *Fisheries Management and Ecology*, **15**(1), 1-9.

Jutila, E., Jokikokko, E., Kallio-Nyberg, I., Saloniemi, I. and Pasanen, P. (2003). Differences in sea migration between wild and reared Atlantic salmon (*Salmo salar* L.) in the Baltic Sea. *Fisheries Research*, **60**(2-3), 333-343.

Kahle, D.J. and Wickham, H. (2013). ggmap: spatial visualization with ggplot2. *R J.*, **5**(1), p.144.

Kallberg, H. (1958). Observations in a stream tank of territoriality and competition in juvenile salmon and trout. *Rep. Inst. Freshw. Res. Drottninigholm*, **39**, 55-98.

Kärgenberg, E., Thorstad, E.B., Järvekülg, R., Sandlund, O.T., Saadre, E., Økland, F., Thalfeldt, M. and Tambets, M. (2020). Behaviour and mortality of downstream migrating Atlantic salmon smolts at a small power station with multiple migration routes. *Fisheries Management and Ecology*, **27**(1), 32-40.

Keefer, M.L., Taylor, G.A., Garletts, D.F., Helms, C.K., Gauthier, G.A., Pierce, T.M. and Caudill, C.C. (2012). Reservoir entrapment and dam passage mortality of juvenile Chinook salmon in the Middle Fork Willamette River. *Ecology of Freshwater Fish*, **21**(2), 222-234.

Keenleyside, M.H. and Yamamoto, F.T. (1962). Territorial behaviour of juvenile Atlantic salmon (*Salmo salar* L.). *Behaviour*, **19**(1-2), 139-168.

Kemp, P.S. and O'hanley, J.R. (2010). Procedures for evaluating and prioritising the removal of fish passage barriers: a synthesis. *Fisheries Management and Ecology*, **17**(4), 297-322.

Kemp, P.S. (2015). Impoundments, barriers and abstractions: impact on fishes and fisheries, mitigation and future directions. *Freshwater fisheries ecology*, 717-769.

Kemp, P.S., Russon, I.J., Waterson, B.J., O'Hanley, J. and Pess, G.R. (2008). Recommendations for a" coarse-resolution rapid-assessment" methodology to assess barriers to fish migration, and associated prioritization tools.

Kennedy, B.M., Gale, W.L. and Ostrand, K.G. (2007). Relationship between smolt gill Na+, K+ ATPase activity and migration timing to avian predation risk of steelhead trout (*Oncorhynchus mykiss*) in a large estuary. *Canadian Journal of Fisheries and Aquatic Sciences*, **64**(11), 1506-1516.

Kennedy, G.J.A. and Greek, J.E. (1988). Predation by cormorants, *Phalacrocorax carbo* (L.), on the salmonid populations of an Irish river. *Aquaculture Research*, **19**(2), 159-170.

Kennedy, R.J. and Crozier, W.W. (2010). Evidence of changing migratory patterns of wild Atlantic salmon *Salmo salar* smolts in the River Bush, Northern Ireland, and possible associations with climate change. *Journal of Fish Biology*, **76**(7), 1786-1805.

Kennedy, R.J., Rosell, R., Millane, M., Doherty, D. and Allen, M. (2018). Migration and survival of Atlantic salmon *Salmo salar* smolts in a large natural lake. *Journal of fish biology*, **93**(1), 134-137.

Kessel, S.T., Cooke, S.J., Heupel, M.R., Hussey, N.E., Simpfendorfer, C.A., Vagle, S. and Fisk, A.T. (2014). A review of detection range testing in aquatic passive acoustic telemetry studies. *Reviews in Fish Biology and Fisheries*, **24**, 199-218.

Kierly, O., Lidgard, D., McKibben, M., Connolly, N. and Baines, M. (2000). Grey seals: status and monitoring in the Irish and Celtic Seas.

King, S. and O'Hanley, J.R. (2016). Optimal fish passage barrier removal—revisited. *River research and applications*, **32**(3), 418-428..

Klemetsen, A., Amundsen, P.A., Dempson, J.B., Jonsson, B., Jonsson, N., O'connell, M.F. and Mortensen, E. (2003). Atlantic salmon *Salmo salar* L., brown trout *Salmo trutta* L. and

Arctic charr *Salvelinus alpinus* (L.): a review of aspects of their life histories. *Ecology of Freshwater Fish*, **12**(1), 1-59.

Klimley, A.P., MacFarlane, R.B., Sandstrom, P.T. and Lindley, S.T. (2013). A summary of the use of electronic tagging to provide insights into salmon migration and survival. *Environmental Biology of Fishes*, **96**, 419-428.

Klinard, N.V. and Matley, J.K. (2020). Living until proven dead: addressing mortality in acoustic telemetry research. *Reviews in Fish Biology and Fisheries*, **30**(3), 485-499.

Klinard, N.V., Halfyard, E.A., Matley, J.K., Fisk, A.T. and Johnson, T.B. (2019). The influence of dynamic environmental interactions on detection efficiency of acoustic transmitters in a large, deep, freshwater lake. *Animal Biotelemetry*, **7**(1), 1-17.

KLTAP, (2015). A guide for constructing stream crossings on local roads and private drives to provide for fish passage, Accessed at: http://www2.ku.edu/~kutc/pdffiles/FishPassageGuide2015.pdf [accessed 02 May 2022].

Kneebone, J., Hoffman, W.S., Dean, M.J. and Armstrong, M.P. (2014). Movements of striped bass between the exclusive economic zone and Massachusetts state waters. *North American Journal of Fisheries Management*, **34**(3), 524-534.

Koed, A., Baktoft, H. and Bak, B.D. (2006). Causes of mortality of Atlantic salmon (*Salmo salar*) and brown trout (*Salmo trutta*) smolts in a restored river and its estuary. *River research and applications*, **22**(1), 69-78.

Koed, A., Birnie-Gauvin, K., Sivebæk, F. and Aarestrup, K. (2020). From endangered to sustainable: Multi-faceted management in rivers and coasts improves Atlantic salmon (*Salmo salar*) populations in Denmark. *Fisheries Management and Ecology*, **27**(1), 64-76.

Koed, A., Jepsen, N., Aarestrup, K. and Nielsen, C. (2002). Initial mortality of radio-tagged Atlantic salmon (*Salmo salar* L.) smolts following release downstream of a hydropower station. In *Aquatic Telemetry: Proceedings of the Fourth Conference on Fish Telemetry in Europe* (31-37). Springer Netherlands.

Lacroix, G.L., Knox, D. and McCurdy, P. (2004a). Effects of implanted dummy acoustic transmitters on juvenile Atlantic salmon. *Transactions of the American Fisheries Society*, **133**(1), 211-220.

Lacroix, G.L., McCurdy, P. and Knox, D. (2004b). Migration of Atlantic salmon postsmolts in relation to habitat use in a coastal system. *Transactions of the American Fisheries Society*, **133**(6), 1455-1471.

Larinier, M. (1998). Upstream and downstream fish passage experience in France. In *Fish migration and fish bypass channels, Vienne, AUT, 24-26 septembre 1996* ( 127-145).

Larinier, M. (2000). Dams and fish migration. *World Commission on Dams, Toulouse, France*.

Larinier, M. (2001). Environmental issues, dams and fish migration. *FAO fisheries technical paper*, **419**, 45-89.

Larinier, M. (2008). Fish passage experience at small-scale hydro-electric power plants in France. *Hydrobiologia*, **609**, 97-108.

Lefèvre, M.A., Stokesbury, M.J.W., Whoriskey, F.G. and Dadswell, M.J. (2013). Migration of Atlantic salmon smolts and post-smolts in the Rivière Saint-Jean, QC north shore from riverine to marine ecosystems. *Environmental Biology of Fishes*, **96**, 1017-1028.

Lefrancois, C., Odion, M. and Claireaux, G. (2001). An experimental and theoretical analysis of the effect of added weight on the energetics and hydrostatic function of the swimbladder of European sea bass (*Dicentrarchus labrax*). *Marine Biology*, 139, 13-17.

Lennox, R.J., Aarestrup, K., Cooke, S.J., Cowley, P.D., Deng, Z.D., Fisk, A.T., Harcourt, R.G., Heupel, M., Hinch, S.G., Holland, K.N. and Hussey, N.E. (2017). Envisioning the future of aquatic animal tracking: technology, science, and application. *BioScience*, **67**(10), 884-896.

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

Lilly, J., Honkanen, H.H., Rodger, J.R., Del Villar, D., Boylan, P., Green, A., Pereiro, D., Wilkie, L., Kennedy, R., Barkley, A. and Rosell, R. (2023). Migration patterns and navigation cues of Atlantic salmon post-smolts migrating from 12 rivers through the coastal zones around the Irish Sea. *Journal of Fish Biology*.

Lilly, J., Honkanen, H.M., Bailey, D.M., Bean, C.W., Forrester, R., Rodger, J.R. and Adams, C.E., 2022. Investigating the behaviour of Atlantic salmon (Salmo salar L.) post-smolts during their early marine migration through the Clyde Marine Region. *Journal of Fish Biology*, *101*(5), 1285-1300.

Lilly, J., Honkanen, H.M., McCallum, J.M., Newton, M., Bailey, D.M. and Adams, C.E. (2021). Combining acoustic telemetry with a mechanistic model to investigate characteristics unique to successful Atlantic salmon smolt migrants through a standing body of water. *Environmental Biology of Fishes*, 1-19.

Limburg, K.E. and Waldman, J.R. (2009). Dramatic declines in North Atlantic diadromous fishes. *BioScience*, **59**(11), 955-965.

Linnaeus, C. (1758). Systema Naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis. Vol. 1. 10th Edition. L. Salvius, Holmia (Stockholm), 824

Lothian, A.J. and Lucas, M.C. (2021). The role of individual behavioral traits on fishway passage attempt behavior. *Ecology and Evolution*, **11**(17), 11974-11990.

Lothian, A.J., Newton, M., Barry, J., Walters, M., Miller, R.C. and Adams, C.E. (2018). Migration pathways, speed and mortality of Atlantic salmon (*Salmo salar*) smolts in a Scottish river and the near-shore coastal marine environment. *Ecology of Freshwater Fish*, **27**(2), 549-558

Lucas, M. and Baras, E. (2001). Migration of Freshwater Fishes Blackwell Science Ltd.

Lucas, M.C. and Frear, P.A. (1997). Effects of a flow-gauging weir on the migratory behaviour of adult barbel, a riverine cyprinid. *Journal of Fish Biology*, **50**(2), 382-396.

Lund, U. and Agostinelli, C. (2018). CircStats: circular statistics, from "topics in circular statistics". *Available in: https://CRAN. R-project. org/package= CircStats. Accessed on: July*, *13*, p.2021.

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

Maia, R. (2017). The WFD implementation in the European member states. *Water Resources Management*, **31**(10), 3043-3060.

Mangel, M. and Satterthwaite, W.H. (2008). Combining proximate and ultimate approaches to understand life history variation in salmonids with application to fisheries, conservation, and aquaculture. *Bulletin of Marine Science*, **83**(1), 107-130.

Marmulla, G. and Ingendahl, D. (1996). Preliminary results of a radio telemetry study of returning Atlantic salmon (L.) and sea trout (L.) in River Sieg, tributary of River Rhine in Germany. In *Underwater Biotelemetry, Proceedings of the First Conference and Workshop on Fish Telemetry in Europe* ( 109-117). University of Liège.

Marschall, E.A., Mather, M.E., Parrish, D.L., Allison, G.W. and McMenemy, J.R. (2011). Migration delays caused by anthropogenic barriers: modeling dams, temperature, and success of migrating salmon smolts. *Ecological Applications*, **21**(8), 3014

Martin, F., Hedger, R.D., Dodson, J.J., Fernandes, L., Hatin, D., Caron, F. and Whoriskey, F.G. (2009). Behavioural transition during the estuarine migration of wild Atlantic salmon (*Salmo salar* L.) smolt. *Ecology of Freshwater Fish*, **18**(3), 406-417.

Martin, J.H.A. and Mitchell, K.A. (1985). Influence of sea temperature upon the numbers of grilse and multi-sea-winter Atlantic salmon (*Salmo salar*) caught in the vicinity of the River Dee (Aberdeenshire). *Canadian Journal of Fisheries and Aquatic Sciences*, **42**(9), 1513-1521.

Martínez, J.L., Moran, P., Perez, J., De Gaudemar, B., Beall, E. and Garcia-Vazquez, E. (2000). Multiple paternity increases effective size of southern Atlantic salmon populations. *Molecular Ecology*, **9**(3), 293-298.

Matley, J.K., Klinard, N.V., Martins, A.P.B., Aarestrup, K., Aspillaga, E., Cooke, S.J., Cowley, P.D., Heupel, M.R., Lowe, C.G., Lowerre-Barbieri, S.K. and Mitamura, H. (2022). Global trends in aquatic animal tracking with acoustic telemetry. *Trends in Ecology and Evolution*, **37**(1), 79-94.

Mawle, G.W. and Milner, N.J. (2003). The Return of Salmon to Cleaner Rivers-England and Wales. *Salmon at the Edge*, 186-199.

McCleave, J.D. and Stred, K.A. (1975). Effect of dummy telemetry transmitters on stamina of Atlantic salmon (*Salmo salar*) smolts. *Journal of the Fisheries Board of Canada*, **32**(4), 559-563.

McCormick, S. D. (2013). Smolt Physiology and endocrinology. In S.D. McCormick, A.P.Farrel, and C.J. Brauner (Eds.), *Euryhaline Fishes (199-251). Academic Press.*

McCormick, S.D. (1994). Ontogeny and evolution of salinity tolerance in anadromous salmonids: hormones and heterochrony. *Estuaries*, **17**, 26-33.

McCormick, S.D., Moriyama, S. and Björnsson, B.T. (2000). Low temperature limits photoperiod control of smolting in Atlantic salmon through endocrine mechanisms. *American Journal of Physiology-Regulatory, Integrative and Comparative Physiology*, **278**(5), R1352-R1361.

McCormick, S.D., Naiman, R.J. and Montgomery, E.T., 1985. Physiological smolt characteristics of anadromous and non-anadromous brook trout (Salvelinus fontinalis) and Atlantic salmon (Salmo salar). *Canadian Journal of Fisheries and Aquatic Sciences*, *42*(3), 529-538.

McCormick, S.D., Shrimpton, J.M., Moriyama, S. and Björnsson, B.T. (2002). Effects of an advanced temperature cycle on smolt development and endocrinology indicate that temperature is not a zeitgeber for smolting in Atlantic salmon. *Journal of Experimental Biology*, **205**(22), 3553-3560.

McCormick, S.D., Shrimpton, J.M., Moriyama, S. and Björnsson, B.T. (2007). Differential hormonal responses of Atlantic salmon parr and smolt to increased daylength: a possible developmental basis for smolting. *Aquaculture*, **273**(2-3), 337-344.

McIlvenny, J., Youngson, A., Williamson, B.J., Gauld, N.R., Goddijn-Murphy, L. and Del Villar-Guerra, D. (2021). Combining acoustic tracking and hydrodynamic modelling to study migratory behaviour of Atlantic salmon (*Salmo salar*) smolts on entry into high-energy coastal waters. *ICES Journal of Marine Science*, **78**(7), 2409-2419.

Meixler, M.S., Bain, M.B. and Walter, M.T. (2009). Predicting barrier passage and habitat suitability for migratory fish species. *Ecological Modelling*, **220**(20), 2782-2791.

Metcalfe, N.B. and Thorpe, J.E. (1990). Determinants of geographical variation in the age of seaward-migrating salmon, *Salmo salar*. *The Journal of Animal Ecology*, 135-145.

Metcalfe, N.B., Huntingford, F.A., Graham, W.D. and Thorpe, J.E. (1989). Early social status and the development of life-history strategies in Atlantic salmon. *Proceedings of the Royal Society of London. B. Biological Sciences*, **236**(1282), 7-19.

Mills, D. (1971). Salmon and trout: a resource, its ecology, conservation and management. *ST. MARTIN'S PRESS: NEW YORK, N. Y., 1971. 351 P, ILLUS, MAPS. PR.$ 14. 95.*

Mills, D. (1991). *Ecology and management of Atlantic salmon*. Springer Science and Business Media.

Mills, D.H. (1967). Predation on fish by other animals. *Biological basis of freshwater fish production. Wiley, New York*, 377-397.

Mills, D. (1994). Evidence of straying from wild Atlantic salmon, *Salmo salar* L., smolt transportation experiments in northern Scotland. *Aquaculture Research*, **25(**S2), 3–8. doi:https://doi.org/10.1111/are.1994.25.s2.3.

Milner, N.J., Elliott, J.M., Armstrong, J.D., Gardiner, R., Welton, J.S. and Ladle, M. (2003). The natural control of salmon and trout populations in streams. *Fisheries Research*, **62**(2), 111-125.

Moffett, I.J.J., Allen, M., Flanagan, C., Crozier, W.W. and Kennedy, G.J.A. (2006). Fecundity, egg size and early hatchery survival for wild Atlantic salmon, from the River Bush. *Fisheries Management and Ecology*, **13**(2), 73-79.

Montgomery, J., Carton, G., Voigt, R., Baker, C. and Diebel, C. (2000). Sensory processing of water currents by fishes. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences*, **355**(1401), 1325-1327.

Moore, A., Ives, S., Mead, T.A., and Talks, L. (1998). The migratory behaviour of wild Atlantic salmon (*Salmo salar* L.) smolts in the River Test and Southampton water, southern England. Hydrobiologia, **371/372**, 295-304.

Moore, A., Privitera, L., Ives, M.J., Uzyczak, J. and Beaumont, W.R. (2018). The effects of a small hydropower scheme on the migratory behaviour of Atlantic salmon *Salmo salar* smolts. *Journal of Fish Biology*, **93**(3), 469-476.

Moore, A., Russell, I.C. and Potter, E.C.E. (1990). The effects of intraperitoneally implanted dummy acoustic transmitters on the behaviour and physiology of juvenile Atlantic salmon, *Salmo salar* L. *Journal of Fish Biology*, **37**(5), 713-721.

Moore, D.S., Chaput, G.J. and Pickard, P.R. (1995). The effect of fisheries on the biological characteristics and survival of mature Atlantic salmon (*Salmo salar*) from the Miramichi River. *Canadian Special Publication of Fisheries and Aquatic Sciences*, 229-248.

Moore, M., Berejikian, B.A. and Tezak, E.P. (2013). A floating bridge disrupts seaward migration and increases mortality of steelhead smolts in Hood Canal, Washington State. *PloS one*, **8**(9), p.e73427.

Mork, K.A., Gilbey, J., Hansen, L.P., Jensen, A.J., Jacobsen, J.A., Holm, M., Holst, J.C., Ó Maoiléidigh, N., Vikebø, F., McGinnity, P. and Melle, W. (2012). Modelling the migration of post-smolt Atlantic salmon (*Salmo salar*) in the Northeast Atlantic. *ICES Journal of Marine Science*, **69**(9), 1616-1624.

Mueller, T. and Fagan, W.F. (2008). Search and navigation in dynamic environments–from individual behaviors to population distributions. *Oikos*, **117**(5), 654-664.

Muir, W.D., Marsh, D.M., Sandford, B.P., Smith, S.G. and Williams, J.G. (2006). Post-hydropower system delayed mortality of transported Snake River stream-type Chinook salmon: unraveling the mystery. *Transactions of the American Fisheries Society*, **135**(6), 1523-1534.

Muir, W.D., Smith, S.G., Williams, J.G., Hockersmith, E.E. and Skalski, J.R. (2001). Survival estimates for migrant yearling Chinook salmon and steelhead tagged with passive integrated transponders in the lower Snake and lower Columbia rivers, 1993–1998. *North American Journal of Fisheries Management*, **21**(2), 269-282.

NASCO (2018). *Nasco Rivers Database Report*. Available at: https://nasco.int/wp-content/uploads/2020/10/Rivers-database-All-Jurisdiction-Report.pdf (Accessed: 24 March 2024).

Nash, A.J., Vollset, K.W., Hanssen, E.M., Berhe, S., Salvanes, A.G., Isaksen, T.E., Barlaup, B.T. and Lennox, R.J. (2022). A tale of two fishes: depth preference of migrating Atlantic salmon smolt and predatory brown trout in a Norwegian lake. *Canadian Journal of Fisheries and Aquatic Sciences*, **79**(12), 2216-2224.

Newton, M., Barry, J., Dodd, J.A., Lucas, M.C., Boylan, P. and Adams, C.E. (2019). A test of the cumulative effect of river weirs on downstream migration success, speed and mortality of Atlantic salmon (*Salmo salar*) smolts: An empirical study. *Ecology of Freshwater Fish*, **28**(1), 176-186.

Newton, M., Barry, J., Dodd, J.A., Lucas, M.C., Boylan, P. and Adams, C.E. (2016). Does size matter? A test of size-specific mortality in Atlantic salmon *Salmo salar* smolts tagged with acoustic transmitters. *Journal of Fish Biology*, **89**(3), 1641-1650.

Newton, M., Barry, J., Lothian, A., Main, R., Honkanen, H., Mckelvey, S., Thompson, P., Davies, I., Brockie, N., Stephen, A. and Murray, R.O.H. (2021). Counterintuitive active directional swimming behaviour by Atlantic salmon during seaward migration in the coastal zone. *ICES Journal of Marine Science*, **78**(5), 1730-1743.

Newton, M., Dodd, J.A., Barry, J., Boylan, P. and Adams, C.E. (2018). The impact of a small-scale riverine obstacle on the upstream migration of Atlantic Salmon. *Hydrobiologia*, **806**, 251-264.

Nilsson, C., Reidy, C.A., Dynesius, M. and Revenga, C. (2005). Fragmentation and flow regulation of the world's large river systems. *Science*, **308**(5720), 405-408.

Norrgård, J.R., Greenberg, L.A., Piccolo, J.J., Schmitz, M. and Bergman, E. (2013). Multiplicative loss of landlocked Atlantic salmon *Salmo salar* L. smolts during downstream migration trough multiple dams. *River Research and Applications*, **29**(10), 1306-1317.

Nunn, A.D. and Cowx, I.G. (2012). Restoring river connectivity: prioritizing passage improvements for diadromous fishes and lampreys. *Ambio*, **41**, 402-409.

Nyqvist, D., Elghagen, J., Heiss, M. and Calles, O. (2018). An angled rack with a bypass and a nature-like fishway pass Atlantic salmon smolts downstream at a hydropower dam. *Marine and Freshwater Research*, **69**(12), 1894-1904.

Nyqvist, D., Greenberg, L.A., Goerig, E., Calles, O., Bergman, E., Ardren, W.R. and Castro-Santos, T. (2017). Migratory delay leads to reduced passage success of Atlantic salmon smolts at a hydroelectric dam. *Ecology of Freshwater Fish*, **26**(4), 707-718.

O'Connell, M.F., Dempson, J.B. and Chaput, G. (2006). *Aspects of the life history, biology, and population dynamics of Atlantic salmon (Salmo salar L.) in eastern Canada* (p. 47). Fisheries and Oceans Canada, Science.

O'Connor, J.P., O'Mahony, D.J., O'Mahony, J.M. and Glenane, T.J. (2006). Some impacts of low and medium head weirs on downstream fish movement in the Murray–Darling Basin in southeastern Australia. *Ecology of Freshwater Fish*, **15**(4), 419-427.

O'Hanley, J.R. and Tomberlin, D. (2005). Optimizing the removal of small fish passage barriers. *Environmental Modeling and Assessment*, **10**, 85-98.

O'Hanley, J.R. (2011). Open rivers: barrier removal planning and the restoration of free-flowing rivers. *Journal of Environmental Management*, **92**(12), 3112-3120.

Ohashi, K. and Sheng, J. (2018). Study of Atlantic salmon post-smolt movement in the Gulf of St. Lawrence using an individual-based model. *Regional Studies in Marine Science*, **24**, 113-132.

Økland, F., Thorstad, E.B., Finstad, B., Sivertsgård, R., Plantalech, N., Jepsen, N. and McKinley, R.S. (2006). Swimming speeds and orientation of wild Atlantic salmon post-smolts during the first stage of the marine migration. *Fisheries Management and Ecology*, **13**(4), 271-274.

Oktaviani.J. (2018). Salmon stocks and Fisheries in England and Wales in 2018. *Sereal Untuk*, **51**(1), 51. https://doi.org/10.1017/CBO9781107415324.004

Olsén, K.H., Grahn, M., Lohm, J. and Langefors, Å. (1998). MHC and kin discrimination in juvenile Arctic charr, *Salvelinus alpinus* (L.). *Animal Behaviour*, **56**(2), 319-327.

Ounsley, J.P., Gallego, A., Morris, D.J. and Armstrong, J.D. (2020). Regional variation in directed swimming by Atlantic salmon smolts leaving Scottish waters for their oceanic feeding grounds—a modelling study. *ICES Journal of Marine Science*, **77**(1), 315-325.

Ovidio, M. and Philippart, J.C. (2002). The impact of small physical obstacles on upstream movements of six species of fish: synthesis of a 5-year telemetry study in the River Meuse basin. In *Aquatic Telemetry: Proceedings of the Fourth Conference on Fish Telemetry in Europe* (55-69). Springer Netherlands.

Parrish, D.L., Behnke, R.J., Gephard, S.R., McCormick, S.D. and Reeves, G.H. (1998). Why aren't there more Atlantic salmon (*Salmo salar*)?. *Canadian Journal of Fisheries and Aquatic Sciences*, **55**(S1), 281-287.

Pelletier, C., Hanson, K.C. and Cooke, S.J. (2007). Do catch-and-release guidelines from state and provincial fisheries agencies in North America conform to scientifically based best practices?. *Environmental Management*, **39**, 760-773.

Pepin, P. (1991). Effect of temperature and size on development, mortality, and survival rates of the pelagic early life history stages of marine fish. *Canadian Journal of Fisheries and Aquatic Sciences*, **48**(3), 503-518.

Pincock, D.G. (2012). False detections: what they are and how to remove them from detection data. *Vemco Application Note*, **902**, 1-11.

Plantalech Manel-la, N., Chittenden, C.M., Økland, F., Thorstad, E.B., Davidsen, J.G., Sivertsgård, R., McKinley, R.S. and Finstad, B. (2011). Does river of origin influence the early marine migratory performance of *Salmo salar*?. *Journal of Fish Biology*, **78**(2), 624-634.

Poff, N.L. and Hart, D.D. (2002). How dams vary and why it matters for the emerging science of dam removal: an ecological classification of dams is needed to characterize how the tremendous variation in the size, operational mode, age, and number of dams in a river basin influences the potential for restoring regulated rivers via dam removal. *BioScience*, **52**(8), 659-668.

Poff, N.L., Allan, J.D., Bain, M.B., Karr, J.R., Prestegaard, K.L., Richter, B.D., Sparks, R.E. and Stromberg, J.C. (1997). The natural flow regime. *BioScience*, 47(11), 769-784.

Pringle, C.M. (2001). Hydrologic connectivity and the management of biological reserves: a global perspective. *Ecological Applications*, **11**(4), 981-998.

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

R Core Team. (2019). *R: A language and environment for statistical computing*. R project. https://www.R-project.org/

Rahel, F.J. and McLaughlin, R.L. (2018). Selective fragmentation and the management of fish movement across anthropogenic barriers. *Ecological Applications*, **28**(8), 2066-2081.

Rand, P.S., Hinch, S.G., Morrison, J., Foreman, M.G.G., MacNutt, M.J., Macdonald, J.S., Healey, M.C., Farrell, A.P. and Higgs, D.A. (2006). Effects of river discharge, temperature, and future climates on energetics and mortality of adult migrating Fraser River sockeye salmon. *Transactions of the American Fisheries Society*, **135**(3), 655-667.

Randall, R.G. (1989). Effect of sea-age on the reproductive potential of Atlantic salmon (*Salmo salar*) in eastern Canada. *Canadian Journal of Fisheries and Aquatic Sciences*, **46**(12), 2210-2218.

Raymond, H.L. (1979). Effects of dams and impoundments on migrations of juvenile chinook salmon and steelhead from the Snake River, 1966 to 1975. *Transactions of the American Fisheries Society*, **108**(6), 505-529.

Raymond, H.L. (1988). Effects of hydroelectric development and fisheries enhancement on spring and summer chinook salmon and steelhead in the Columbia River basin. *North American Journal of Fisheries Management*, 8(1), 1-24.

Rechisky, E.L. and Welch, D.W. (2010). Surgical implantation of acoustic tags: Influence of tag loss and tag-induced mortality on free-ranging and hatchery-held spring Chinook (*O. tschawytscha*) smolts. *PNAMP Special Publication: tagging, telemetry and marking neasures for monitoring fish populations—A compendium of new and recent science for use in informing technique and decision modalities: Pacific Northwest Aquatic Monitoring Partnership Special Publication*, ***2***, 71-96.

Rechisky, E.L., Welch, D.W., Porter, A.D., Jacobs-Scott, M.C. and Winchell, P.M. (2013). Influence of multiple dam passage on survival of juvenile Chinook salmon in the Columbia River estuary and coastal ocean. *Proceedings of the National Academy of Sciences*, **110**(17), 6883-6888.

Reid, J.E. and Chaput, G. (2012). Spawning history influence on fecundity, egg size, and egg survival of Atlantic salmon (*Salmo salar*) from the Miramichi River, New Brunswick, Canada. *ICES Journal of Marine Science*, **69**(9), 1678-1685.

Renardy, S., Takriet, A., Benitez, J.P., Dierckx, A., Baeyens, R., Coeck, J., Pauwels, I.S., Mouton, A., Archambeau, P., Dewals, B. and Pirotton, M. (2021). Trying to choose the less bad route: Individual migratory behaviour of Atlantic salmon smolts (*Salmo salar* L.) approaching a bifurcation between a hydropower station and a navigation canal. *Ecological Engineering*, **169**, p.106304.

Richter, B.D., Braun, D.P., Mendelson, M.A. and Master, L.L. (1997). Threats to imperiled freshwater fauna: amenazas a la fauna dulceacuicola en riesgo. *Conservation biology*, **11**(5), 1081-1093.

Riddell, B. and Tautz, A.F. (2003). State of Pacific salmon and their habitats: Canada and the United States. *Proceedings from the World Summit on Salmon*, 63-76.

Righton, D.R., Metcalfe, J.D. and Connolly, P. (2001). Electronic tags reveal behavioural differences between North Sea and Irish Sea cod. *Nature*, **411**(156.10), p.1038.

Rikardsen, A. H., Hansen, L. P., Jensen, A. J., Vollen, T., and Finstad, B. (2008). Do Norwegian Atlantic salmon feed in the northern Barents Sea? Tag recoveries from 70 to 78° N. *Journal of Fish Biology*, **72**(7), 1792–1798. https://doi.org/10.1111/j.1095-8649.2008.01823.x

Riley, W.D. (2007). Seasonal downstream movements of juvenile Atlantic salmon, *Salmo salar* L., with evidence of solitary migration of smolts. *Aquaculture*, **273**(2-3), 194-199.

Riley, W.D., Bendall, B., Ives, M.J., Edmonds, N.J. and Maxwell, D.L. (2012). Street lighting disrupts the diel migratory pattern of wild Atlantic salmon, *Salmo salar* L., smolts leaving their natal stream. *Aquaculture*, **330**, 74-81.

Riley, W.D., Ibbotson, A.T., Gregory, S.D., Russell, I.C., Lauridsen, R.B., Beaumont, W.R., Cook, A.C. and Maxwell, D.L. (2018). Under what circumstances does the capture and tagging of wild Atlantic salmon *Salmo salar* smolts affect probability of return as adults?. *Journal of Fish Biology*, **93**(3), 477-489.

Riley, W.D., Ibbotson, A.T., Maxwell, D.L., Davison, P.I., Beaumont, W.R.C. and Ives, M.J. (2014). Development of schooling behaviour during the downstream migration of Atlantic salmon *Salmo salar* smolts in a chalk stream. *Journal of Fish Biology*, **85**(4), 1042-1059.

Roff, D.A. (1988). The evolution of migration and some life history parameters in marine fishes. *Environmental Biology of Fishes*, **22**, 133-146.

Rosenberg, D.M., McCully, P. and Pringle, C.M. (2000). Global-scale environmental effects of hydrological alterations: introduction. *BioScience*, **50**(9), 746-751.

Roshier, D.A. and Reid, J.R.W. (2003). On animal distributions in dynamic landscapes. *Ecography*, **26**(4), 539-544.

Ross, M.J. and McCormick, J.H. (1981). Effects of external radio transmitters on fish. *The Progressive Fish-Culturist*, **43**(2), 67-72.

Rowell, T.J., Nemeth, R.S., Schärer, M.T. and Appeldoorn, R.S. (2015). Fish sound production and acoustic telemetry reveal behaviors and spatial patterns associated with spawning aggregations of two Caribbean groupers. *Marine Ecology Progress Series*, **518**, 239-254.

Ruggles, C.P. (1980). 10. Sampling migrating salmon. *Guidelines for sampling fish in inland waters, EIFAC, Technical Paper*, **33**, 143-58.

Russell, I.C., Aprahamian, M.W., Barry, J., Davidson, I.C., Fiske, P., Ibbotson, A.T., Kennedy, R.J., Maclean, J.C., Moore, A., Otero, J. and Potter, T. (2012). The influence of the freshwater environment and the biological characteristics of Atlantic salmon smolts on their subsequent marine survival. *ICES Journal of Marine Science*, **69**(9), 1563-1573.

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

Sanderson, B., Buhariwalla, C., Adams, M., Broome, J., Stokesbury, M. and Redden, A. (2017). August. Quantifying detection range of acoustic tags for probability of fish encountering MHK devices. In *Proceedings of the 12th European Wave and Tidal Energy Conference, Cork, Ireland*.

Saunders, R.L., Henderson, E.B., Glebe, B.D. and Loudenslager, E.J. (1983). Evidence of a major environmental component in determination of the grilse: larger salmon ratio in Atlantic salmon (*Salmo salar*). *Aquaculture*, **33**(1-4), 107-118.

Saura, M., Caballero, A., Caballero, P. and Moran, P. (2008). Impact of precocious male parr on the effective size of a wild population of Atlantic salmon. *Freshwater Biology*, **53**(12), 2375-2384.

Scarnecchia, D.L. (1984). Climatic and oceanic variations affecting yield of Icelandic stocks of Atlantic salmon (*Salmo salar*). *Canadian Journal of Fisheries and Aquatic Sciences*, **41**(6), 917-935.

Serrano, I., Rivinoja, P., Karlsson, L. and Larsson, S. (2009). Riverine and early marine survival of stocked salmon smolts, *Salmo salar* L., descending the Testebo River, Sweden. *Fisheries Management and Ecology*, **16**(5), 386-394.

Shaw, E.A. (2013). Weir management: challenges, analysis and decision support (*Doctoral dissertation, University of Sheffield).*

Sheehan, T. F., Barber, J., Dean, A., Deschamps, D., Gargan, P., Goulette, G., Maxwell, H., Tavner, I., Bradbury, I. R., Robertson, M. J., and Maoiléidigh, N. Ó. (2017). *The International Sampling Program: Continent of Origin and Biological Characteristics of Atlantic salmon Collected at West Greenland in 2017*. Northeast Fisheries Science Centre. https://repository.library.noaa.gov/view/noaa/22017

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

Shephard, S. and Gargan, P. (2021). Wild Atlantic salmon exposed to sea lice from aquaculture show reduced marine survival and modified response to ocean climate. *ICES Journal of Marine Science*, **78**(1), 368-376.

Sibert, J.R. and Nielsen, J.L. eds. (2001). *Electronic Tagging and Tracking in Marine Fisheries: Proceedings of the Symposium on Tagging and Tracking Marine Fish with Electronic Devices, February 7–11, 2000, East-West Center, University of Hawaii* (Vol. 1). Springer Science and Business Media.

Sigourney, D.B., Zydlewski, J.D., Hughes, E. and Cox, O. (2015). Transport, dam passage, and size selection of adult Atlantic Salmon in the Penobscot River, Maine. *North American Journal of Fisheries Management*, **35**(6), 1164-1176.

Silva, A.T., Bærum, K.M., Hedger, R.D., Baktoft, H., Fjeldstad, H.P., Gjelland, K.Ø., Økland, F. and Forseth, T. (2020). The effects of hydrodynamics on the three-dimensional downstream migratory movement of Atlantic salmon. *Science of the Total Environment*, **705**, p.135773.

Silva, A.T., Santos, J.M., Ferreira, M.T., Pinheiro, A.N. and Katopodis, C. (2011). Effects of water velocity and turbulence on the behaviour of Iberian barbel (*Luciobarbus bocagei*, Steindachner 1864) in an experimental pool-type fishway. *River Research and Applications*, **27**(3), 360-373.

Simpfendorfer, C.A., Heupel, M.R. and Hueter, R.E. (2002). Estimation of short-term centers of activity from an array of omnidirectional hydrophones and its use in studying animal movements. *Canadian Journal of Fisheries and Aquatic Sciences*, **59**(1), 23-32.

Smith, S.G., Muir, W.D. and Marsh, D.M. (2006). *Survival Estimates for the Passage of Spring-Migrating Juvenile Salmonids through Snake and Columbia River Dams and Reservoirs, 2005-2006 Annual Report* (No. DOE/BP-00004922-7). Bonneville Power Administration (BPA), Portland, OR (United States).

Smith, S.G., Muir, W.D., Williams, J.G. and Skalski, J.R. (2002). Factors associated with travel time and survival of migrant yearling Chinook salmon and steelhead in the lower Snake River. *North American Journal of Fisheries Management*, **22**(2), 385-405.

Stefansson, S.O., Nilsen, T.O., Ebbesson, L.O., Wargelius, A., Madsen, S.S., Björnsson, B.T. and McCormick, S.D. (2007). Molecular mechanisms of continuous light inhibition of Atlantic salmon parr–smolt transformation. *Aquaculture*, **273**(2-3), 235-245.

Stich, D.S., Zydlewski, G.B., Kocik, J.F. and Zydlewski, J.D. (2015). Linking behavior, physiology, and survival of Atlantic salmon smolts during estuary migration. *Marine and Coastal Fisheries*, **7**(1), 68-86.

Stock, J.D. and Schlosser, I.J. (1991). Short-term effects of a catastrophic beaver dam collapse on a stream fish community. *Environmental Biology of Fishes*, **31**, 123-129.

Storebakken, T. (2009). *Atlantic salmon, Salmo salar. Nutrient requirements and feeding of finfish for aquaculture* **7**, 79–102. https://doi.org/10.1079/9780851995199.0079.

Svendsen, J.C., Eskesen, A.O., Aarestrup, K., Koed, A. and Jordan, A.D. (2007). Evidence for non-random spatial positioning of migrating smolts (Salmonidae) in a small lowland stream. *Freshwater Biology*, **52**(6), 1147-1158.

Taggart, J.B., McLaren, I.S., Hay, D.W., Webb, J.H. and Youngson, A.F. (2001). Spawning success in Atlantic salmon (*Salmo salar* L.): a long-term DNA profiling-based study conducted in a natural stream. *Molecular ecology*, **10**(4), 1047-1060.

Tallis, H. and Polasky, S. (2009). Mapping and valuing ecosystem services as an approach for conservation and natural-resource management. *Annals of the New York Academy of Sciences*, **1162**(1), 265-283.

Tamario, C., Sunde, J., Petersson, E., Tibblin, P. and Forsman, A. (2019). Ecological and evolutionary consequences of environmental change and management actions for migrating fish. *Frontiers in Ecology and Evolution*, **7**, p.271.

Tentelier, C. and Piou, C. (2011). Obstacles to migration constrain nest distribution of Atlantic salmon. *Ecology of Freshwater Fish*, **20**(3), 400-408.

Tetzlaff, D., Soulsby, C., Bacon, P.J., Youngson, A.F., Gibbins, C. and Malcolm, I.A. (2007). Connectivity between landscapes and riverscapes—a unifying theme in integrating hydrology and ecology in catchment science?. *Hydrological Processes: An International Journal*, **21**(10), 1385-1389.

The state of Wild North Atlantic Salmon (2019) *NASCO*. Available at: https://nasco.int/atlantic-salmon/state-of-salmon/ (Accessed: 18 June 2023).

Thorpe, J.E. (1986). Age at first maturity in Atlantic salmon, *Salmo salar* L: freshwater period influence and conflicts with smolting. *Canad. Spec. Pub. Fish. Aqua. Sci.*, **89**, 7-14.

Thorpe, J.E., Miles, M.S. and Keay, D.S. (1984). Developmental rate, fecundity and egg size in Atlantic salmon, *Salmo salar* L. *Aquaculture*, **43**(1-3), 289-305.

Thorpe, J.E., Ross, L.G., Struthers, G. and Watts, W. (1981). Tracking Atlantic salmon smolts, *Salmo salar* L., through loch Voil, Scotland. *Journal of Fish Biology*, **19**(5), 519-537.

Thorstad, E., Kland, F., Finstad, B., Sivertsgrd, R., Bjorn, P. and McKinleyd, R. (2004). Migration speeds and orientation of Atlantic salmon and sea trout post-smolts in a Norwegian fjord system. *Environmental Biology of Fishes*, **71**, 305-311.

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

Thorstad, E.B., Økland, F. and Finstad, B. (2000). Effects of telemetry transmitters on swimming performance of adult Atlantic salmon. *Journal of Fish Biology*, **57**(2), 531-535.

Thorstad, E.B., Økland, F., Aarestrup, K. and Heggberget, T.G. (2008). Factors affecting the within-river spawning migration of Atlantic salmon, with emphasis on human impacts. *Reviews in Fish Biology and Fisheries*, **18**, 345-371.

Thorstad, E.B., Uglem, I., Finstad, B., Chittenden, C.M., Nilsen, R., Økland, F. and Bjørn, P.A. (2012a). Stocking location and predation by marine fishes affect survival of hatchery-reared Atlantic salmon smolts. *Fisheries Management and Ecology*, **19**(5), 400-409.

Thorstad, E.B., Whoriskey, F., Rikardsen, A.H. and Aarestrup, K. (2011). Aquatic nomads: the life and migrations of the Atlantic salmon. *Atlantic Salmon Ecology*, **1**(6), 1-32.

Thorstad, E.B., Whoriskey, F., Uglem, I., Moore, A., Rikardsen, A.H. and Finstad, B. (2012b). A critical life stage of the Atlantic salmon *Salmo salar*: Behaviour and survival during the smolt and initial post-smolt migration. *Journal of Fish Biology*, **81**(2), 500-542.

Tipping, J.M. (1998). Return Rates of Transported Steel head Smolts with and without a Rest Period before Release. *The Progressive Fish-Culturist*, **60**(4), 284-287.

Todd, C.D., Hughes, S.L., Marshall, C.T., MacLEAN, J.C., Lonergan, M.E. and Biuw, E.M. (2008). Detrimental effects of recent ocean surface warming on growth condition of Atlantic salmon. *Global Change Biology*, **14**(5), 958-970.

Trust, S. (2015). *Salmon at weirs* 1–2.

Tucker, S., Mark Hipfner, J. and Trudel, M. (2016). Size-and condition-dependent predation: A seabird disproportionately targets substandard individual juvenile salmon. *Ecology*, **97**(2), 461-471.

Udyawer, V., Dwyer, R.G., Hoenner, X., Babcock, R.C., Brodie, S., Campbell, H.A., Harcourt, R.G., Huveneers, C., Jaine, F.R., Simpfendorfer, C.A. and Taylor, M.D. (2018). A standardised framework for analysing animal detections from automated tracking arrays. *Animal Biotelemetry*, ***6***(1), 1-14.

Utne, K.R., Skagseth, Ø., Wennevik, V., Broms, C.T., Melle, W. and Thorstad, E.B. (2022). Impacts of a changing ecosystem on the feeding and feeding conditions for Atlantic salmon during the first months at sea. *Frontiers in Marine Science*, p.342.

Verspoor, E., Stradmeyer, L. and Nielsen, J.L. eds. (2007). The Atlantic salmon: genetics, conservation and management. *John Wiley & Sons*.

Virtanen, E. and Forsman, L. (1987). Physiological responses to continuous swimming in wild salmon (*Salmo salar* L.) parr and smolt. *Fish Physiology and Biochemistry*, **4**, 157-163.

Voegeli, F.A., Lacroix, G.L. and Anderson, J.M. (1998). Development of miniature pingers for tracking Atlantic salmon smolts at sea. *Hydrobiologia*, **371**(0), 35-46.

Vogel, E.F., Biuw, M., Blanchet, M.A., Jonsen, I.D., Mul, E., Johnsen, E., Hjøllo, S.S., Olsen, M.T., Dietz, R. and Rikardsen, A. (2021). Killer whale movements on the Norwegian shelf are associated with herring density. *Marine Ecology Progress Series*, **665**, 217-231.

Waldman, J.R. and Quinn, T.P. (2022). North American diadromous fishes: Drivers of decline and potential for recovery in the Anthropocene. *Science Advances*, **8**(4), p.eabl5486.

Waples, R.S. (1995). Evolutionarily significant units and the conservation of biological diversity under the Endangered Species Act. *Evolution and the aquatic ecosystem: defining unique units in population conservation*.

Welch, D.W., Batten, S.D. and Ward, B.R. (2007). Growth, survival and tag retention of surgically implanted acoustic tags in steelhead trout (*O. mykiss*). *Hydrobiologia*, **582**, 289-299.

Welch, D.W., Rechisky, E.L., Melnychuk, M.C., Porter, A.D., Walters, C.J., Clements, S., Clemens, B.J., McKinley, R.S. and Schreck, C. (2008). Survival of migrating salmon smolts in large rivers with and without dams. *PLoS biology*, **6**(10), p.e265.

Went, A.E.J. (1973). Movements of salmon *Salmo salar* (L.) to and from Irish waters. *Journal of Fish Biology*, **5**(6), 659-671.

Westerberg, H. (1982). Ultrasonic tracking of Atlantic salmon (*Salmo salar* L.)-II. Swimming depth and temperature stratification. *Drottingholm report*, **60**, 102-120.

Whalen, K.G., Parrish, D.L. and McCormick, S.D. (1999). Migration timing of Atlantic salmon smolts relative to environmental and physiological factors. *Transactions of the American Fisheries Society*, **128**(2), 289-301.

White, J., Fitzgerald, C., Gargan, P., de Eyto, E., Millane, M., Chaput, G., Boylan, P., Crozier, W.W., Doherty, D., Kennedy, B. and Lawler, I. (2023). Incorporating conservation limit variability and stock risk assessment in precautionary salmon catch advice at the river scale. *ICES Journal of Marine Science*, **80**(4), 803-822.

Wickham, H. (2011). ggplot2. *Wiley interdisciplinary reviews: computational statistics*, **3**(2), 180-185.

Wild Trout Trust. (2020). *Trout Lifecycle | Wild Trout Trust*. [online] Available at: <https://www.wildtrout.org/content/trout-lifecycle> [Accessed 3 June 2020].

Williams, J.G., Smith, S.G. and Muir, W.D. (2001). Survival estimates for downstream migrant yearling juvenile salmonids through the Snake and Columbia rivers hydropower system, 1966–1980 and 1993–1999. *North American Journal of Fisheries Management*, **21**(2), 310-317.

Wilson, A.D., Hayden, T.A., Vandergoot, C.S., Kraus, R.T., Dettmers, J.M., Cooke, S.J. and Krueger, C.C. (2017). Do intracoelomic telemetry transmitters alter the post-release behaviour of migratory fish?. *Ecology of Freshwater Fish*, **26**(2), 292-300.

Wilson, B., Thompson, P.M. and Hammond, P.S. (1997). Habitat use by bottlenose dolphins: seasonal distribution and stratified movement patterns in the Moray Firth, Scotland. *Journal of Applied Ecology*, 1365-1374.

Windsor, M.L., Hutchinson, P., Hansen, L.P. and Reddin, D.G. (2012). Atlantic salmon at sea: Findings from recent research and their implications for management. NASCO document CNL (12) 60. Edinburgh, UK. 20

Winfield, I.J. (2016). Recreational fisheries in the UK: natural capital, ecosystem services, threats, and management. *Fisheries Science*, **82**, 203-212.

Winter, J.D. (1996). Advances in underwater biotelemetry. *Fisheries Techniques*, 555-590.

WWF, (2001). The status of wild Atlantic salmon: a river by river assessment.

Zale, A.V., Brooke, C. and Fraser, W.C. (2005). Effects of surgically implanted transmitter weights on growth and swimming stamina of small adult westslope cutthroat trout. *Transactions of the American Fisheries Society*, **134**(3), 653-660.

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

Zydlewski, G.B., Haro, A. and McCormick, S.D. (2005). Evidence for cumulative temperature as an initiating and terminating factor in downstream migratory behavior of Atlantic salmon (*Salmo salar*) smolts. *Canadian Journal of Fisheries and Aquatic Sciences*, **62**(1), 68-78.