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The Effect of In-stream Structures on the Freshwater Migration of Atlantic salmon (*Salmo salar*)

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This thesis is dedicated to my parents.

I wish you were both here to see me finish.

In memory of Sue (1957 – 2015) and Alan (1951 – 2016)

Abstract

Atlantic salmon *Salmo salar* are an anadromous fish which undertake long distance migrations between ontogenetic specific habitats throughout their lifecycle. There is a need for free passage of salmon along river corridors in both upstream and downstream directions.

Previously, river barriers have been shown to have serious, negative impacts on the survival of downstream migrating salmonids. There is little information available regarding the natural migration and mortality in un-impacted rivers against which to contrast data from studies on impacted river systems. Chapter 2 investigates the cumulative impact of barriers on the downstream migration of Atlantic salmon *(Salmo salar)* smolts in the River Foyle, Northern Ireland. Migrating smolts were implanted with acoustic transmitters and monitored via a passive acoustic telemetry array during their downstream migration. Fish were released in two tributaries of similar length; one tributary with seven barriers along its length and the other devoid of such structures. There was no evidence to suggest river barriers heightened mortality, or that there were post-passage effects of weirs on downstream migrating smolts. This suggests that elevated mortality at obstacles in other studies is not inevitable in all river systems. Migration through rivers with natural riffle-pool migration may result in similar effects as those from low-head weirs.

A significant constraint of the use of acoustic telemetry in fishes is the transmitter size relative to that of the fish. In chapter 3, the widely accepted, but regularly debated, “2% transmitter mass: body mass” rule in biotelemetry was extended with no significant effect on survival. The results of this chapter indicate the potential to tag smaller, wild Atlantic salmon smolts which are a better representation of the wider population from which they originate

The effect of small (less than 5 meters in height) river barriers on upstream migrating adult Atlantic salmon is relatively unknown. In chapter 4, the behaviour and passage success of adult salmon at a small but complex overspill weir was investigated. A radio telemetry array was implemented at the barrier to enable identification of the behaviour of tagged

individuals as they approached and attempted to pass the structure. Fish exhibited large variations in their behaviour, and in general, avoided fish passes cited on the obstacle in favour of what was deemed the most difficult point of passage. Larger fish, in terms of fork length, were delayed longer than smaller individuals, suggesting that river barriers may potentially exert an anthropogenic selection pressure on salmon populations. Such phenomena has been reported on larger structures. This chapter also raises important questions into the effect of delay on migrating salmonids. Individuals which are delayed for longer or require a greater number of passage attempts use more energy than those which are not delayed or pass on their first attempt. The post passage effects of increased energy expenditure remain unknown and require future investigation.

Radio telemetry is not confined by a specific medium and can be utilised in both the terrestrial and aquatic environment. Thus, the fate of Atlantic salmon tagged with radio transmitters can be identified. Chapter 5 utilises tag fate identification to determine the rates of illegal exploitation of Atlantic salmon in the River Foyle, Northern Ireland. Illegal exploitation rates are high within the system and a significant proportion of the wild population is removed by illegal means. Radio telemetry has the potential to enable the identification of illegal activities which by their nature are unseen.

The work presented in this these has challenged the popular view of salmon migration in a variety of aspects. As with any research it has uncovered a number of future research questions which should be addressed, the most pertinent of which is the effect of increased energy expenditure at riverine obstacles and the post passage effects of heightened delay at such obstacles

Contents

List of Tables

List of Figures

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Authors Declaration

The material presented in this thesis is the result of original research, conducted between January 2012 and September 2015, under the supervision of Professor Colin E. Adams and Dr. Patrick Boylan. This work has not been submitted, in whole or in part towards the fulfilment of any other degree. This work is based solely on data collected and analysed by myself. Any published and unpublished material not of my own is acknowledged in the text.

Signature ______________________________

Printed name: Matthew Newton

Chapter 1

A general introduction to habitat connectivity, Atlantic salmon (*Salmo salar*) migration and the passability of instream obstacles

1.1. Migration and Habitat Connectivity

Successful completion of the life cycle of many animal species relies not on a single high quality habitat but on multiple habitats which support different ontogenetic stages (Ovidio and Philippart 2002, Melnychuk *et al.* 2010). Migration is evolutionarily advantageous co-ordinated, seasonal movement where individuals increase fitness benefits by exploiting alternative habitats (Gross *et al.* 1988, Alerstam *et al.* 2003). Migration by the arctic tern *Sterna paradisaea,* for example*,* is possibly one of the longest on record at around 24,000Km, travelling from breeding zones in the high arctic to feeding grounds in the southern oceans (Egevang *et al.* 2010). The cost of migration is outweighed by the benefits of extended day length at high latitudes of the northern hemisphere which provide sufficient food resources with a reduced pathogen and parasite prevalence during breeding (Alerstam *et al.* 2003, Buehler and Piersma 2008). For species where habitats are separated geographically, it is not just habitat quality that is important but also the migration and connectivity between habitat patches which form a critical element of the life cycle. For example, migration pathway in the Eurasian spoonbills (*Platalea leucorodia leucorodia*) significantly decreases survival during the spring migration as a result of crossing the Sahara desert (Lok *et al.* 2015).

Landscape connectivity, the degree to which a landscape facilitates or impedes movement between resources and habitats is fundamental for organisms to complement or supplement their resource requirements and complete their life history strategy (Taylor *et al.* 1993, Junge *et al.* 2014). Corridors of linear habitat (habitat corridors), connect two or more pieces of habitat together within a dissimilar matrix (Beier and Noss 1998). The ability of an organism to utilise the mosaic of habitats distributed across the landscape relies heavily on the biophysical nature of the corridor(s) connecting the habitat patches together (Taylor *et al.* 1993). Some habitat corridors facilitate un-impeded movement where as others restrict it, often to varying degrees, depending upon the behaviour and biology of the individual (Taylor *et al.* 1993).

It is generally agreed by conservation biologists that habitat connectivity is critically important to enhance population viability (Beier and Noss 1998, Cote *et al.* 2009). Connectivity enables gene pool maintenance, re-colonisation post disturbance and population recruitment (Elosegi *et al.* 2010). Habitat connectivity is not pre-defined, but is made up of several variables such as; the physical aspect of the landscape (landuse type, vegetation cover, moisture etc.), the distance between individual patches, and the behaviour of the species itself. What constitutes as a corridor for one species is likely to differ to that of another, thus not all corridors are created equally. For example, one species may be reluctant to cross certain types of agricultural areas whilst moving freely through others. The linear continuity of a corridor, such as the; length, amount and severity of barriers or gaps and the presence of alternative pathways may influence the ease at which animals can navigate through the landscape (Henein and Merriam 1990).

What constitutes as a barrier or obstacle varies between species and is dependent on the mode and ability of movement (Henein and Merriam 1990). Although arctic terns are able to undertake extensive migrations, relatively free of obstructions, in South Africa, the fencing of protected areas, rangelands and transitional boundaries has severely disrupted ungulate migrations and is reflected in the decline in abundance of several migratory species (Bolger *et al.* 2008). Similarly the Ulaanbaatar-Beijing railroad in Mongolia is thought to be primary factor in preventing the historic east-west migration of Mongolian gazelle (Bolger *et al.* 2008).

Terrestrial landscapes enable animals in a single habitat patch to move via one of numerous potential paths to another habitat patch. Movement between habitat patches in aquatic systems, particularly rivers, is primarily longitudinal and confined to the river corridor (Cote *et al.* 2009), although lateral movement within floodplain reaches are sometimes imperative (Lucas and Baras 2001). Pringle (2003) defined aquatic connectivity as the:

> *"water-mediated transfer of matter, energy and/or organisms within or between elements of the hydrological cycle".*

The river corridor is highly susceptible to fragmentation with a single damming event having the potential to immediately isolate adjacent habitats (Jager *et al.* 2001, Cote *et al.* 2009, Branco *et al.* 2012). Connectivity is highly variable among rivers, natural waterfalls and even rapids may create migration barriers for some species, often resulting in variable community structure both up and downstream of such structures (Elosegi *et al.* 2010). In-river structures, both artificial and natural, such as; fords, dams, weirs, culverts, rapids and waterfalls can have major impacts on fish communities when they prevent free movement along the riverine corridor (Baras *et al.* 1994, Lucas and Frear 1997, Jager *et al.* 2001, O'Hanley and Tomberlin 2005, Kemp *et al.* 2008). Barriers may not form complete obstructions but be passable under certain circumstances, they still have the ability to impact on fish movement and are historically related to declines in anadromous fish stocks (Mills 1989).

Fragmentation of essential habitats often leads to the extinction of fishes (Roscoe and Hinch 2010). In addition, ecosystem functioning in general relies heavily on longitudinal connectivity, for example, the spawning migrations of salmon periodically transport nutrients from the ocean to the headwater of rivers where carcasses fertilise stream beds (Elosegi *et al.* 2010). Salmonid migration is also imperative for the translocation and re-distribution of the freshwater pearl mussel *Margaritifera margaritifera* which attaches to the gills of fish as parasites, and transported to new habitats by migrating salmonids, prior to release and dispersal (Arvidsson *et al.* 2012). River fragmentation and connectivity is also at the forefront of legislation, the European Union Water Framework Directive (WFD) requires that Member States achieve 'good ecological status of water bodies which have been heavily modified, by 2015'. One of the key requirements for the directive is the need for unimpeded fish migration, bringing to light the need to mitigate the ability of fish to migrate up and downstream unconstrained. To meet minimum requirements for the WFD the river or water course must be in a state where there is connectivity between all river zones from estuary to source in both upstream and downstream directions. One of the most established ways to do this is through mitigating the impact riverine barriers have on ecological processes as described by the River Continuum Concept (Vannote *et al.* 1980).

A diadromous life history is particularly enigmatic since fish must cross the marine-freshwater boundary (Gross *et al.* 1988, Thorstad *et al.* 2012). Fish exhibiting a diadromous life cycle are likely to be most vulnerable to changes in connectivity as they navigate between salt-free and salt-rich environments whilst undertaking challenging physiological transformations in order to survive in these ecosystems (Thorstad *et al.* 2012). Anadromous species exhibit a remarkable and complex type of diadromous migration where fish hatch in freshwater prior to migrating into marine habitats for feeding and eventually make a return migration to freshwater for spawning, overwintering or both (Gross *et al.* 1988). An anadromous lifecycle is continuously threatened by river fragmentation, habitat connectivity and the impact of riverine barriers since there is a need for individuals to transcend the river corridor, both as they migrate to sea as juveniles and also on their return to spawn as adults. Such a life cycle is exemplified in the Atlantic salmon *Salmo salar* L. 1758.

The life cycle of the Atlantic salmon has been described in detail by various authors (Dunkley and Shearer 1982; Jones 1959, Mills 2000, Klemetsen *et al.* 2003, Aas *et al.* 2010). In general, the life cycle of Atlantic salmon is as follows (Fig. 1): Spawning and egg laying begins in autumn, spawning takes place on silt free, well oxygenated gravels. After spawning, adult mortality is high although some individuals do return to spawn in subsequent years. The eggs hatch into alevins in spring (March – April) and make their way up through the gravels to emerge as feeding fry. Fry, at the end of the first year in freshwater are known as parr (Mills 1989). They may remain at this stage for up to six (in the British Isles normally one to two) years, at the end of which they turn silver and become smolts. Smolts migrate downstream to the marine environment where they feed and grow for one winter (grilse or one sea winter [1SW] fish) or longer (multi-sea winter [MSW]). Mature adults then return to natal rivers and streams to spawn.

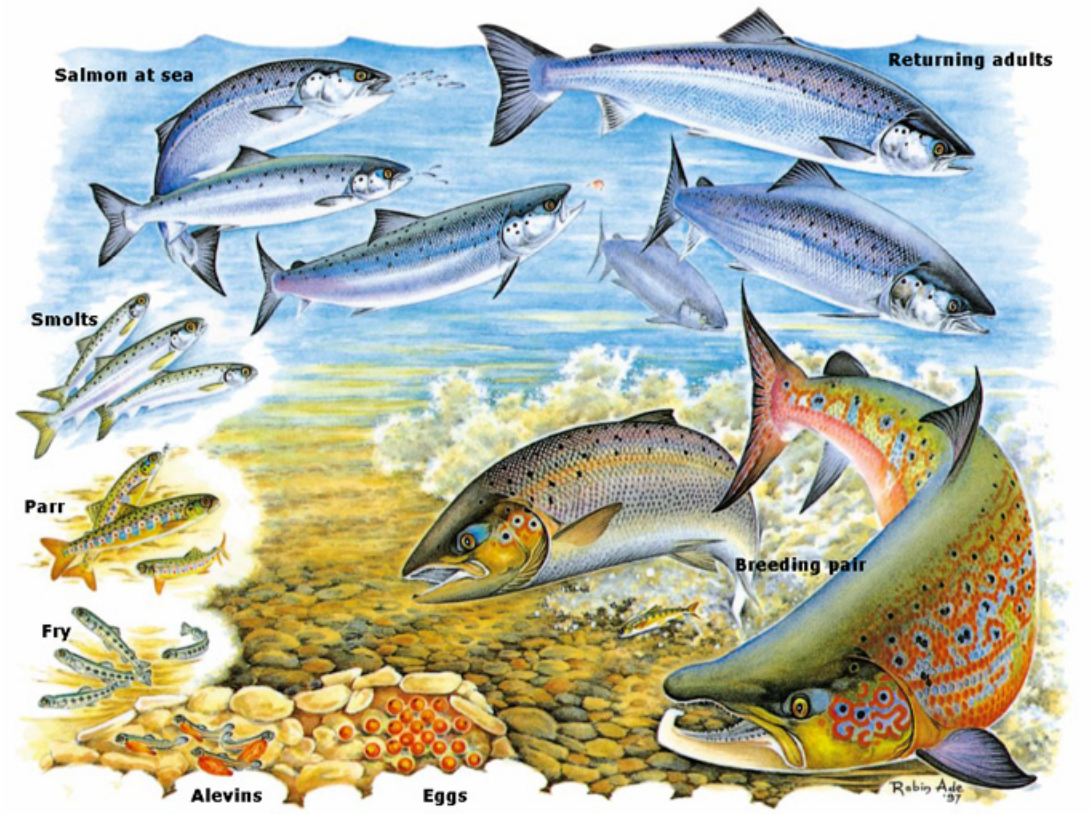

Figure 1.1 The life cycle of the Atlantic salmon: From NASCO courtesy of Atlantic salmon trust and Robin Ade

Theoretically, diadromous life-histories have evolved via natural selection where breaching the marine-freshwater boundary enhances an individual's fitness which exceeds the migratory cost (Gross *et al.* 1988). Within salmonids, body size has a significant positive correlation with an individual's fitness. In females, egg size and number increases with maternal body size (Thorpe *et al.* 1984, Moffet *et al.* 2006, Jonsson *et al.* 2016) consequently, a large fish will produce a greater number of large eggs, which subsequently leads to large fry (Thorpe *et al.* 1984, Heinimaa and Heinimaa 2004) which intern have higher survival (Einum *et al.* 2002, Moffet *et al.* 2006). Larger fry initially have a competitive advantage over smaller individuals, resulting in higher initial survival rates due to the fact they are able to control and exploit favourable feeding territories. Multi-sea winter males also exhibit greater reproductive success than 1SW fish due to their aggressive behaviour (Garant *et al.* 2016). In temperate latitudes, marine ecosystems are more productive than freshwaters, hence migration from freshwater to salt-water enables greater food intake, resulting in increased growth and thus fitness (Gross *et al.* 1988). Pacific salmon may experience a 10-50% increase in daily growth rate for the first week in marine waters (Neilson *et al.* 1985). As reported in Gross *et al.* (1988), a review of seven salmonid species life history traits indicated that diadromous populations produced more eggs, as a function of their body size, than non-diadromous populations. An experimental increase of freshwater food ability in arctic charr (*Salvalinus alpinus*) decreased the incidence of anadromous migration (Nordeng 1983). Increase in body size and ultimately fitness through food availability is a primary benefit to the anadromous life cycle of Atlantic salmon.

If natural anadromous populations of salmon are to survive, both the downstream juvenile and upstream adult migrations are essential. The confinement of fish movement to within the river corridor makes fragmentation by barriers a serious threat. Permanent barriers cause severe impacts on populations from reduction in suitable habitat sites through to increasing mortality rates and even increased predation risks (O'Hanley and Tomberlin 2005). It is also evident that riverine barriers which cause a temporary delay and subsequent slow migration, impacts on survival to spawning grounds through a number of processes, ultimately affecting population viability (Naughton *et al.* 2005).

1.2. Barrier Passability

The ability of a fish to successfully navigate past an obstacle is highly dependent on the leaping and swimming capabilities of the individual, the hydraulic and physical characteristics of the barrier and the local environmental conditions (temperature [effect on swimming ability], water depth and water velocity) at the time of passage. The swimming and leaping capabilities of a fish are directly related to its biomechanical morphology, as such there is a high degree of variability in the ability of different species, life stages of a species and even individuals within that species, to negotiate riverine barriers (Baras *et al.* 1994, Winter and Van Densen 2001, O'Hanley and Tomberlin 2005, Lucas *et al.* 2009).

As a consequence to the multitude of variables which enable or prevent passage, barriers can either be a permanent obstruction or simply cause a brief delay until favourable conditions arise for the barriers to become negotiable (Winter and Van Densen 2001, Kemp *et al.* 2008, Lucas *et al.* 2009). For example culverts may create an impassable barrier during high flows when velocities are too high and may also be impassable under low flows when water depths are too low, both scenarios preventing fish movement upstream. However, there are times when conditions across or within the barrier will enable passage, hence a partial barrier to migration. The specific time at when a barrier becomes passable to an individual will vary from one to another, for example, large fish require deeper water to swim through compared to smaller fish, yet larger fish are able to swim at higher speeds than smaller fish, hence the window of opportunity for passage varies simply on fish size characteristics, combine this with environmental and barrier type variability and passage of a barrier becomes highly complex.

It is important to recognise that barriers do not only cause impediments to migration, but also impact on fish species indirectly by altering the natural flow regime and hydrological conditions of the river. Barriers often impact on sediment yields as well as discharge, hydrological regimes and both water temperature and quality. Currently over 50% of large scale river systems (Virgin Mean Annual Discharge > 350 $m^3 s^{-1}$) are affected by dams (Nilsson *et al.* 2005) with water residence time increasing threefold resulting in reduced supply of sediments to coastal regions (Vörösmarty *et al.* 2003). Alteration of the natural thermal regime along with severe habitat fragmentation, combined with the effect of river barriers will result in decreases of biodiversity, particularly for anadromous fish species (Elosegi *et al.* 2010).

Passage efficiency and barrier passability are possibly the most common phrases used to describe the impediment of instream barriers to fish. In this thesis the term barrier passability will be used, however definition of this passability varies widely within literature. In the most basic form, barriers maybe assigned a value on whether they are passable or not, for example dams without fish pass constructions are generally impassable whereas those with fish passes are deemed passable. However, as for the majority of barriers, only a partial impediment is present with passability being temporally variable, quantitative values are required in order to give a level of passability for any given time or the number of available days of passage for certain species within the migration season.

Passage efficiency also varies when considering whole populations or single individuals. At the individual scale, passage efficiency can be derived through the total number of attempts to pass a barrier before eventually doing so, whilst at a population level efficiency maybe measured through the number of successful passages compared to the total population (Haro *et al.* 2004). A significant problem however is the fact that fish may not attempt to pass a barrier as migrating fish utilise suitable habitat downstream.

O'Hanley and Tomberlin (2005) defined passability as:

> *"The fractional rate, within the range (0,1), at which fish are able to pass through a barrier while migrating upstream"*

This definition is primarily suited to migrating adult salmonids whose movement during migration is generally in a single direction (marine to freshwater) however only upstream passability is considered. The time taken to pass barriers is also an essential element when considering passability. Delayed migration may impact on survival rates through; increased energetic costs, heightened predation risk and timing of arrival at destination which may ultimately disrupt key life cycle events such as spawning, there for a delay factor should be measured when considering passability (Castro-Santos and Haro 2003).

In many catchments, measurement of the impact of multiple barriers is often required, using the total delay time or proportion of fish ascending all barriers are useful tools in defining passability. Cumulative passability can be measured empirically through the use of telemetry. Due to constraints, primarily resource driven (monetary), a large proportion of studies investigating the effect of barriers on salmonids is undertaken at local scales often examining one barrier and its short term consequences (Caudill *et al.* 2007). Due to this, the vast majority of such research is undertaken at large scale dams or hydro-electric projects, however both share similar characteristics and it is a question of scale of impacts rather than identifying separate consequences (SNIFFER, 2011). As is often the case, individual passabilities of barriers are assumed to be independent. This general assumption means that a fish passing one barrier are not affected post passage and thus passability at a subsequent barrier does not account for previous encounter histories. However this is not the case, with telemetry studies indicating cumulative effects of riverine barriers (Thorstad *et al.* 2008, Cote *et al.* 2009, Lucas *et al.* 2009). Determining pasability at cumulative barriers can be difficult, Kemp and O'Hanley (2010) suggest an idealised form of cumulative passability, whereby passability of numerous sequential barriers is taken as the lowest passability score, on the basis that fish which can pass the barrier with the lowest score will also be able to pass other barriers which are deemed more easily passable. Within this thesis passability is defined within each chapter referring specifically to each individual study.

1.3. Monitoring Barrier Passability

Traditionally, the migration of Atlantic salmon within rivers has been studied by physical counts of fish passing set points; traps, fences, or weirs through the use of manual counts and automatic fish counters (Lucas and Baras 2000). Mark and recapture studies as well as catch statistics have also previously been used. Such methods prove problematic when teasing apart various factors thought to have an intrinsic relationship with migration patterns due to unknown quantity of fish present downstream from the counting location (Thorstad *et al.* 2008). Favourable migration conditions may be present yet little migration activity documented due to the lack of individuals in the downstream area. Similarly increased activity may be seen however this activity may not be directly related to environmental conditions but could be due to an increase in fish entering from the sea (Thorstad *et al.* 2008). This variability needs to be accounted for and considered in such studies when creating statistical analysis and the robustness of such data can be questionable.

Should social factors, such as upstream movements in groups, be of greater importance to fish than currently recognised, a dilemma is created for fisheries managers in respect to statistically weighting large groups of fish which pass counters (Thorstad *et al.* 2008). When one individual selects a successful passage route across a barrier, many individuals seem to follow however such social mechanisms are still to be studied and considered (Thorstad *et al.* 2008).

The use of catch rate from recreational fisheries also involves un-reliable variables, such as fish susceptibility to capture, and catches may not be linked with migratory behaviour (Thorstad *et al.* 2008, Lennox *et al.* 2015). Mark and recapture studies have in general highlighted important information about fish migrations (Lucas and Baras 2000). The method identifies limited information on the migration behaviour between the two capture points and variables which maybe affecting this behaviour. Information gained is also limited to individuals which are recaptured, often a small proportion of the initial marked population. The ultimate result of the study (recapture) may be due to a particular migration behaviour different to un-recaptured individuals and hence not a true representative sample (Lucas and Baras 2000, Thorstad *et al.* 2008)

Cote *et al*. (2009) have developed a new tool in assessing longitudinal connectivity of river systems, based on the ability of a single organism being able to move un hindered between two points within a network, such as sea to source (Cote *et al.* 2009). The Dendritic Connectivity Index (DCI; Cote *et al*. 2009) requires two specific data inputs: Barrier location and a passability score for each barrier. Whilst location is relatively easy, passability is not. Barriers have significant impacts on fish migration, quantifying this impact is challenging due to the difficulties involved with defining and measuring passability itself. Common methods use a combination of physical barrier properties and known fish physiological parameters to define a passability rate. Passability is dynamic; fish physiological capacity varies by species, within species, and across environmental conditions. The physical properties of barriers may also vary due to variations in discharge. This variability, both environmental and physiological makes defining passability at a single barrier challenging let alone at a catchment or national scale (Bourne *et al.* 2011). The restoration and protection of aquatic connectivity is widely recognised and accepted as a conservation goal, hence the development of methods to measure this connectivity within dendritic systems (Bourne *et al.* 2011).

> *"Common to all methods is the difficulty in assessing barrier passability - The dynamic component of connectivity"*
>
> *Bourne et al, 2011*

In order to meet the obligations of the WFD, water resource managers and regulators require methodologies that enable assessment of barrier porosity to fish migration, along with the development of a barrier inventory which will allow for prioritisation for mitigation based on a value of positive gains (Kemp *et al.* 2008). It has been recognised there is limited information defining barrier porosity to migration, this factor alone makes it difficult for organisations to prioritise barriers for mitigation (Kemp *et al.* 2008).

Ovidio and Philippart (2002) found that some barriers, initially thought to be minor barriers were in fact severe obstacles to migration. In some instances this was due to lack of water depth across the obstacle. Barriers which were expected to be complete barriers or pose relatively large obstacles to movements were in fact relatively porous, 100% (11) brown trout ascended a barrier with a slope of >50%

1.4. Telemetry

Animal tracking technology (telemetry) has given an insight into animal behaviour and revealed novel information in both terrestrial and aquatic habitats, revealing information that only a few decades ago was impossible to achieve through the use of traditional sampling methods (Lucas and Baras 2000, Adams *et al.* 2012, Cooke *et al.* 2013, Thorstad *et al.* 2013). The use of electronic transmitters is a proven and effective technology for identifying movements and migrations of various aquatic species in coastal, estuarine and freshwater ecosystems (Cooke *et al.* 2004, 2013). A significant advantage of telemetry techniques is that it is possible to monitor and repeatedly locate individuals over long periods of time without the requirement for multiple re-capture events. The developments and benefits of telemetry have previously been covered extensively by a number of authors (Lucas and Baras 2000, Hodder *et al.* 2007, Halttunen *et al.* 2009, Cooke and Thorstad 2011, Adams *et al.* 2012, Cooke *et al.* 2013, Thorstad *et al.* 2013). Typically, within telemetry, a transmitter, which is attached to an individual, transmits information wirelessly to a receiver where it is stored and recorded. This information can be used to inform the position of the individual at a specific time and provide data on measurements of environmental and physiological parameters (Thorstad *et al.* 2013).

The work described in this thesis has made extensive use of both acoustic and radio telemetry methods to glean information on the migration of Atlantic salmon. An important assumption in telemetry studies is that the transmitter does not influence the behaviour and physiology of the individual and that observations made on the tagged individuals reflect that of the population as a whole. Correspondingly numerous studies have been conducted to investigate the potential effect of the transmitter on the fish, one strand of the work described here examines this further.

1.5. Upstream Migration

Upstream movement maybe categorised into three main stages (Thorstad *et al.* 2008). Initial upstream movement (steady migration phase) will take individuals to within reach of their natal spawning grounds. Baisez *et al.* (2011) indicated the initial upstream migration ceased when water temperatures reached 15.5 ± 2.7^{o}C, with survival rates highly correlated with lower temperatures. Once the initial upstream phase is completed, a 'search phase' has been witnessed in studies (Økland *et al.* 2001, Finstad *et al.* 2005), where fish move up and downstream of the position held for spawning (Aas *et al.* 2010), fish maybe selecting spawning areas or finding a suitable holding location until ready to spawn. A final holding phase, is often noted where fish may hold for many months until ready for spawning, this is normally a short distance downstream of spawning gravels. The final stage of freshwater migrations sees adults move up from holding pools to spawning grounds where reproduction takes place (Bardonnet and Baglinière 2000).

1.5.1. Return Adult Migration in Pristine Systems

In order to evaluate the effects of in-stream barriers on populations it is important to have data from 'pristine' systems which remain wholly undisturbed by anthropogenic impacts where factors such as flow and temperature (which generally determine passage at barriers) have less influence on the migration behaviour of Atlantic salmon (Økland *et al.* 2001). The River Tana in northern Scandinavia is one of the very few large river systems with abundant and pristine salmon populations with no anthropogenic obstructions (Erkinaro *et al.* 1999).

(Økland *et al.* 2001) analysed the return freshwater migration of MSW Atlantic salmon in the subarctic River Tana. No difference in discharge was detected between days with and those without migration movements, however once fish had begun migration movements, migration speed was positively correlated with discharge suggesting migration is influenced by external factors in pristine rivers. Conversely (Erkinaro *et al.* 1999) indicated that for 1SW salmon this relationship was not evident, with no correlation between migration speed and river flow (Karppinen *et al.* 2004). In the River Tana, all riffle areas (Tana bru – 38km from the river mouth, Storfossen – 69km from river mouth) along the migration route are passable, giving further evidence that migration motivation is influenced by external factors since small passable riffles and rapids prevent migration upriver (Økland *et al.* 2001). Migration delay at these areas varied with discharge, under high flows (>300m^3/s) passage was quicker than under low flows (< 300 m^3/s) (Erkinaro *et al.* 1999). Average migration delay at two riffle areas on the River Tana for 1SW fish were much lower (19.5 hours and 2.7 days) (Karppinen *et al.* 2004) compared to MSW fish delays (2.2 days and 4.6 days) recorded by Erkinaro *et al*. (1999). This variation in delay maybe due to environmental factors or possible behavioural differences between MSW and 1SW fish (Karppinen *et al.* 2004).

The evidence suggests that 1SW and MSW fish exhibit differing behaviour during pristine migration, it is therefore likely differences are also exhibited when encountering river barriers. The analysis of this behaviour is essential due to the significance of defining mitigation options; it is possible that 1SW and MSW fish require different passage criteria. The identification of migration delays, and variance in delay depending on life history strategy, within pristine rivers demonstrates the importance of understanding the effects of natural and anthropogenic barriers to migration of salmonids. These bottlenecks create delays where individual fish accumulate exacerbating susceptibility to fishing, disease and predators (Karppinen *et al.* 2004).

1.5.2. Single river barriers

Chanseau and Larinier (1999) studied the movements and behaviour of adult Atlantic salmon in the vicinity of a hydroelectric power plant, over three years, 11 of 32 tagged fish ascended the barrier. Of 1851 detections at the fish pass entrance, on only 16 occasions did fish enter the pass (0.86% attraction efficiency). Telemetry data indicated fish moving between the fish pass entrance and a holding pool 500 meters downstream. Gowans *et al.* (1999) observed similar behaviour where tagged individuals approached a fish pass but less than 50% of these approaches resulted in entry to the ladder and mean delay at the ladder was calculated at 14.8 days (36 minutes – 66 days). Rivinoja *et al.* (2001) also indicate failure of fish passage efficiency with 26% of tagged fish passing dam Norrfors in Sweden. This result is supported by Perä and Karlström (1996) with only 14% of fish (81 of 485) locating the fish pass at the same dam. Webb (1990) found six of eleven tagged fish did not ascend Pitlochry fish ladder (River Tay, Scotland), however following improvements to the pass Gowans *et al.* (1999) showed 100% of fish detected below the pass eventually ascended but only after a significant delay averaging 14.8 days (range 36 mins – 66 days), thus showing the importance of monitoring behaviour at river barriers.

These 'yo-yo' migrations and delayed passage, cause increased energetic costs through excess swimming behaviour, costs which cannot be recuperated since adult anadromous fish cease feeding in freshwater (Jones 1959, Mills 1989, Bardonnet and Baglinière 2000), however see Johansen (2001). A reduction in fat reserves potentially reduces fitness of individuals during mate competition eventually leading to lower over winter survival (Lundqvist *et al*. 2008). Various studies have indicated successful migrants (i.e. individuals which reached spawning grounds) had lower approach and passage times when compared with unsuccessful individuals (Chanseau and Larinier 1999, Naughton *et al.* 2005, Lundqvist *et al.* 2008, Makiguchi *et al.* 2011). Thorstad *et al*. (2003) released tagged fish which were detected after a median of 21 hours below a hydropower impoundment, and did not pass for 0–71 days (median = 20). The initial rapid upstream movement and subsequent length of time to passage at the barrier indicates a significant impact on migration. This is supported by Roscoe *et al*. (2011) with 49% of tagged fish released downstream of a dam (Seton river, British Columbia) reaching spawning grounds, compared with 98% of tagged fish released above the dam. Females had a lower survival rate (39% of 38) compared with males (71% of 17). Lundqvist *et al*. (2008) also illustrated the impact of a single impoundment, with only 30% (of 478) of all tagged fish successfully passing, mitigation to improve passage rate to 75% is estimated to result in a 500% escapement return within 10 years in the study. Contrary to this, Caudill *et al*. (2007) found that migration success of Chinook salmon (Oncorhynchus tshawytscha) and steelhead (sea-run Oncorhynchus mykiss) was highly dependent on passage time through the Columbia River system as a whole rather than at individual barriers.

1.5.3. Cumulative river barriers

Rivers often have more than one barrier along its length and the cumulative impact of these may have a critical impact on the successful spawning migration of Atlantic salmon. Gowans *et al.* (2003) estimated proportions of fish passing individual obstacles to range between 63-100% in the study, however cumulatively only 4 of 54 tagged fish were successful (7.4%) in reaching spawning areas. Cumulative barriers on the River Aulne (France) caused similar impacts with only 4.3% of individuals being capable of passing the 28 barriers required to reach spawning grounds (Baisez *et al.* 2011). Baisez *et al.*(2011) indicated that mortality was highly dependent on fish passing barriers, those delayed furthest downstream over the summer period experienced a higher mortality rate (56%) compared to those delayed in the middle (38%) and the upper (13%) parts of the river, primarily due to temperature increases. In this river it is key that fish can ascend to the upper reaches in order to survive high summer temperatures, barriers delay travel time preventing fish reaching the upper catchment where cool water enhances summer survival (Baisez *et al.* 2011).

The measurement of this cumulative impact is rare, however the idea that slowed migration as a whole can have serious negative impacts is common (Chanseau and Larinier 1999, Naughton *et al.* 2005, Holbrook *et al.* 2011). A large majority of studies on single barriers emphasise that when passage is required at several dams, cumulative effects of even slightly reduced passage can be substantial (Holbrook *et al.* 2011). Various studies indicate a negative correlation between successful migrants (individuals which reach spawning grounds) and migration rates through entire systems (Chanseau and Larinier 1999, Naughton *et al.* 2005, Holbrook *et al.* 2011).

Endogenous (i.e. physiological) mechanisms impacting upon passage success were often not assessed, though they were a powerful means of evaluating mechanisms of failure (Roscoe and Hinch 2010). A common research theme throughout the literature is the behaviour of Atlantic salmon in response to hydro-power installations and the fish passes related to these impoundments, yet small scale barriers are vastly understudied (Kemp and O'Hanley 2010). Indeed a tagged salmon by Ovidio and Phillipart (2002) was unable to surmount a barrier 1.4m in height due to water depth below the barrier and on the face itself. Conversely Chanseau *et al*. (1999) indicated Atlantic salmon could negotiate barriers <1.5m within 24hr on the Pau River (France) yet severe delays were encountered at barriers >2.5m in height with passage being highly dependent on fish passage facilities and pool depth.

1.6. Downstream Migration

The sea-ward migration of *S.salar* smolts is a critical transition from one life history stage to another. This downstream migration is heavily influenced by photoperiod, discharge and water temperature. The movement of smolts is reviewed by McCormick *et al.* (1998) and their known mortality and behaviour by Thorstad *et al*. (2012). The downstream migration of smolts and the effects of river barriers on their movements has received far less attention than the upstream stage of migration.

The documentation of natural mortality of smolts is rare, indeed research is generally conducted in relation to anthropogenic factors, such as hydropower or abstraction sites. Smolts, during their migration are preyed upon by both avian and mammalian species as well as other fish predators. A summary of studies where mortality occurs without direct links or association to anthropogenic factors indicate a possible natural mortality rate of between 0.3 and 7% km^{-1} (Thorstad *et al.* 2012)

The majority of smolt migration research has been conducted in relation to hydropower facilities. Since smolts, in general, follow the main flow of a river, they are subsequently drawn into turbine intakes, thus migration of smolts through turbines is common due to the bulk of flow directed into the turbines for power generation. Hence hydropower turbines represent a major barrier for migrating juveniles with the potential to cause direct mortality from blade strikes or shear injuries (Deng *et al*. 2005) but may also result in delayed mortality or reduced reproductive potential (Thorstad *et al*. 2012).

Delays at river obstructions have the potential to increase the time smolts are exposed to predators and thus inducing anthropogenically heightened mortality. Gauld *et al*. (2013) demonstrated for the first time that the downstream migration of anadromous brown trout (*Salmo trutta*) smolts may be significantly impeded by low-head over spill weirs with losses varying between 9% and 44% between years. The delay in migration exposes fish to potential predation threats for a greater period of time thus inducing heightened mortality. Apart from Gauld *et al.* (2013) there are no studies identifying the impacts of instream obstacles, free from hydropower on the downstream migration of smolts.

1.7. Summary

There is a clear requirement for the need for Atlantic salmon to be able to pass freely along river corridors to complete their life cycle, it is also necessary to ensure that larger, higher fecund females are able to ascend rivers and negotiate obstacles in order to enable recruitment of strong fry. Similarly there is a need for smolts to be able to pass downstream un-impeded without anthropogenically heightened mortality. A key problem with river barriers is their temporal effect on migrations which still remains relatively unknown. Currently there is little empirical evidence identifying the impact of small, low-head obstructions on the freshwater migration of Atlantic salmon.

This thesis uses telemetry methods to identify the impact of riverine barriers on the upstream migration of adult Atlantic salmon and also the downstream migration of Atlantic salmon smolts. Specifically in each of the following chapters I address these questions:

Chapter 2: The cumulative effect of river weirs on downstream migration success, speed and mortality of Atlantic salmon (*Salmo salar*) smolts.

Question: Do cumulative riverine barriers negatively impact the downstream migration of Atlantic salmon smolts?

Approach: A comparison of smolt migration rate and mortality in two rivers from the same catchment. One river was 'impacted' with seven river barriers along its length, the other 'un-impacted' with no river barriers. Acoustic telemetry was used to determine migration rates and survival during the downstream migration

Chapter 3: Does Size Matter? A Test of Size Specific Mortality on the Downstream migration of salmon *Salmo salar* smolts tagged with Acoustic Transmitters.

Question: Can small wild Atlantic salmon smolts, representative of the population, be used in acoustic telemetry studies?

Approach: Survival of wild Atlantic salmon smolts implanted with acoustic transmitters was tested against body size characteristics (e.g. fork length, Transmitter mass: body mass ratio) to determine the effect of the transmitter on survival.

Chapter 4: The Impact of a small scale riverine obstacle on the upstream migration of Atlantic salmon (*Salmo salar* L.)

Question: What is the behaviour of returning adult Atlantic salmon on approach to a small scale riverine barrier?

Approach: A radio telemetry array was constructed at the downstream foot of a weir. The array was designed so that tagged, approaching fish would be detected and their behaviour identified. The array enabled the identification of passage route choice, extent of delay and wider movements of the fish

Chapter 5: An estimate of the rate of illegal net fishing for sea-migrant Atlantic salmon, *Salmo salar*, in a dendritic river system in the western Atlantic.

Question: What is the fate of tagged Atlantic salmon?

Approach: Atlantic salmon were oesophageal tagged with radio transmitters. The movements of tagged fisher were identified daily over the migration period. The fate of tags could be determined, ultimately identifying the extent of illegal exploitation of the wild stock.

Chapter 2

The cumulative effect of river weirs on downstream migration success, speed and mortality of Atlantic salmon (*Salmo salar*) smolts.

2.1. Introduction

Habitat corridors, which connect larger pieces of habitat together within a dissimilar matrix are essential in facilitating gene pool coherence, recolonisation post disturbance and population recruitment (Beier and Noss 1998; Elosegi *et al.* 2010). Species decline and extinction is often preceded by the fragmentation of its distribution (Ceballos & Ehrlich 2002; Baguette *et al.* 2013). Terrestrial connectivity enables animals to cross from one habitat patch to another, often using one of several paths. In aquatic riverine habitats however, longitudinal movement, along the river channel, tends to be dominant (Cote *et al.* 2009) although in floodplain reaches, lateral movements are sometimes imperative (Lucas & Baras 2001). Hydrological connectivity and the water-mediated transport of organisms, energy and matter, is thus critical to ecosystem functioning. Species that exhibit migration within river habitats and between river and ocean habitats (e.g. anadromous and catadromous fishes) are inevitably highly vulnerable to river corridor fragmentation.

In-river structures, both natural and artificial, such as waterfalls, dams, weirs, fords, and culverts can have major impacts on fish communities, preventing free movement along the riverine corridor (Baras *et al.* 1994; Lucas & Frear 1997; Jager *et al.* 2001; O'Hanley & Tomberlin 2005; Kemp *et al.* 2008). It is estimated within England and Wales alone there are some 25,000 in-river, man-made, obstructions, of which 3,000 are significant and require mitigation in order to meet objectives set by the Water Framework Directive (Directive 2000/60/EC), and EU Eel legislation (EC No. 1100/2007) (Environment Agency 2009).

The impacts of large engineered in-river structures (>5 m head height; predominantly hydropower dams), particularly on fish populations and assemblages is well documented (Gowans *et al.* 2003; Antonio *et al.* 2007; Meixler *et al.* 2009; Branco *et al*. 2012). The effects of low-head obstacles (<5 m head height) has however received much less attention, yet they too have also been shown to have serious implications for fish passage (Lucas & Frear 1997; Ovidio & Philippart 2002; O'Connor *et al.* 2006; Gauld *et al.* 2013). Determining the likelihood of fish passage at river obstacles is highly complex due to numerous environmental and biological variables. Swimming and leaping capabilities of fish of different sizes and species, as well as the heterogeneity of environmental variables associated with riverine systems such as flow and temperature, all affect the probability of successful barrier (natural or man-made) passage (Baras & Lucas 2001). As such, any single barrier may prevent migration, cause a temporary delay in migration, or have no effect whatsoever depending on the environmental conditions and organism biology. Passage at small scale barriers is likely to be highly temporal as a result of changing environmental conditions, particularly flow (Kemp & O'Hanley 2010). Such barriers are likely to be permeable to some species or some individuals of that species, for example to some, but not all, size classes (Lucas & Frear 1997, O'Connor *et al.* 2006; Lucas *et al.* 2009), resulting in temporary and variable delays to migration

Downstream migration patterns of fish over small scale obstacles, remains relatively poorly described and quantified, however reluctance of fish to progress downstream when confronted with an in-stream barrier has been documented (Haro *et al.* 1997; Jepsen *et al.* 1998). Elevated mortality resulting from physical damage of passage through hydropower turbines is regularly reported (Hvidsten & Johnsen 1997; Thorstad *et al.* 2012). It is also possible that physical damage occurs from downstream passage of over spill weirs through contact with the weir face or stream bed due to hydrological forces present at such structures. This impact, although not necessarily causing instant mortality, may result in a delayed response, affecting individuals during the subsequent migration. Thus to fully understand the impact of low head impoundments, and how these man-made structures compare with passage within a natural system without engineered structures, it is essential to understand post-passage impacts in addition to pre-passage behaviour (Roscoe *et al.* 2011).

Migration delays and increased mortality (between 9% and 44% of tagged fish) have been shown in downstream migrating anadromous trout *(Salmo trutta)* smolts at a single low head weir 3m in height, the delay may vary depending on yearly flow regimes (Gauld *et al.* 2013). Using mortality rates from the lower end of the range recorded by Gauld *et al.* (2013) mortality induced by low-head obstacles might result in a high cumulative loss over several structures in series. The measurement of this cumulative impact for small engineered structures is rare, although it has been demonstrated for medium-sized and larger obstacles (Gowans *et al.* 2003; Holbrook *et al.* 2011). However the idea that delayed migration in general can have serious negative impacts is common (Chanseau & Larinier 1999; Naughton *et al.* 2005; Caudill *et al.* 2007; Holbrook *et al.* 2011). Downstream migrating smolts are subjected to predation from mammalian, avian and fish predators; where the impact of a barrier is a delay or an overall reduction in travel speed during migration, this can negatively impact survival rates due to increased exposure to predation risks (Jepsen *et al.* 1998; Koed *et al.* 2002). Furthermore, various studies on salmonids indicate a negative correlation between migration success and migration speeds through entire systems (Chanseau & Larinier 1999; Naughton *et al.* 2005, Holbrook *et al.* 2011).

There is a paucity of studies that have examined smolt migration in pristine or natural systems (Welch *et al.* 2008), thus information on natural migration speeds, delay and particularly mortality resulting from natural riverine structures, such as rapids, pools and riffles, is lacking. Studies on impacted rivers alone also lack any credible control against which to test migration behaviour; such information would allow any direct effect of riverine barriers to be assessed in terms of delayed migration or mortality within regulated rivers (Thorstad *et al.* 2007).

Only recently has technology become available that allows us to address some of these behavioural questions. Acoustic telemetry enables the real-time movement of fish to be studied, allowing the environmental factors which enable migration or cause delay to be measured, whilst at the same time assessing mortality and migration success. Here acoustic telemetry was used to investigate the cumulative effects of seven small man-made obstacles on the seaward migration of Atlantic salmon smolts.

2.2. Methods

2.2.1. Study Area

The study was carried out in the River Foyle system (55°00'N; 07°20'W). The river has a catchment area of 4450km^2 and forms part of the border between the Republic of Ireland and Northern Ireland (UK) (Fig. 1). The whole Foyle system is designated an EU Special Area of Conservation (SAC) for Atlantic salmon. There are two main tributaries within the catchment; the River Finn, which is free from anthropogenic river obstacles apart from a fish counting weir at Killy Gordon (Fig. 1), the form of which has been shown to have no impact on upstream fish movement (Smith *et al.* 1997). In contrast, the second major tributary, the River Mourne, has seven low-head anthropogenic obstacles along its length (Fig. 1, Table 1). Here the Rivers Finn and Mourne will be referred to as 'un-impacted' and 'impacted' rivers respectively the impact refers only to the presence of a barrier within the river in the descriptive sense and not in relation to the fish or their subsequent behaviour. The confluence of these two rivers form the upper reach of the tidal River Foyle, and represents a transitional/estuarine habitat with surface salinity levels (Practical Salinity Units [PSU]) at its most upstream point (L1, Fig.1) averaging 0.14psu, increasing to 26.6psu at Culmore Point, where the river enters a large sea lough, Lough Foyle (Fig. 1). The section, from the confluence of the un-impacted and impacted tributaries to the entry of the sea lough, will be referred to as 'estuarine.' Lough Foyle salinity levels average 26psu at its most inland location (Culmore Point), where it is strongly influenced by freshwater run-off, to 35psu at its most northerly point where salinity rarely falls below 32psu (salinity data provided by Department of Environment Marine Environment Division, Northern Ireland). The Lough Foyle section will be referred to as a 'sea lough' and classified as the early marine phase migration for emigrating salmon smolts.

2.2.2. Smolt Capture and Tagging

This study was conducted across two years. In 2013 fish (n = 39) were tagged in both the impacted and un-impacted rivers. In 2014 fish (n = 29) were released only in the impacted river, repeating the study on the impacted river from 2013.

In 2013, salmon smolts (identified by silver complexion and loss of parr marks) were captured by electro-fishing in the upper reaches of both rivers between 14th and 15th April. Due to technical problems salmon smolts were sampled by rod and line in April 2014. Smolts were placed into a holding tank filled with aerated river water. Fish deemed large enough for tagging and which were also clearly smolting, were anaesthetised with clove oil (0.5mg per litre); mass (M, g) and fork length (L_F, mm) were recorded prior to being placed on a v-shaped surgical pillow saturated with river water. An incision (11-13mm) was made along the ventral abdominal wall anterior to the pelvic girdle. A coded acoustic transmitter (either, Model LP-7.3, 7.3mm diameter, 18mm length, 1.9g mass in air, Thelma Biotel AS, Trondheim, Norway [2013], or Model V7-2x, 7 mm diameter, 18 mm length, 1.4 g mass in air, Vemco Ltd, Nova Scotia, Canada [2014]) was inserted into the peritoneal cavity. The incision was closed with two independent sterile sutures (6-0 ETHILON, Ethicon Ltd, Livingston, UK). Fish were aspirated with 100% river water throughout the procedure. Tags were programmed to have an acoustic transmission repeat cycle of 30s ± 50%, giving a tag life span in excess of 90 days.

On completion of tagging, fish were placed into a recovery bucket filled with aerated river water and allowed to recover before being placed into a keep box which was positioned in-river overnight. No mortality occurred at any stage throughout the tagging period. Fish were released the day after tagging close to their capture site within their respective tagging groups (Fig. 2.1).

2.2.3. Acoustic Tracking

Movement of tagged smolts was determined using fixed position automatic listening stations (ALS) (Vemco: VR2W). All ALS were deployed prior to tagging and release of fish, ALS were recovered in the July of each year, i.e. post migration and expected tag life. Six ALS were positioned in the impacted river (M1 – M7), each located slightly upstream from a river obstacle (Fig. 2.1). All such structures were over-spill sloping weirs, apart from M1 which comprised a degraded historic weir and a series of rapids. Barriers ranged from 0.75-4.3m head height (Table 2.1).

Five ALS were assigned to the un-impacted river (F1 - F5), located at deep holding pools or glides where river flow was generally slow and similar to the conditions created artificially above man made obstacles (i.e. deep, slow moving impounded water located immediately upstream of riverine barriers) (Fig. 2.1). An additional four ALS were positioned downstream of the confluence of the study rivers (L1 – L4) at the tidal limit of the River Foyle. To ensure adequate spatial coverage and detection of emigrating smolts from both rivers, data from these were combined to create a single detection zone henceforth named L4. A further three ALS were located downstream within the estuarine part of the River Foyle (L5 - L7). Entrance to the sea lough was defined as detection at L6 or L7. Two final receivers covered the exit from the Sea Lough into the Atlantic Ocean with successful early marine migration being defined as detection at either L8 or L9.

Range tests were undertaken throughout the array to ensure complete gated coverage at each location to prevent acoustic breaches by tagged individuals. More specifically at ALS L8 and L9 (Fig. 2.1), to ensure detection coverage was adequate to determine survival, an acoustic tag (Model LP-7.3, 139dB re 1 μPa power, Thelma Biotel AS, Trondheim, Norway 2013) was suspended at 3 m depth and trolled (~1500 m x 4; ebbing and flooding tide) by a drifting boat (engine off) to test for acoustic breaches. Data identified an acoustic range of 450m and thus receivers were deployed so as to create overlap in detection ranges of ALS L8 and L9. Tag failure rate reported by manufacturers is low (<2%); for Thelma tags of the same model used here, Gauld *et al.* (2013) reported control tag failure rates of 0% within field test environments. It is assumed relevant precautionary steps were taken to maximise detection efficiency within the study and enable the determination of tag fate. In 2014, three receivers were also located in a transect stretching 2 km out from the North coast of Ireland, adjacent to Lough Foyle (L10 – L12, [Fig. 2.1]).

Here, freshwater migration is defined as the movement of tagged fish from the most upstream receiver (M1 or F1) downstream to L4. In 2014, receivers L1 to L4 were removed for logistical reasons, and freshwater migration in the impacted river was calculated as occurring between M1 and M7 in 2014. It is assumed that fish which were detected at the first upstream receivers (M1, F1) but not detected leaving freshwater died within the freshwater section and are thus defined as freshwater mortalities. This is a reasonable assumption as de-smoltification is rare in Atlantic salmon smolts (McCormick *et al.* 1998). Successful estuarine migration is defined by the movement of fish between L4 and L6 + L7 in 2013 and between M7 and L6 + L7 in 2014 (due to the removal of L4), similarly fish that were detected at L4 (M7 in 2014) but not at L6 + L7 are assumed to have died within the estuary section (estuarine mortality). Successful early marine phase migration is defined as movement between L6 or L7 to where the lough discharges into open sea (L8/L9), finally fish detected at L6 + L7 but not at L8/L9 were assumed to have died within the sea lough section (early marine mortality).

Freshwater travel time of smolts was calculated as the time between the last detection at receiver M1 or F1, until first detection at the estuarine receiver L4 (M7 in 2014). Estuarine travel time was calculated as the last detection on L4 (M7 in 2014) until the first detection at L6 or L7. Data from 2013 for the impacted river were recalculated to account for receiver location change (removal of L4 in 2014) i.e. freshwater travel calculated as M1 to M7 and estuarine travel as M7 to L6 or L7 (same distances at 2014), enabling a direct comparison between years. Analysis is thus conducted spatially within one year (impacted vs un-impacted, 2013) and temporally (impacted 2013 vs impacted 2014).

Delay, a measure of how long an individual fish remained in the upstream vicinity of a potential manmade (impacted) or within a natural (un-impacted) pool was calculated as the time between first and last detection at each individual freshwater ALS, located immediately upstream of a weir (impacted river) or within a natural pool (un-impacted river) for each individual.

Distance travelled between detection sites was calculated using the centre line of the river with ARC GIS software. It is recognised that this is not the shortest or longest possible route an individual may use; however it is likely to be representative of the actual migration distance. Freshwater travel distance in the impacted river (M1 – L1) was 50 km, 16% longer than the un-impacted river (F1 – L1) survival results are reported on a kilometer by kilometer basis and migration speed in km.d^{-1} to reflect this variation.

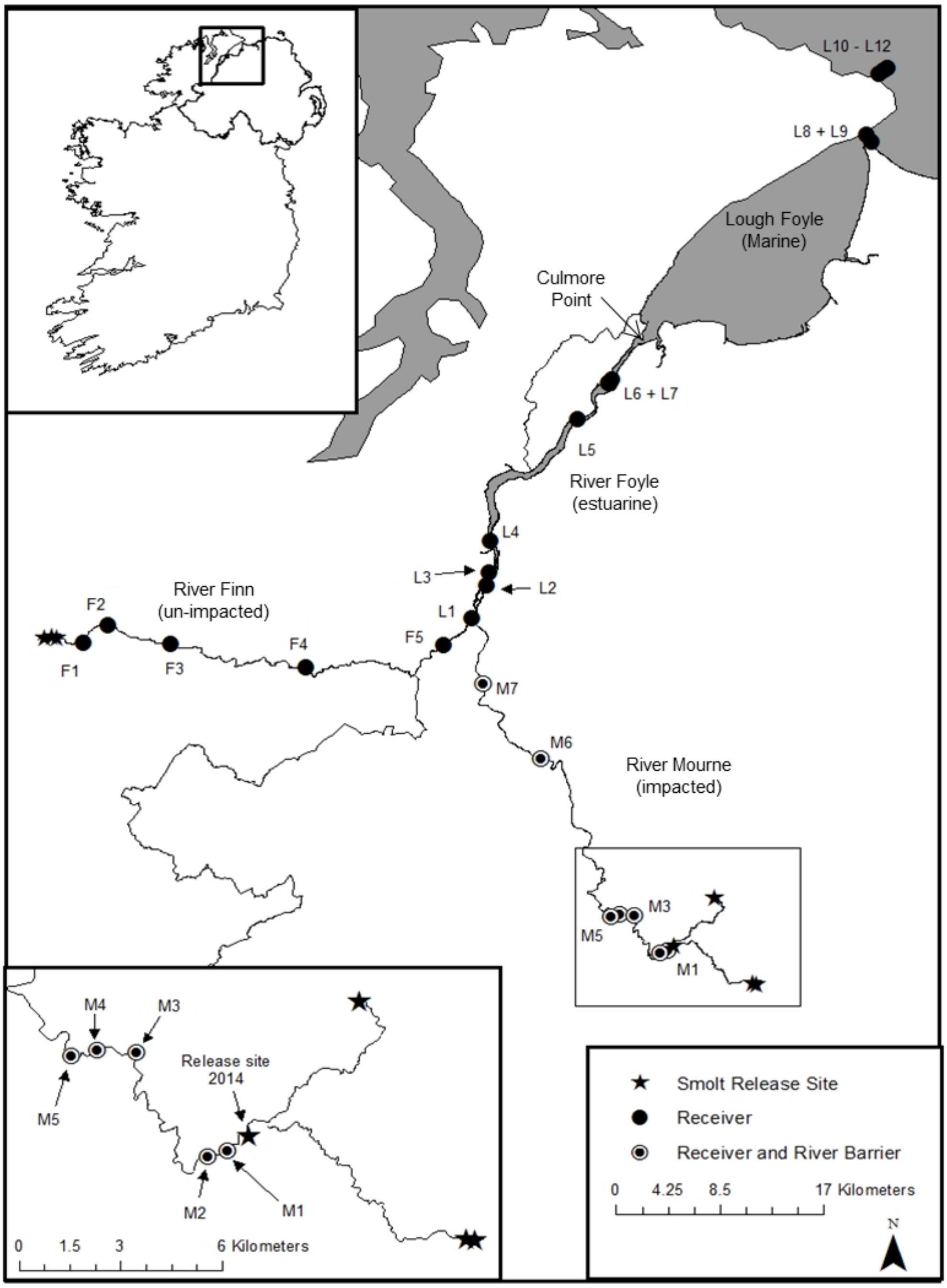

Figure 2.1 Location of the Foyle catchment in Ireland, on the border between Northern Ireland and the Republic of Ireland (top left). Automatic listening station (ALS) deployment throughout the catchment is presented in the main map. Bottom left is a larger version of the headwater of the impacted river where river barriers and release sites are in close proximity. River flow is in a northerly direction, the River Foyle is tidal downstream from the confluence of Rivers Finn and Mourne (L1).

2.2.4. Environmental Data

River flow data for the rivers were provided in the form of discharge data for the impacted river (provided by the Department of Agriculture and Rural Development, Northern Ireland), and stage (used as a proxy for discharge, provided by the Office of Public Works, Ireland) for the un-impacted river. Mean daily discharge from the impacted river was used to assess flow conditions for the study period in both 2013 and 2014. Data from the previous ten years were also analysed to identify long term trends in river flow for the impacted river.

2.2.5. Statistical Analysis

All analysis was performed using R statistical software (R version 3.1.3 [2015-03-09]) programming (R Core Team, 2013). Welch-t-tests were used to test for differences in fork length between populations, differences in delay times between rivers and speed of travel. Normality of data were confirmed using Shapiro wilks test. Where normality was un-confirmed or assumptions of t-tests not met, Wilcoxon Mann-Whitney rank sum tests were performed. Fisher's exact tests were used were used to determine if the observed frequencies of mortalities was different from expected frequencies between years, rivers and phases of migration. A one-way ANOVA was used to test for differences in the mean delay at each river barrier in both the impacted and un-impacted river.

2.3. Results

Sixty eight fish were tagged during the study period; impacted 2013, *n* = 20, mean fork length [L_F] = 144.3 ± SD 9.1, mean mass [M] = 31.3 ± SD 4.9g, un-impacted 2013, *n* = 19, L_F = 132.2 ± SD 10.8, M = 24.8 ± SD 6.3g, impacted 2014, *n* = 29, L_F = 135.2 ± SD 27.3, M = 28.8 ± SD 7.0g. There was a significant difference in fish length between rivers (*t.test*, *t* = 2.94, *p* = 0.005, d.f. = 36.5, mean ± S.D impacted = 144.3 ± 9.1 mm, un-impacted = 132.2 ± 10.8 mm) but no difference in length between years (*t* = 1.49, *p*= 0.14, d.f. = 46.9 mean ± S.D 2013 = 144.3 ± 9.1 mm, 2014 = 135.2 ± 27.3 mm).

Data from the ALS receiver array was used to estimate survival for these fish. Data from ALS M5 was removed from analysis due to acoustic noise severely reducing detection efficiency throughout the study period. Fish which were not detected at the first receiver within the array (M1, F1) were eliminated from all further analysis, a lower proportion of fish (41%, n = 12) were detected within the array in 2014 compared to 85% (n = 17) in 2013. There was no difference fork length or tag mass to body mass ratios between fish tagged in 2014 detected within the array and those not detected as reported in (Newton *et al.* 2016) . The exact fate of undetected fish cannot be directly determined.

Total escapement (survivorship of fish from first upstream detection zone [M1, F1] to lough exit at either L8/L9) of tagged fish in the impacted river in 2013 was 18% (n = 3), and 19% (n = 3) from the un-impacted river (Fig. 2.2). In 2014 loss of ALS L8 prevented total coverage of the lough exit and thus exact escapement cannot be determined A single fish was detected at L9, with no individuals detected at L10 - L12 thus at least one individual did reach the open ocean. Data from 2013 indicates that 50% of fish were detected at either receiver (detection probability of 50%) at L8 and L9. Thus a cautious estimation may indicate two fish likely successfully migrated to the open ocean in 2014.

Freshwater survival within the un-impacted river was higher (100% per km, n = 17) but not statistically different (*p*=0.53, *Fisher's exact test*) than the impacted system (99.9% km^{-1}) in 2013. No difference in the number of mortalities between years (*p* = 0.62, *Fisher's exact test*) was observed for the impacted river. Survival rates decreased marginally during estuarine migration in both rivers (impacted 2013 = 99.4% km^{-1}, un-impacted 2013 = 99%

km^{-1}) (Fig. 2.2) for those fish which initiated migration (L1/F1 to L6 + L7) but not in 2014 (impacted 2014 = 100%). Significantly (p < 0.01, *Fisher's exact test*) lower survival occurred in the early marine phase of migration (L6 + L7 to L9) in both rivers (impacted 2013 = 97.4% km^{-1}, un-impacted 2103 = 97.5% km^{-1}) and years (impacted 2014 = 97.3% km^{-1}), than in the freshwater and estuarine phase (L1/F1 to L6 + L7 [Fig. 2.2]).

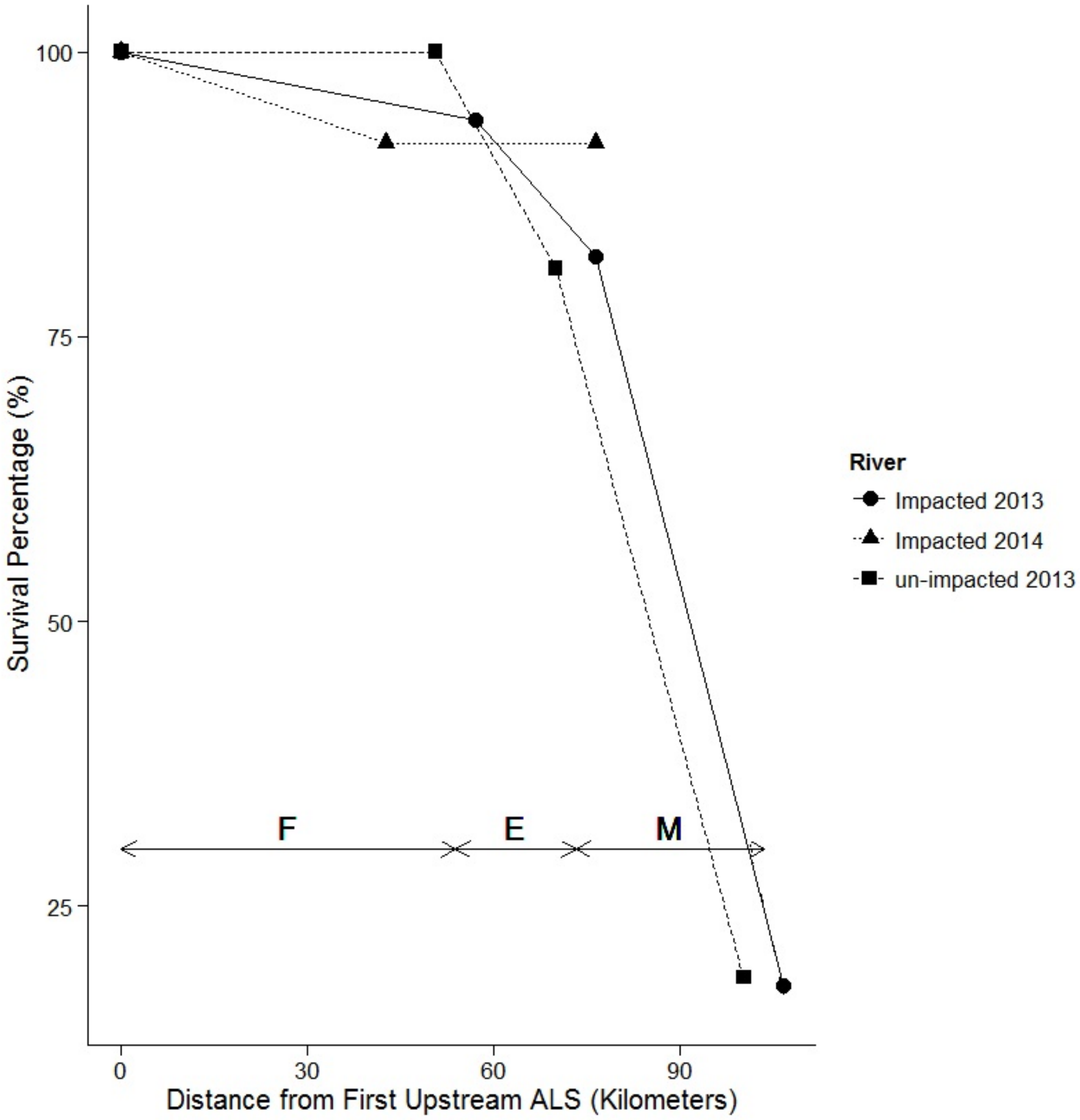

Figure 2.2 Survivorship curve of tagged salmon smolts from three release groups for freshwater (F), estuarine (E), and sea lough (M) elements of the migration. Distance 0 is the most upstream ALS with distances calculated from this point.

2.3.1. Migration Delay

Mean delay per fish in 2013 was not significantly different (Wilcoxon-Mann-Whitney, *W* = 159, *p* = 0.86) between the un-impacted river (*n* = 18, median = 0.16hr, range 0-18.2hr) and impacted river (*n* = 17, median = 0.17hr, range 0-126.74hr). Mean delay was lower in 2014 in the impacted river (n = 12, median = 0.5hr, range = 0-72.5hr), than in 2013 but not significantly so (*W* = 84, *p* = 0.44). Total Delay at some individual obstacles (Table 2.1) within the impacted river was significantly different between years (M3, *W* = 29, *p* = 0.03; M4, *W* = 24, *p* = 0.03, M7, *W* = 85.5, *p* = 0.03) but not at others (M1, M2, M6).

Analysis of variance (ANOVA) testing identified no difference in delay at individual obstacles for the un-impacted river (*F* [4,15] = 1.4, *p* = 0.3) or impacted river in either 2013 (*F* [5,57] = 1.8, *p* = 0.1) or 2014 (*F* [5,62] = 0.7, *p* = 0.6). Two individuals in 2013 were delayed for 118 and 126 hours respectively at M2, exaggerating the mean delay time from that measured for other fish (Table 2.1. Median delay at M2 = 0.07hrs), similarly two fish in 2014 were delayed for 49 and 72 hours compared to a median of 0.16hrs (Table 1).

Table 2.1 Summary of obstacle type with mean and median delay of ALS deployments across the study period. Delay is not calculated at M5 due to receiver being compromised by excess noise.

Station Name	**Obstacle Type**	**Head Height (meters)**	**Hydropower off-take**	**Mean (Median) Delay (Hours)**	
				2013	**2014**
F1	N/A	N/A	N/A	0.06 (0.02)	NA
F2	N/A	N/A	N/A	0.17 (0)	NA
F3	N/A	N/A	N/A	0.18 (0.008)	NA
F4	N/A	N/A	N/A	0.08 (0.08)	NA
F5	N/A	N/A	N/A	1.97 (0.38)	NA
M1	Broken weir above rapids	4.3	Disused and dry	1.18 (0.05)	6.17 (0.06)
M2	Sloping Weir	0.75	Y	18.86	5.48 (0.16)

				(0.07)	
M3	Sloping Weir	1.89	N	0.18 (0.14)	0.56 (0.31)
M4	Two sloping weirs approx. 30 meters apart	1.5+ 0.75	Y un-Commissioned in 2013. Working in 2014	0.15 (0.11)	6.21 (0.97)
M5	Over spill weir	0.75	N	NA	NA
M6	Vertical weir	1.2	N	0.07 (0.07)	0.04 (0)
M7	Sloping weir	3.4	Y	0.86 (0.22)	0.06 (0.03)

2.3.2. Freshwater Migration

Ground speed was highly variable within river groups. The range in ground speed for the un-impacted river was 2.3 – 17.3 km.d^{-1} and for the impacted river 1.8 – 103.3 km.d^{-1} across both years. Freshwater ground speed in 2013 was greater in the impacted river (mean ± SD, 12.3 ± 13.01 km.d^{-1}) but not significantly different (Wilcox rank sum, W = 145, p = 0.34) to that of the un-impacted river (mean ± SD 6.4 ± 4.4 km.d^{-1}). Freshwater ground speed in 2014 did not differ (mean ± SD 17.5 ± 15.7 km.d^{-1}) to that in 2013 (mean ± SD 17.2 ± 22.6 km.d^{-1}) and was not significantly different (Wilcox rank sum, W = 179.5, p = 0.37).

2.3.3. Estuary and Early Marine Migration

Mean travel time of fish migrating through the estuary was 75 hrs (range 11 hrs – 20 days) at a mean speed of 15 km.d^{-1} (range = 0.9 – 52 km.d^{-1}). There was no difference in estuarine ground speed between rivers (W= 105, p = 0.06) or between years (W = 114, p = 0.54). There was no significant difference between freshwater or estuarine ground speeds (t = 0.013, p = 0.99). Data on movements within the sea lough are limited to six individuals in 2013. Mean travel time through the sea lough (30 km) was 59 hrs with a mean ground speed of 19.4 km.d^{-1} (range = 4.9 – 48.1 km.d^{-1}). A single individual was successful in reaching L9 in 2014 and did so in 30 hrs at a speed of 24 km.d^{-1}.

2.3.4. Inter-annual variation in River Discharge

River discharge between the two study years contrasted markedly. Flow in the Mourne (impacted river) in 2014 fell below the Q90 exceedance for an extended proportion (16 days) of the migration period, compared to 2013 when it fell below this level only for three days. Indeed river flow in 2013 was considerably higher with seven days being above Q90 compared to only three in 2014. A peak in discharge in mid-April, 2013 sustained moderate flows throughout the migration period. No such peak was present in 2014 resulting in declining low flows from 10th April through to May 6th (Fig. 2.3).

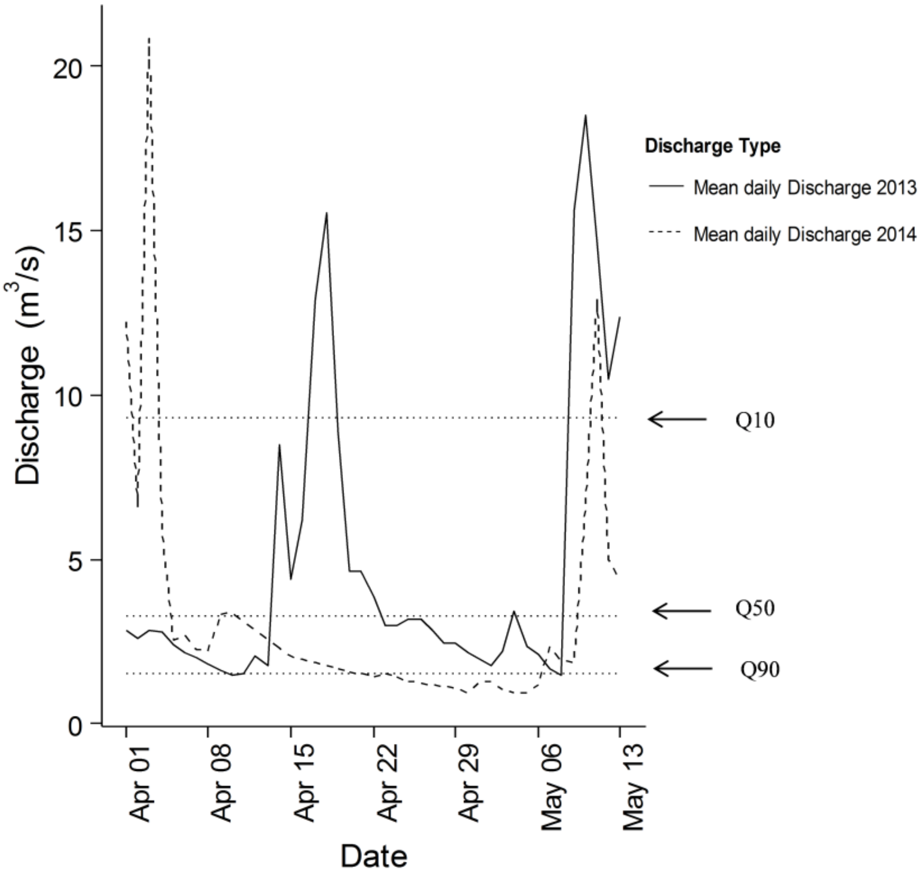

Figure 2.3 Mean daily flow taken from flow gauging station on the impacted river for 2013 and 2014. Also are flow exceedance percentiles, Q90, Q50 and Q10 flows calculated from mean daily flows of the previous ten years of the study period.

2.4. Discussion

This study is the first to directly compare downstream wild Atlantic salmon smolt migration in a river impacted by multiple low head obstacles with a river un-impacted in this way in a single catchment and thus subject to the same general environmental conditions. Surprisingly, survival rates during the freshwater phase of migration in the impacted river were high across both years (93%), and this study found no difference in survival rates between impacted and un-impacted rivers in one year (2013). This contradicts the conventional view that in-stream obstructions, including small ones, increase mortality of smolts, thereby reducing escapement of smolts in a catchment (Aarestrup & Koed 2003; Thorstad *et al.* 2012; Gauld *et al.* 2013). It has been shown recently that for some rivers with large hydro-electric dams, survival rates for Pacific salmon (*Oncorhynchus* species) smolts are higher than in rivers which lack dams (Welch *et al.* 2008). In individual catchments, salmon populations are exposed to a unique set of environmental variables which may impact upon mortality, hence barrier effects on smolts might reasonably be expected to be site and catchment specific.

The freshwater survival rate of Atlantic salmon smolts for the impacted river in this study is broadly in line with that reported in UK rivers with no anthropogenic barrier effects e.g. the River Conway, UK, 99.4% km^{-1} (Moore *et al.* 1995), River Test, UK, 95% km^{-1} (Moore *et al.* 1998), and more generally 93% - 99.7% km^{-1} (Thorstad *et al.* 2012). Salmon populations exhibit both ecological and genetic differences between rivers; combined with precise natal homing, natural selection may well generate local adaptations to cope with modifications within the natal water body for that population (Taylor 1991; Heinimaa *et al.* 1998; Garcia de Leaniz *et al.* 2007). There were also no differences in mortality between smolts migrating from different rivers in the estuarine migration phase thus suggesting no evidence of post-passage effects of low head impoundments on downstream migrating smolts.

Despite high freshwater and estuarine survival, overall escapement to sea (18%) was relatively low when compared with other studies of river and estuarine smolt migration; River Tweed, UK 19-45% (Gauld *et al.* 2013), Nova Scotia, Canada, 39-74% (Halfyard *i.* 2012), River Lærdalselva, Norway, 85% (Urke *et al.* 2013), Romsdalsfjord System, Norway 35% , (Thorstad *et al.* 2007). Lough Foyle contains a variety of marine fish species, of which spurdog (*Squalus acanthias)* are thought to be present in high densities. Spurdog are a known predator of Pacific salmon smolts (*Oncorhynchus* species) in the Strait of Georgia, and are also a significant source of mortality for seaward migrating smolts, a single individual having been recorded with 17 smolts within its gut (Beamish *et al.* 1992; Friedland *et al.* 2012). Previous studies in Norway estimated that cod (*Gadus morhua*) were taking 24.8% of Atlantic salmon smolts from the River Surna (Hvidsten & Møkkelgjerd 1987), with cod and saithe (*Gadus virens*) populations combined, responsible for 20% of smolt mortality in the River Orkla (Hvidsten & Lund 1988). These and other gadoid species are present within Lough Foyle (McGonigle *et al*. 2011), yet there is little information available on additional predator species, such as birds or mammals, or population numbers of potential predators and their diet, thus it is difficult to directly estimate their effect on smolt emigration, particularly in areas such as sea loughs and river mouths where predator density is likely to be high (Larsson 1985; Greenstreet *et al*. 1993; Dieperink *et al.* 2002; Woody *et al.* 2002; Serrano *et al.* 2009; Thorstad *et al.* 2012).

The fact that survival was not affected by annual variations in flow is somewhat surprising. Exceedingly low flows experienced by migrating smolts in 2014 (18 consecutive days below Q90) did not impact on mortality, migration speeds or delay in freshwater migration through the impacted system when compared with data from a hydrologically typical year in 2013. In contrast, an extended low flow period of 18 days below Q95 in the river Tweed resulted in 44% of smolts failing to pass a single barrier, compared to 9% failure in a 'normal' spring (Gauld *et al.* 2013). Despite studies identifying a positive relationship between flow and smolt survivorship at both large barriers (Kjelson & Brandes 1989; McCormick *et al.* 1998) and small scale barriers (Gauld *et al.* 2013), results of the study presented here contrast markedly with these earlier results.

Delay and mortality at riverine barriers is regularly reported, however there is rarely a comparison of delay in an impacted river to that of a natural system (Thorstad *et al.* 2012; Cooke & Hinch 2013). This study demonstrated that delays (or natural 'holding' behaviour) resulting from natural pools and impoundments to migration in natural systems can be equivalent and not significantly different to, those of impacted rivers. Also, site specific delays can differ significantly between years even when delay throughout the whole system does not. Because of the existence of natural, but unpredictable, holding behaviour in un-impacted and impacted river systems, it may not be feasible to directly compare downstream passage time of smolts in an impacted reach to that of an un-impacted reach within the same river. Indeed what is perceived or postulated as a delay above an obstacle may actually be a natural ‘holding’ pattern in a pool created by the obstacle. Holding is a natural phenomenon and delay should be measured across a whole emigration period and stream reach rather than at, perhaps, individual sites. Thus care must be taken when attributing the cause of a delay solely to a man-made river obstacle.

A common limitation in telemetry studies, and applicable here, is that of low sample size, the primary driver of which is transmitter cost. Individuals within a species may differ greatly in their behaviour and behavioural response to environmental variables (Dall *et al.* 2012). Thus it is sometimes difficult to determine whether results from small sample sizes accurately reflect the wider population they represent. Low sample sizes must be contrasted with the benefit of data collected which cannot be generated through other techniques. Although sample size in this study is relatively small, the high survival rate of fish through freshwater and estuarine portions, across years, supports the primary conclusions. Similarly despite the low number of fish detected reaching the open ocean, mortality rate per kilometer is not dissimilar to those reported in other studies of estuarine and marine migration. However there is an ever present need for greater numbers of fish utilised within telemetry studies. In reality, to accurately represent a significant proportion of an individual smolt population may require thousands of individuals to be tagged due to the vast numbers of downstream migrating juveniles. Our study raises important questions regarding the migration of Atlantic salmon smolts, in that not all systems with multiple obstacles, expected to have cumulative effects, cause elevated mortality, and that migration through rivers with natural riffle-pool sequences may be no different to that of a system with low head anthropogenic obstacles. It is clear there is a requirement for further studies, with greater sample sizes, of natural migration of smolts in un-impacted rivers, before it is possible to attribute mortality and delay to a direct consequence of weirs, dams and engineered in-river structures.

Chapter 3

Does size matter? A test of size-specific mortality in Atlantic salmon *Salmo salar* smolts tagged with acoustic transmitters.

*Note: This chapter is published in the Journal of Fish Biology

3.1. Introduction

Recent technological advances have dramatically improved our ability to track fishes in the wild (Cooke *et al.* 2013, Thorstad *et al.* 2013). Fuelled by the need to understand the movements of diadromous fishes, particularly salmon smolts, during their estuarine and early marine migration, acoustic transmitters have been miniaturised, thus opening up new and exciting aspects of fisheries research. Previously limited to larger species or older life stages, acoustic telemetry now has the potential to track small fishes through freshwater, estuarine and marine environments for considerable periods of time (Thorstad *et al.* 2013). Like all battery-powered electronic transmitters, one significant remaining constraint of this technology, for fishes, is the transmitter size relative to that of the fish, which currently precludes use of the technique on small species and very early life stages.

In fishes, the “2% rule” (Winter 1996) has been accepted frequently as a ‘rule of thumb’ for maximum tag mass to body mass ratios (tag burden), despite criticism in recent years (Jepsen *et al.* 2005). Empirical studies have shown negative effects on fishes when tag burden is greater than this and have been used to support this position (McCleave and Stred 1975, Ross and McCormick 1981, Marty and Summerfelt 1986, Adams *et al.* 1998, Lefrançois *et al.* 2001, Sutton and Benson 2003).

More recently, the boundaries of telemetry transmitter burden impacts on small fishes have been explored, stimulated in part by the study of Brown *et al.* (Brown *et al.* 1999) showing no effect on swimming performance of surgically implanted acoustic transmitters (7 x 12 mm, 0.6 g in air) up to 12% of body mass in juvenile hatchery rainbow trout, *Oncorhynchus mykiss* (Walbaum, 1792) (mean L_F 88.9, mean mass 7.4 g). Studies on

Pacific salmon (*Oncorhynchus* spp.) from hatcheries have attempted to determine a maximum tag burden for surgically intracoelomic implanted transmitters. However, species, tag size, survival rate and other measures of performance have varied between studies. For example Zale *et al*. (Zale *et al.* 2005) reported a small decrease in swimming performance with transmitter mass (mass 1-5 g in air, volume 0.5-1.5 cm^3) of up to 4% body mass in cutthroat trout, *Oncorhynchus clarkii lewisi* (Richardson, 1837) (mean L_T 240 mm, mean mass 132.8 g). Yearling Chinook salmon, *Oncorhynchus tshawytscha*, (Walbaum, 1792) (mean L_F 166 mm and mass 50.5 g) exhibited 80 - 100% survival rates with a combined intracoelomic implantation of an acoustic transmitter (7 x 20.5 mm, 1.8 g in air) and passive integrated transponder (PIT) tag (2.15×12.0 mm, 0.1 g in air) up to 5.6% of their body mass (Ammann *et al.* 2013). However, growth and survival impacts in *O.tshawytscha* (L_F 80 – 109 mm, mass 6.8 – 16.3 g) surgically implanted with an acoustic transmitter (mean mass 0.64 g in air; 0.28 ml volume) and a PIT tag (mass 0.10 g in air, 0.04 ml volume) were evident at transmitter burdens greater than 6.7% (Brown *et al.* 2010).

For many salmonids, seaward-migrating smolts are relatively small, so tag burden issues are particularly acute in these studies. In Coho salmon, *Oncorhynchus kisutch*, (Walbaum, 1792) smolts L_F 95 – 130 mm, a maximum transmitter size to body size of 17% L_F and 7% by mass showed no adverse effects on survival, growth or physiology using transmitters of 6 x 19 mm, and mass of 0.9 g in air (Chittenden *et al.* 2009). Small *O. mykiss* pre-smolts (L_F 110 – 170 mm, mass 16.8 – 53.3 g) have been shown to survive intrcoelomic implantation with acoustic transmitters 8 mm diameter, 24 mm long, mass 1.4 g (with a 12 mm PIT tag embedded in the body of the tag) (Welch *et al.* 2007), however greatest survival rate in that study was with *O. mykiss* larger than 140 mm L_F.

Although there is a paucity of studies that have directly examined the effects of tag burden specifically on Atlantic salmon, *Salmo salar* L. 1758 smolts in the wild, there is good reason for concern that tag size effects may introduce unwanted biases to smolt movement and mortality studies. Many tracking studies on *S. salar* smolts have been conducted on *S. salar* which have been reared in hatcheries and are typically larger than wild *S. salar*. For study of stocked smolts, this is acceptable, but their use as a surrogate for wild *S. salar* is a poor choice. Hatchery fishes, express different physiological, behavioural and ecological traits to those of wild smolts (*e.g.* Jonsson *et al.* 1991). Physical condition along with physiological status also differs between wild and hatchery fishes due to their exposure to different selection regimes, thus migration preparedness and survival is likely to differ significantly between hatchery origin and wild smolts (McCormick *et al.* 1998). Fishes reared in hatchery conditions lack exposure to predators and this may result in increased mortality for hatchery origin individuals when released to the wild. Thorstad *et al.* (2012*a*), for example, reported low survival (12%) for hatchery reared smolts released to the wild, potentially due to reduced freshwater migratory behaviour.

Also, resulting from tag burden concerns, in most salmon smolt acoustic telemetry studies using widely available 7 x 20 mm sized transmitters, and where wild fishes are used, often only the largest individuals are selected for tagging (*e.g.* Lefèvre *et al.* 2012). Since the size of fishes is thought to play a significant role in survival, bias in initial selection may falsely represent true behaviour and/or mortality (Gingerich *et al.* 2012, Deng *et al.* 2015). There is a pressing need for smolt migration studies which focus on wild rather than hatchery reared fish and access the full size range of the natural migrating smolt populations. One route to enabling this, is to better evaluate the effects that exceeding the ‘2% rule’ may have on wild migrating smolts implanted with acoustic transmitters, particularly under natural conditions. The effect of tag burden, beyond 2% of body mass, on mortality is tested here with wild *S. salar* smolts implanted with acoustic transmitters.

3.2. Methods

The Foyle catchment (4450 km^2, 54◦ 736′ N; 007◦ 083′ W) is situated on the border between Northern Ireland (U.K.) and the Republic of Ireland (Fig. 3.1). Two main tributaries of the catchment are the rivers Finn and Mourne, both of which have significant migrations of *S. salar* smolts. The average size of these smolts is relatively small at around 135 mm L_F and 26 g (Loughs Agency 2010). These two rivers form the River Foyle at their confluence, which is a transitional/estuarine water under tidal influences. Salinity levels range from 0.14 at the confluence of the rivers Mourne and Finn (River Foyle) to 22 at Culmore point (Fig. 3.1). This section of river (confluence to Culmore point) will be referred to as the estuarine section. At Culmore point, the Foyle discharges into a large sea lough, Lough Foyle. Lough Foyle is a shallow embayment, covering approximately 186

km^2, 20% of which is intertidal mudflats. At its mouth, the lough narrows to a 1 km wide channel before discharging into the Atlantic Ocean. Salinity in the sea lough ranges from 22 at Culmore point to 35 at its mouth and represents the early marine phase of migration for migrating smolts (Fig. 3.1).

Wild *S. salar* smolts (n = 68) were tagged over a 2 year period (2013 to 2014). Individuals were captured by electrofishing (backpack) in the upper tributaries of the Mourne and Finn in 2013 and by rod and line only in the Mourne in 2014. *S. salar* were implanted with acoustic transmitters and released close to their capture site (Fig. 3.1) following a short period of recovery (approximately 30 minutes) post capture. *S. salar* were anaesthetised with clove oil (0.5 mg l^{-1}); their mass (g) and fork length (L_F, mm) were recorded prior to being placed on a v-shaped surgical sponge saturated with river water. The gills were aspirated with 100% river water throughout the procedure. An incision (11-13 mm) was made along the abdominal wall, anterior to the pelvic girdle. A coded acoustic transmitter (either, Model LP-7.3, 7.3mm diameter, 18mm length, 1.9g mass in air, Thelma Biotel AS, www.thelmabiotel.com or Model V7-2x, 7 mm diameter, 18 mm length, 1.9 g mass in air, Vemco Ltd, , www.vemco.com) was inserted into the intracoelomic cavity. The incision was closed with two independent sterile sutures (6-0 ETHILON, Ethicon Ltd, http://www.ethicon.com/) with a surgeons knot. On completion of the procedure, *S. salar* were placed into a keep-box which was positioned in an area of gentle flow in the river overnight; *S. salar* were released in their tagging groups the following day. No mortality occurred before release. Work was undertaken in accordance with UK Home Office licencing.

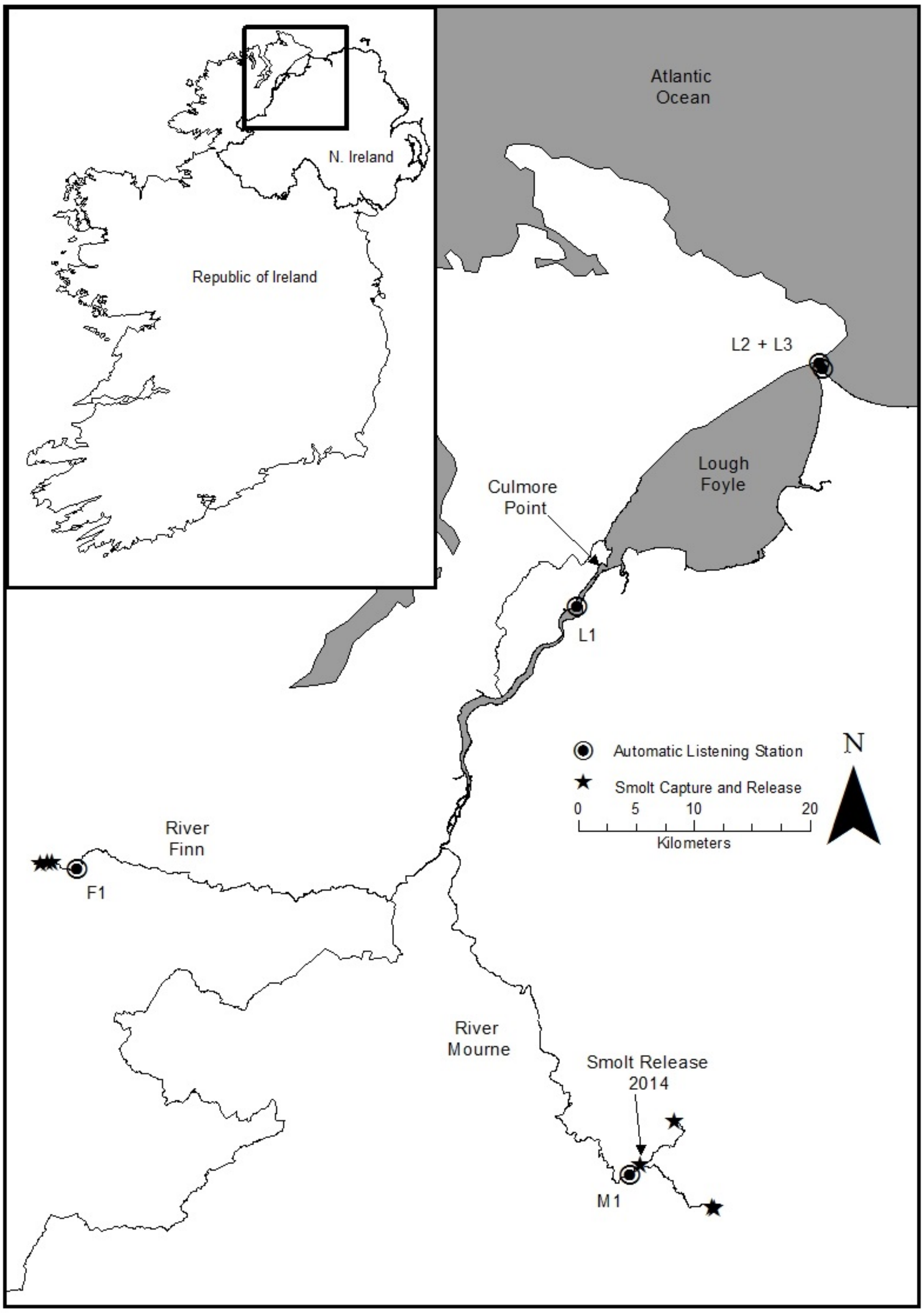

Figure 3.1 The Foyle catchment showing location on the border between Northern Ireland and the Republic of Ireland within the small inset, and the study site location. The large map outlines the study site. Black circles ◉ indicate Automatic Listening Station (ALS) with ALS name (M1, F1, L1, L2, L3) along with smolt capture and release points; ★ (in 2013) and individual capture and release site for 2014. The river section, between the confluence of the Mourne and Finn, and Culmore point is estuarine.

Extensive range tests were undertaken throughout the array, and specifically at ALS L2 and L3 (Fig.1) to ensure detection coverage at this location was adequate to determine escapement success. To test for acoustic breaches at L2 and L3, an acoustic transmitter (Model LP-7.3, 139 dB re 1 μPa power, Thelma Biotel AS, Trondheim, Norway 2013) was suspended at 3 m depth and trolled (~1500 m x 4; ebbing and flooding tide) by a drifting boat (engine off). Tests identified an acoustic range of 450 m ensuring an overlap in detection ranges of ALS L2 and L3. Transmitter failure rate reported by manufacturers is low (<2%); for Thelma transmitters of the same model used here, Gauld *et al*. (2013) reported control transmitter failure rates of 0% within field test environments. Thus relevant precautionary steps were taken to maximise detection efficiency within the study and enable the determination of transmitter fate.

The hypothesis that tag burden affects survival in *S. salar* smolts was tested by examining the influence of four characteristics (F_L, *S. salar* mass, transmitter length to F_L ratio and transmitter mass to body mass ratio) on mortality. Tests were conducted on all tagged (AT) *S. salar* to investigate outright mortality, along with a subset of these which initiated migration (ST) to investigate the effect of tag burden during migration. ST *S. salar* were analysed separately as a subset of AT as they were deemed to have initiated migration and thus maybe exposed to delayed mortality post tag implantation. *S. salar* were grouped depending on their survival outcome, data normality were confirmed by Shapiro-Wilk tests, Welch's two sample *t*-tests were used to compare between each group (survive vs. mortality) for each variable. All analysis was conducted using R (R version 3.1.3 [2015-03-09]) statistical computing package (R Development Core Team, 2014).

3.3. Results

Sixty eight wild *S.salar* smolts were implanted with acoustic transmitters (39 in 2013 and 29 in 2014) over a 2 year period. *S. salar* fork length (L_F) ranged from 115 to 168 mm and mass from 15 to 44 g (Table I). A lower proportion of *S. salar* (41%) were detected within the array in 2014 compared to 85% in 2013. There was no difference in L_F or transmitter mass to body mass ratio between fish tagged in the Mourne 2014 detected within the array and those not detected (L_F, *t-test*, $t = -0.8$, d.f. = 23.3, $P = >0.05$. transmitter mass: body mass, *t-test*, $t = 1.3$, d.f. = 27.0, $P = >0.05$). Similarly there was no difference between *S. salar* detected in the array and those not in 2013 in the Mourne (L_F, *t-test*, $t = -1.4$, d.f. = 2.9, $P = >0.05$. transmitter mass: body mass, *t-test*, $t = 1.2$, d.f. = 2.6, $P = >0.05$) or between all *S. salar* in the study (L_F, *t-test*, $t = -0.9$, d.f. = 35.7, $p = >0.05$. transmitter mass: body mass, *t-test*, $t = 0.9$, d.f. = 36.6, $P = >0.05$). All *S. salar* were detected in the array from the river Finn in 2013. The exact fate of undetected *S. salar* cannot be directly determined.

Across the size range of *S. salar* tagged in this study (L_F 115 – 168 mm, mass 15 – 44 g), (Table 3.1) there was no evidence to support the hypothesis that tag burden had any effect on survival. T-tests between all measured parameters of *S. salar* size and transmitter size to *S. salar* size ratios showed no significant difference between successful [*S. salar* detected at L1 (Fig. 3.1)] and unsuccessful migrants (Table 3.1). This holds true for all tagged *S. salar* (AT, $n = 68$) as well as a subset of these *S. salar* (ST, $n = 41$) which were deemed to have initiated migration.

Table 3.1: Tests of the differences in a range of *S. salar* and tag parameters in smolts that were successful [detected at ALS L1 (Figure 1)] and unsuccessful in migrating to the sea lough [not detected at ALS L1 (Figure 1)], and descriptive statistics for each variable. Tag mass: Body mass (Mass %) and Tag length: L_F (Length %) ratios are expressed as a percentage. *S. salar* are grouped as all tagged *S. salar* (AT) and a subset of these *S. salar* which were detected within the acoustic array and deemed to initiate migration (ST)

Group	Test variable	Successful (*n*) Mean ± SD	Unsuccessful (*n*) Mean ± SD	Range	d.f.	*t*-value	*P*-value
AT	L_F (mm)	(41) 138.8 ± 12.7	(27) 138.3 ± 13.8	115-168	56.8	-0.2	0.8
	Length %	(41) 14.5 ± 1.3	(27) 14.6 ± 1.4	11.9-17.4	57.0	0.3	0.8
	Mass (g)	(41) 28.6 ± 6.5	(27) 28.1 ± 7.1	15-44	58.4	-0.2	0.8
	Mass %	(41) 7.2 ± 1.9	(27) 7.2 ± 1.9	4.3-12.7	62.3	0.2	0.9
ST	L_F (mm)	(33) 139.1 ± 12.2	(8) 143.0 ± 13.5	115 – 168	9.5	0.8	0.5
	Length %	(33) 14.5 ± 1.3	(8) 14.1 ± 1.3	11.9 – 17.4	10.0	-0.8	0.4
	Mass (g)	(33) 28.6 ± 6.6	(8) 30.65 ± 7.3	15 – 44	9.5	0.8	0.5
	Mass %	(33) 7.1 ± 2.0	(8) 6.5 ± 1.3	4.3 – 12.7	14.3	-1.1	0.3

Indeed, the smallest tagged *S. salar* within the study (L_F = 115 mm, mass = 15 g) successfully migrated through fresh water and the estuary. Of the 10 smallest fish within the study (mean L_F = 120.1 ± 3 mm, mean mass = 18.5 ± 3 g) six were successful migrants, entering the sea lough. Similarly, of the 10 largest fish within the study (mean L_F = 160.5 ± 5.8 mm, mean mass = 38.0 ± 5.0 g) six were also successful migrants reaching the sea lough. The two fish with highest transmitter mass to body mass ratios (both 12.7%) also survived. Mean time ± S.D. from release to escapement into Atlantic Ocean (last detection within the array for successful migrants) was 24.9 ± 8.8 days (range 11.9 – 44.5 days).

Mortality within the sea lough was high, only seven individuals were detected at L2 and L3 of the initial 41 detected entering the Lough. A two sample *t*-test between *S. salar* which were successful in migrating to L2/3 and those successful in reaching L1 but not L2/3 (Fig.1) showed no difference in transmitter mass to body mass ratio (*t*-test, t = 0.1, d.f. = 10, P = 0.9).

3.4. Discussion

The range of sizes (Table 3.1) of *S. salar* used in this study include some of the smallest *S. salar* smolts used in electronic tagging studies, providing a unique opportunity to determine the effect of tagging on short term (up to 44 days) survival rates and migration patterns of these fish. Mortality of small, wild *S. salar* smolts implanted with acoustic transmitters, was not associated with tag burden, for transmitters 7x20 mm in size and 1.9 g mass in air. Survival of the smallest *S. salar* in the study to the sea lough, with a transmitter mass to body mass ratio of 12.7% and 115 mm L_F along with another *S. salar* of the same tag burden, 12.7% (L_F 123 mm), demonstrate the ability of small *S. salar* to successfully cope with relatively large acoustic transmitters. This is supported by the high survival rate (60%) to the sea lough of the 10 smallest *S. salar* within the study, equivalent to that of the largest 10 (60%). Despite only small numbers of *S. salar* being detected exiting the sea lough, no size difference in mortalities was present. No tagged *S. salar* were recorded on an ALS which had not been recorded previously at an upstream ALS. Combined with no acoustic breaching during range tests and high transmitter reliability, it is assumed the telemetry array design was adequate to determine migration success. High mortality within the lough (83%) was probably due to predation, although mortality by other means (*e.g.* osmoregulatory incompetence) cannot be ruled out. High estuarine predation is commonly reported in smolt migration studies (Hvidsten and Møkkelgjerd 1987, Serrano *et al.* 2009, Hedger *et al.* 2011, Thorstad, *et al.* 2012). Reduced numbers of *S. salar* were detected within the array in 2014 despite this not being related to size. No mortalities occurred during the tagging process. This difference might be due, in part, to the change in capture method between the 2 years but the exact fate of these individuals could not be determined. Indeed the need for further investigation on the effects of capture and handling in fishes telemetry studies has recently been highlighted (Jepsen *et al.* 2015).

Body size is a limiting factor in acoustic tagging studies, and although the effects of tagging on Pacific salmonids (*Oncorhynchus* spp*)* are relatively well studied (Jepsen *et al.* 2005), extrapolation of data across even closely related species should be done with caution (Ebner *et al.* 2009). The findings of the study presented here do not define tag size or a limit to tag mass ratios, however they do specifically demonstrate the potential to successfully implant small wild *S. salar* smolts with acoustic transmitters at a size much smaller than previously reported. Lacroix *et al*. (Lacroix *et al.* 2004) recommend a transmitter mass of 8% body mass and a transmitter length of 16% or less of L_F for juvenile *S. salar* following a laboratory experiment. Several studies utilising *S. salar* smolts for tagging have not identified any abnormal mortality rates despite using transmitter mass: body mass ratios above 2%. Urke *et al*. (Urke *et al.* 2013) although not specifically reporting on the effect of tag size, indicate high survival rates to sea for wild smolts (775 survival, mean L_F 127 mm, mean mass 16.5 g) implanted with acoustic transmitters (7.3 mm diameter, 1.2 g in water) and hatchery *S. salar* (85% survival, mean L_F 157 mm, mean mass 40.8 g) with transmitter mass to body mass ratios equating to approximately 7%. In addition Thorstad *et al*. (2007) indicated no effect of transmitter to body mass ratio (mean = 6%) on survival of wild *S. salar* post smolts (mean L_T 152 mm, mean mass 25 g) implanted with acoustic transmitters (7 x 19 mm 1.9 g in air). Lefèvre *et al*. (Lefèvre *et al.* 2012) utilised transmitter mass (9 x 20 mm, 2.9 g in air) to body mass ratios of up to 14% (mean 12%) with wild *S. salar* smolts and post smolts (>131 mm L_F and >20 g) with no reported effect on mortality.

This study adds to the growing evidence challenging rigid application of the '2% rule' in biotelemetry (Brown *et al.* 1999, Jepsen *et al.* 2005). Brown *et al.* (Brown *et al.* 1999) for example suggest moving away from the 2% rule towards a new standard with a more scientific basis which takes into account the relative buoyancy of a tag and physical dimensions. They argue that there may be a requirement of a fish to compensate for tag buoyancy by transferring gas into their swim bladder. Hence a more buoyant tag may have less impact upon a fish compared with a denser tag of similar dimensions. Jepsen *et al.* (Jepsen *et al.* 2005) similarly argue that any tag/fish size relationship should be driven by the study objectives and empirical evidence. In some cases, large tags may be utilised without significant effects on behaviour and physiology, whilst in other circumstances, effects such as reduced growth and swimming ability may result from the use of smaller tags (Jepsen *et al.* 2005, Thorstad *et al.* 2013). Nevertheless, several longer-term studies have shown growth impacts on fishes with higher tag burdens (Larsen *et al.* 2013) and concerns over subtle impacts on behaviour and the need to minimize impacts in handling and tagging continue to drive forward tag miniaturisation processes (McMichael *et al.* 2010, Deng *et al.* 2015).

Telemetry has helped unlock an understanding of fish migration ecology providing essential knowledge to manage and conserve declining anadromous fish populations. The ability to identify migration routes, bottlenecks, sources of mortality and species interactions will enable development of more effective conservation strategies. The study presented here has shown that the 2% tag mass to body mass ratio is not an immutable threshold for tagging studies. If *S. salar* smolt migration studies are to adequately represent wild salmon behaviour there is a requirement to move away from the 2% tag mass to body mass rule of thumb adhered to in the past, and towards tested criteria which are species-specific and suitable to address study outcomes, without compromising the natural behaviour of the individual.

Chapter 4

The Impact of a small scale riverine obstacle on the upstream migration of Atlantic Salmon (Salmo salar L.)

4.1. Introduction

The loss and fragmentation of habitat truncates movement, reduces connectivity and often precedes the decline and extinction of a species (Ceballos and Ehrlich 2002, Baguette *et al.* 2013). In rivers, habitat connectivity is primarily longitudinal and in general confined to the river corridor. A single impoundment thus has the potential to isolate adjacent habitats completely for many species (Jager *et al.* 2001, Cote *et al.* 2009, Branco *et al.* 2012). In-river structures, both natural and artificial such as waterfalls and weirs, can have major impacts on species that have multiple, life stage dependent, aquatic habitat requirements. The complex life cycles of highly mobile anadromous and catadromous fish are among some of the species most effected (Forty *et al.* 2016). The Atlantic salmon (*Salmo salar)* is one species shown to be highly vulnerable to river corridor fragmentation (Baras *et al.* 1994, Lucas and Frear 1997, Jager *et al.* 2001, O'Hanley and Tomberlin 2005, Kemp *et al.* 2008).

The impacts of large scale obstacles (> 5m hydraulic head height), particularly their effect on fish migrations, are well documented (Gowans *et al.* 2003, Antonio *et al.* 2007, Meixler *et al.* 2009, Branco *et al.* 2012). Considerable effort has been made to mitigate the effects of river obstacles through the development of fish passes, which aim to facilitate the upstream and downstream migration of individuals around or through obstacles (Larinier 1998, Guiny *et al.* 2005, Bunt *et al.* 2012). The efficiency of such facilities is however often questioned. Fish pass facilities themselves may present an obstacle for migrating fish, when fish are unable to locate the entrance in complex hydrological conditions frequently found at the foot of obstacles. For example, the addition of fish screens at the 86m high Pitlochry Dam (Scotland), increased the proportion of fish ascending the dam from 45% of fish which attempted (Webb 1990) up to 100% by guiding fish away from the turbine entrances (Gowans *et al.* 1999).

Fish pass facilities are generally built at large, high head impoundments. Low-head obstacles (defined here as <5m hydraulic head height), in general, lack such passage facility, relying on the fish's own ability to successfully ascend. In Europe there is a legislative framework requiring EU member states to ensure fish passage; Water Framework Directive (Directive 2000/60/EC), and EU Eel legislation (EC No. 1100/2007). It is estimated that within England and Wales there are some 25,000 in-river obstructions, of which 3,000 are significant and require mitigation in order to meet ecological objectives set out in these directives (Environment Agency 2009).

There is a paucity of knowledge on the effects of low head obstacles on fish populations and assemblages, yet they may also present serious deleterious impacts for fish populations through habitat fragmentation (Lucas and Frear 1997, Ovidio and Philippart 2002, O'Connor *et al.* 2006). Determining the likelihood of fish passage at riverine obstacles is highly complex due to variable swimming and leaping capabilities of fish of different size and species, coupled with the heterogeneity of environmental variables associated with riverine systems (Ovidio and Philippart 2002, Sigourney *et al.* 2015). Viewed in the terms of fish passage, any single obstacle may: prevent migration, cause a temporary delay in migration or have no effect. The likelihood is that man-made obstacles will disrupt upstream migration, resulting in at least some delay in the upstream movement of migratory fish.

There is evidence that upstream migrating adult Atlantic salmon are sometimes reluctant to pass obstacles which, in theory, present no physical impediment to their upstream movement (Gerlier and Roche 1998, Ovidio and Philippart 2002). It is expected that low head obstacles are more likely than high head obstacles to result in a temporary delay to migration rather than a complete impediment. Low head obstacles are more likely to be permeable to some species or some individuals of that species, for example to some but not all size classes, at any given time. Given the effects of scaling (smaller streams show greater variability in relative flow conditions compared with larger streams) the prevailing hydrological conditions are also more likely to influence passage at low head obstacles. For example an upstream migrating Atlantic salmon was unable to surmount an obstacle 1.4m in height due to low water depth below the obstacle and insufficient water depth on the face of the weir (Ovidio and Philippart 2002). Conversely Chanseau et al. (1999) indicated Atlantic salmon were successful in ascending low obstacles <1.5m in height within 24hrs on the Pau River (France), in contrast severe delays were encountered at high obstacles, >2.5m in height with passage highly dependent on specific fish passage facilities and downstream pool water depth. Low head obstacle permeability is likely to change significantly with environmental conditions, particularly flow, with fish characteristics (such as species and body size) and environmental conditions combining to create a discrete period of time when passage may be successful (Kemp and O'Hanley 2010).

The biological consequences of a delayed migration is unclear, logically however, increased movement and searching behaviours caused as a direct result of an encounter with an impassable (even if only temporarily) riverine obstacle is likely to result in increased energy expenditure. Fish attempting to ascend through the Baigts hydro-electric station (Gave de Pau River, France) for example, were delayed up to 80 days despite the presence of a fish pass. Telemetry demonstrated that fish moved between the fish pass and a holding pool approximately 500m downstream, expending energy in attempting to pass the barrier (Chanseau and Larinier 1999). The increased energy expenditure associated with obstacle passage may translate into a subsequent cost on gonad production and spawning activity. In Atlantic salmon, energetic costs cannot be recovered as adult salmon cease feeding while in fresh water (Mills 1989, Bardonnet and Baglinière 2000). Ultimately, energy loss associated with obstacle navigation has the potential to reduce the overall fitness of the individual. A number of studies have shown successful migrants (i.e. individuals which reached spawning grounds) had lower approach and passage times at obstacles when compared with unsuccessful individuals (Chanseau *et al.* 1999, Naughton *et al.* 2005, Lundqvist *et al.* 2008, Makiguchi *et al.* 2011), suggesting potentially rapid obstacle passage reduces energetic costs in barrier passage resulting in greater success of reproduction.

Radio telemetry provides a technique to investigate the behaviour and migration pathways of fish in the wild, providing data on temporal and spatial scales that were previously impossible. In the study reported here, a radio-telemetry detection array was established to investigate the movements of wild Atlantic salmon as they approached and attempted to pass a low-head, complex, riverine obstacle during the upstream spawning migration. The aim of this study was to: 1) determine the behaviour of fish prior to attempts to ascend a river obstacle: 2) determine the behavioural response of fish when they are unable to ascend the obstacle: 3) determine the length of any potential delay at a low head obstacle and 4.) determine the characteristics of fish that determine passage success.

4.2. Methods

4.2.1. Study site

The Foyle system (55°00’N; 07°20’W) has a catchment area of 4450 km^2 and forms part of the border between Northern Ireland and the Republic of Ireland; Fig. 4.1. The Foyle system is a designated European Union, Special Area of Conservation (SAC) for Atlantic salmon. The River Mourne, the largest tributary of the catchment, has a number of riverine obstacles along its length, the most downstream of which is located at Sion Mills (54°46.968 N; 7°27.689 W). As there is no spawning habitat downstream of the obstacle at Sion Mills, anadromous fish must pass this obstacle to access spawning grounds upstream. The obstacle at Sion Mills is a complex sloping weir which presents multiple potential channels for passage for migrating fish (Fig. 4.2 & 4.3).

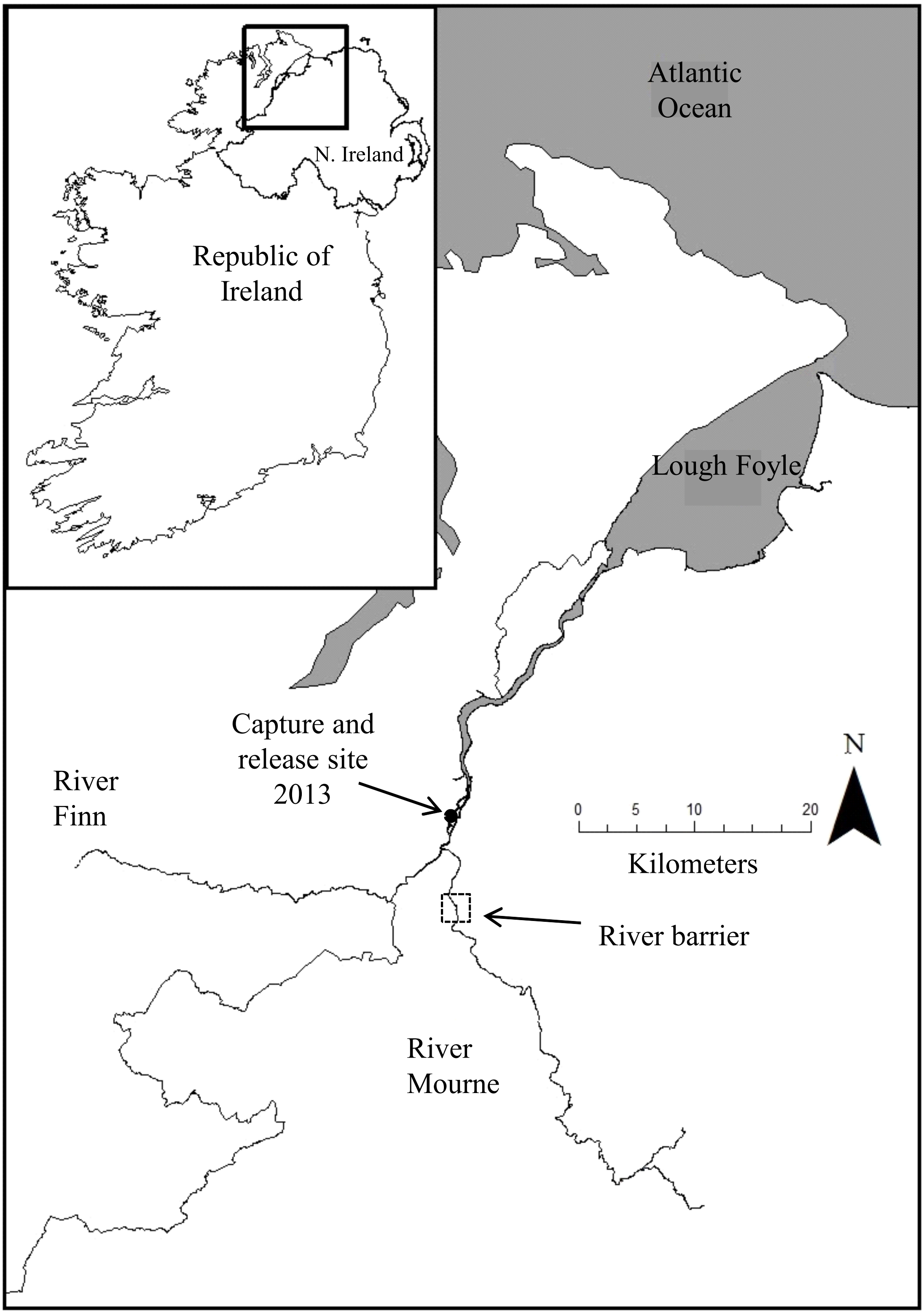

Figure 4.1 The Foyle catchment showing location on the border between Northern Ireland and the Republic of Ireland within the small inset. The large map outlines the river barrier location (Sion mills weir) and telemetry array along with the capture and release site for fish in 2012. Also highlighted is the capture and release site of fish in 2013.

The weir is 265m wide (left bank to right bank) and is positioned at approximately 50° to the main flow of the river (Fig. 4.2.). Its purpose is to deflect water into an old mill lade, which now generates hydropower. The outlet of the lade is completely inaccessible to fish due to the presence of an electric barrier. The weir has a sloping main face, presenting a swim obstacle to fish and, under certain conditions, at the foot of the barrier, a leap obstacle. The foot of the weir falls directly onto a bedrock and boulder substrate. The weir has become degraded and eroded (Fig. 4.3 and Fig. 4.4.) resulting in variation in the effective length of the weir for fish passage (the distance that a passing fish is required to negotiate) varies along its width, i.e. bank to bank (Fig. 4.4). Two fish passes are present; one a Denil pass on the right hand bank and a Larinier pass in the centre of the weir (Fig. 4.3). Beside the Larinier pass are two attraction channels designed to guide flow towards the foot of the pass, enabling fish to locate and ascend this route. Two deep channels are carved in the bedrock leading to the entrance of each fish pass. These are designed to guide fish to suitable passage channels. Both fish passes are highly turbulent and, due to river bed scouring, the Larinier pass now requires a leap for fish to access it.

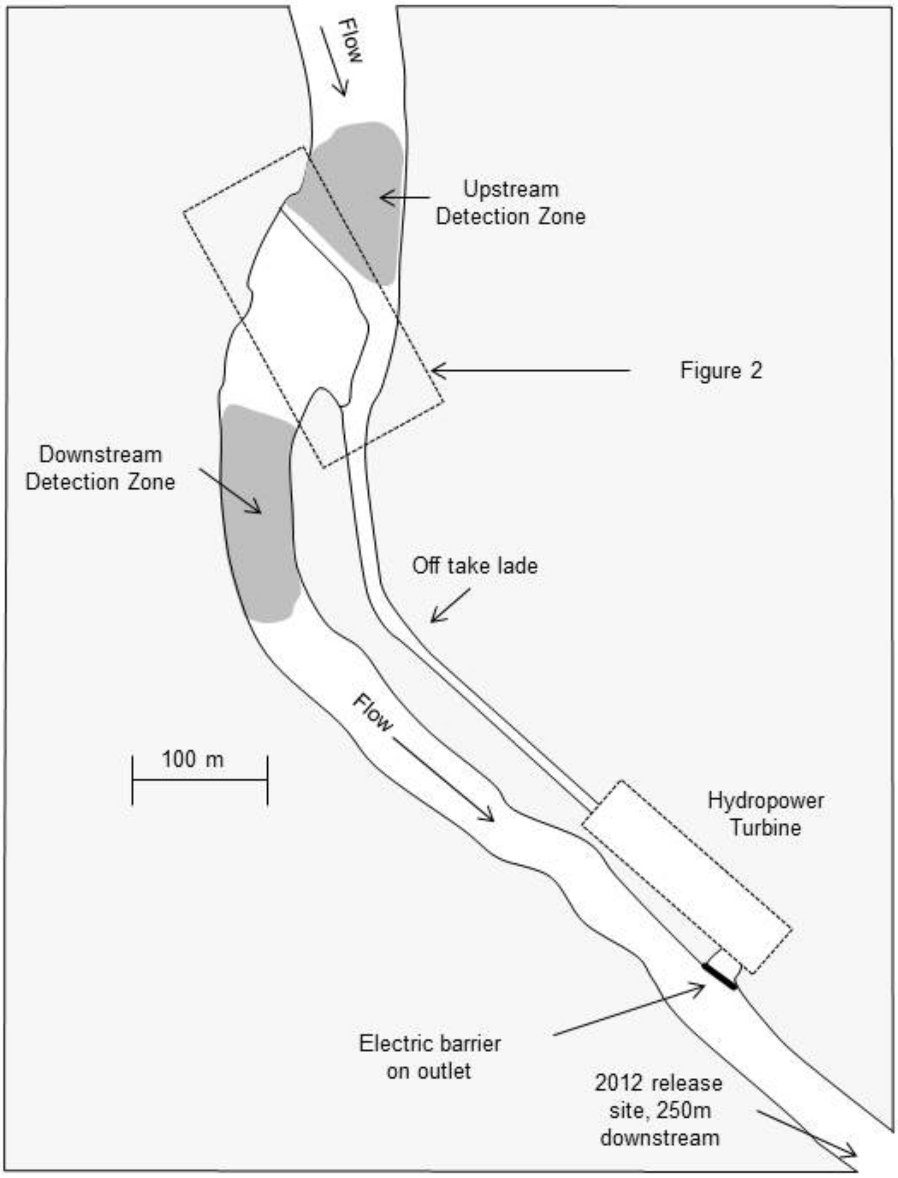

Figure 4.2 Overview of the Sion Mills weir and large scale detection zones, release site for fish in 2012 is 250m downstream from this site.

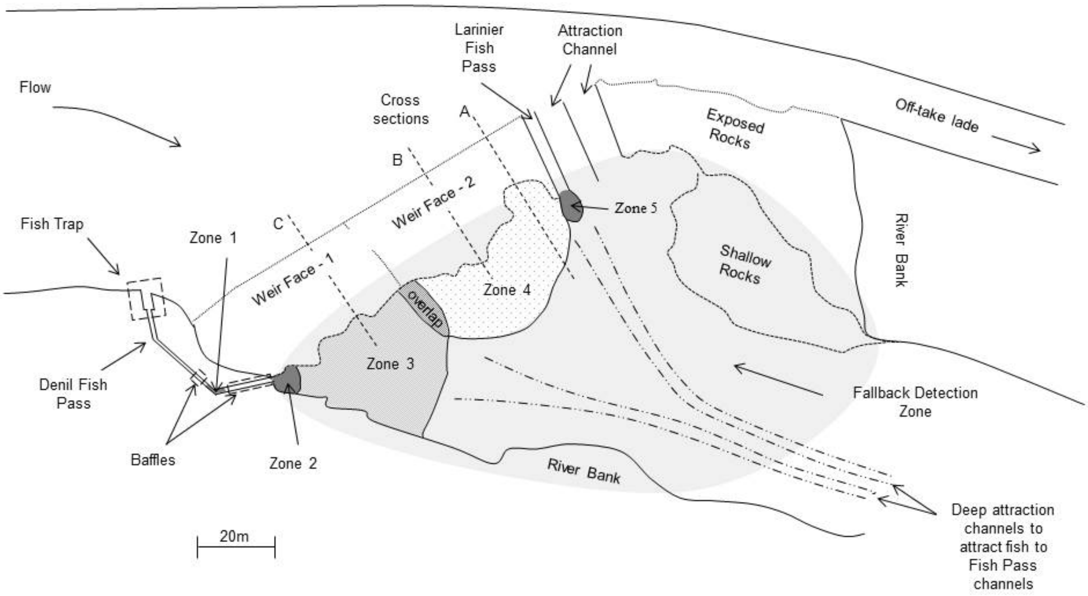

Figure 4.3 Plan of obstacle structure, indication detection zones at the weir face.

The weir profile is best described by three transects which are representative of the wider weir structure at each location. Each transect was selected to most accurately reflect the wider weir face.

<u>Transect A (Fig. 4.4)</u>

Effective passage length = 13m, Head height = 2.17m, Slope = 16.7%. This section of the weir has degraded, shortening the effective length of the obstacle and creating a vertical drop at the foot of the slope. These conditions extend for 6.5m either side of the transect. An outlet drop (at the foot of the weir) of 0.5m is present under regular flow conditions (up to Q20), with an average plunge pool (depression at foot of weir eroded by falling water and suspended material) depth of 1m, this depth is only present at the foot of the weir, with the pool becoming shallow (< 0.5m) yet still providing a large resting place for fish, extending 7.5m downstream from the foot of the weir. Water flowing over the initial 5m section of the weir face is smooth and unbroken before breaking up over rough concrete on the longest section of the face.

Transect B (Fig. 4.4)

Effective passage length = 22m, Head height = 2.42m, Slope = 11%. The full passage length of the weir is intact; water is smooth and unbroken across the initial 5m of the face, before breaking up over rough concrete down the remainder of the face. No outlet water drop at the foot of the weir, water flows directly into shallow and partially exposed rock and boulder substrate creating medium turbulence levels at the foot of the weir.

Transect C (Fig. 4.4)

Effective passage length = 22m, Head height = 2.42m, Slope = 11%. The full passage length of the weir is intact, with the upper section of the face being a much shallower slope than the remainder of the weir. Water is smooth and unbroken across the passage length of the weir face. Water flows onto rock and boulder substrate with specific areas of flow concentration created by larger boulders.

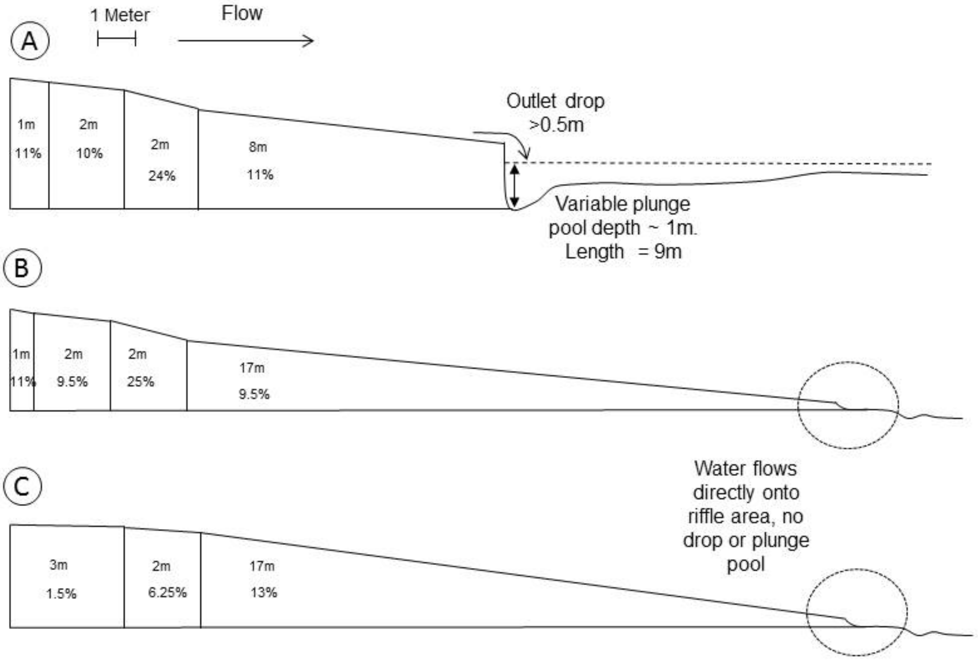

Figure 4.4 Cross section of the weir at points outline in figure 2. These cross sections represent the three possible channel option for fish ascending the main face of the weir. The width (meters) and slope (%) is outlined for each downstream portion of the weir face.

4.2.2. Fish Capture and tagging

Atlantic salmon were captured during the spawning migration of 2012 and 2013. In 2012, Atlantic salmon were collected with a fish trap installed within the upstream section of the Denil fish pass (Fig. 4.1 & 4.2). The trap (3 x 2.5 x 2 meters) was checked periodically (two or more times daily). Fish were removed from the trap by dip net and transferred to a holding box for examination. In 2013 obstacle-naïve fish were collected through draft (seine) netting, downstream of the weir, within the tidal part of the river (Fig. 4.1). Fish were netted during darkness and transferred directly to holding box filled with fresh river water for inspection. Fish were rejected from the study if they indicated any signs of disease or physical damage. Prior to tagging, fish were immersed in an anaesthetic bath of clove oil (Ethanol: clove oil 10:1, 0.5mg per litre). Once anaesthetised, a radio tag (Model: F1835, Advanced Telemetry Systems) was inserted via the oesophagus into the stomach. Fish were then held to recover in fresh water whilst fork length and depth of the fish were measured. Fat content was measured by using a fish fat meter (Distell, Model – FM 692). A panjet was used to mark each fish with alcian blue dye between the pectoral fins on the ventral surface of the fish to enable anglers easy identification and subsequent release of tagged individuals. Fish were placed into a protective sling and weighed. In 2012, fish were then placed into a fish transport box containing aerated river water before being transferred to the release site downstream of the weir (Fig. 4.2). On release fish were held by hand in slow flowing current and allowed to recover. In 2013, following weighing, fish were transferred to a holding pen submerged within the river in an area of gentle flow for recovery and to prevent recapture by subsequent netting attempts. Fish were released at the end of each netting session.

4.2.3. Telemetry array and fish tracking

A telemetry array was installed within the vicinity of the weir to enable the movements of tagged individuals to be assessed (Fig. 4.3). Three fixed automatic listening stations were used to create eight detection zones. Coaxial cable was stripped to create aerials, the length of exposed core was modified to create varying detection ranges. Aerials were either exposed to air (wide detection) or submerged in water (confined detection) and combined with variable gain receivers enabled the establishment of precise detection zones (Fig. 4.2). Range testing was conducted throughout the study period to ensure these detection areas were maintained.

Wide detection zones were used to investigate broad behaviour patterns for fish approaching and leaving the obstacle vicinity. Upstream migrating fish would first be detected at a large detection zone 150 – 450m downstream of the weir, this *'downstream detection'* zone covered a deep pool which had been reported (pers comm) as a holding area for fish (Fig. 4.2). A wide detection zone was installed between the weir and the *downstream detection* zone, the '*fall back detection zone*' (Fig. 4.2). The *fall back detection* zone was used to detect fish which were in the vicinity of the weir but not necessarily directly within confined detection zones at the weir face (Fig 4.3. Zone 1 to 5). A large detection zone upstream, *'upstream detection'* zone enabled identification of fish that had successfully passed the weir.

Detection zones were created at all channel passages where it was physically possible to place equipment (Fig. 4.3). Zone 1 identified when fish had ascended the initial baffled section of the Denil fish pass into a holding pool within the pass itself. Zone 2 detected fish at the entrance to the Denil pass. Zone 3 covered the right hand bank, detecting fish as they approached the weir face, zone 4 detected fish as they approached the left hand bank of the main weir face. There was a small overlap between zones 3 and 4. A combination of the signal strength and the number of tag detections was used to determine whether fish were located in zone 3 or 4. Zone 5 identified fish at the entrance of the Larinier fish pass.

The telemetry array was operational throughout the study period in each year (May to the following January). Out with the obstacle array, from 8 km downstream to 14 km upstream, locations of tagged fish were recorded daily by manual bankside tracking. Wider area searches across the catchment and tributaries were undertaken every two days to try and locate fish which had moved out with the local search area. In January 2013 a fly over with an aerial mounted on a helicopter was undertaken to search all major tributaries of the catchment.

4.2.4. Fish Movement and Behaviour

Fish behaviour was quantified through a number of metrics. '*Total delay*' is defined as the time difference between the first detection of an individual at the weir face (i.e. in zones 1 to 5, Fig. 4.3), and the time at which passage was deemed to have occurred, defined by detection at the *upstream detection* zone. For many fish, *total delay* will include multiple passage attempts. An '*attempt'* is defined here as detection of the fish at the weir face aerials (zone 1 to 5). A new *'attempt'* was assigned when there was a gap in detections at weir face detection zones (1 to 5) of greater than 15 minutes or if the fish was detected continuously on a downstream aerial. *'Passage attempt time'* is the difference in time from the start of an attempt to the end of an attempt. *Passage attempt time* is assumed to represent the time spent searching at the weir face for successful passage. An *attempt* and *passage attempt time* is deemed to have ended when either a fish passes the barrier and is detected on the *upstream detection zone* (also a '*successful passage'*)*,* or when fall back occurs (*'unsuccessful passage*). '*Fall back'* is deemed to have occurred by continuous detections in the *downstream* or *fallback detection* zones (Fig. 4.3), or where there is a gap in the data where the fish is no longer detected at weir face aerials.

'*Fallback*', in this study, is defined by a fish moving downstream between any individual passage attempt. The *fallback 'distance'* and *'location'* were split into 3 categories: *'Short range'* (<80m from weir), here fish remained close to the weir within the *fallback detection* zone but not detected within weir face zones (zone 1:5). *'Medium range;'* fish held between the *fallback detection* zone and the *downstream detection* zone (~130m from weir). '*Long range*;' fish moved downstream and held within a deep pool covered by the *downstream detection* zone (>225m downstream from weir; Fig.3) or further.

To determine if fish were attracted to specific areas of the weir, the proportion of time spent in each zone (zones 1 to 5) during the entire attempt was calculated, and the zone with the highest proportion of time was assumed to be the channel of preference for that fish. Chi-squared tests were used to determine if greater numbers of fish were attracted to specific sections of the weir. If no preference was observed there would be equal numbers of fish exhibiting a preference across each of the detection zones.

A number of non-parametric tests were conducted on behavioural traits. Shapiro-Wilk normality tests were used to test for normality in the data, log10 transformations failed to improve the spread of the data thus leading to the use of Wilcox rank sum tests on the following: 1) A difference in the *total delay* for each fish between years. 2) A difference in the passage attempt time between a successful or unsuccessful first passage attempt. 3) A difference in passage attempt time between first and second attempts

Measures of behaviour were modelled to determine what factors enabled a rapid successful passage over the obstacle with a minimal delay. An initial mixed logistic regression model (Model 1) was developed to identify the variables determining passage success on an individual's first passage attempt. The response variable was binary, either passage success occurred or it didn't, the independent response variables are outlined in table 4.1. A second model (Model 2) was developed to determine the independent variables influencing passage attempt time on an individual's successful passage attempt. The response variable was the *passage attempt time* recorded when the fish successfully crossed the weir, the independent response variables are outlined in table 4.1. Within each model an interaction between mean search flow and mean search temperature as tested to account for the reduction in temperature associated with increased discharge. The predictor variables were selected based on a subjective approach whereby variables most likely to have a known biological mechanistic effect on the response were utilised as opposed to exhaustive searching. Due to low sample size and low *a priori* knowledge of factors effecting behaviour exhaustive searching may identify relationships but the relative importance of this unknown hence a subjective approach in model formulation was undertaken

All analysis was conducted using R (R version 3.1.3 [2015-03-09]) statistical computing package (R Core Team, 2013).

4.2.5. Environmental Data

River flow data for the rivers were provided in the form of discharge data at 15 minute intervals (provided by the Department of Agriculture and Rural Development, Northern Ireland). The discharge at each *passage attempt* was taken as the mean discharge of all data records during the specific *passage attempt.* Temperature data is recorded remotely and provided by the Loughs Agency for every 15 minute period. The temperature for each *passage attempt* was taken as the mean temperature of data records during the specific *passage attempt.*

Day and night values were calculated using the sunriset function in the maptools package developed by Bivand and Lewin-Koh (2016) within R (R Core Team, 2013). Light conditions were used within Chi-squared tests to determine if there was a preference for passage attempts either during daylight or at night

4.2.6. Modelling approach

Fish behaviour within years was likely to be more similar than between years as a result of environmental variables and capture/release method, thus a mixed modelling approach was taken with ‘year’ included as a random effect. Data exploration identified outliers which were removed and independent variables violating the assumption of collinearity were also removed.

Due to the complexities associated with the highly exploratory nature of this study *a priori* information about predictor relevance is relatively unknown. The glmulti function in the glmulti package (Calcagno, 2013) enables the generation of all possible model formulas from a set of specified effects from which model selection is performed. Glmulti is a general wrapper for glm and related functions and generates all possible model formulas from input variables. The glmulti function (Calcagno and Mazancourt 2010), was utilised in conjunction with the glmer (model 1)/lmer (model 1) functions within the lme4 package (Bates *et al*, 2015) to enable use of random effects, uses a genetic algorithm to sample a large number of first order models (the terms within the model are a subset of the full model) and was used to allow selection of the model comprising the best set of independent variables with minimum Akaike Information Criterion. The best candidate models within two AIC units (competing models) were assessed based on Akaike weights which is considered as the weight of evidence in favour of model *i* being the actual best model. In addition, evidence ratio's of the Akaike weights were used to determine strength of support for the best model, and the modelled sum of weights were used to estimate the relative importance of variables under consideration (Burnham and Anderson, 2002. Symonds and Moussalli, 2011). P-values were obtained by likelihood ratio tests of the full model with the effect in question against the model without the effect in question. The model selected based on the best AIC sometimes included independent variables which were not significant. Final models were generated with non-significant variables being dropped as determined by likelihood ratio tests. The code utilised to formulate models is attached within the appendix.

Table 4.1: Description of independent variables used in the model selection process.

Variable	Description	Used in model
Passage Attempt time	The difference in time between the start and the end of an attempt	1,2
Mean search flow	The mean discharge for the duration of a passage attempt	1,2
Mean flow status	Binary response to if the flow was increasing or decreasing	1,2
Standard deviation of search temperature	The standard deviation of discharge during a passage attempt. A measure of flow variability.	1,2
Search flow status	Binary response to whether the discharge was increasing or decreasing	1,2
Mean search temperature	The mean temperature for the duration of an attempt	1,2
Mean Temperature status	Binary response to whether the temperature was increasing or decreasing	1,2

Zone per unit time	The mean number of non-consecutive detections at individual aerials over a period of ten minutes. This is a measure of the amount of searching by a fish at the weir face.	1,2
Fat Content	Fat content of a fish (%)	1,2
Length	Length of a fish	1,2
Sex	Sex of fish (male/female)	1,2
Proportion time in zone 3	Proportion of time spent in zone 3 for the duration of the attempt	2
Proportion time in zone 4	Proportion of time spent in zone 4 for the duration of the attempt	2

4.3. Results

Of the 132 fish tagged (Mean ± S.D for: Fork Length [L_F] = 609.2 ± 41.65 mm, Mass = 2.96 ± 0.51Kg, Fat content = 9.52 ± 3.82%) in this two-year study (12 in 2012 and 120 in 2013), 51 fish (39%) were detected within the telemetry array and 40 (77%) of these fish were deemed to have had a *successful passage attempt* (9 in 2012, 31 in 2013). Of the 11 fish that were detected but failed to pass, one fish arrived at the obstacle but failed in ascending, ten fish were detected in the stream reach immediately downstream of the weir, however were not detected at the weir itself. The ultimate fate of the 11 fish that did not pass the obstacle could not be determined.

The following results are based on 36 salmon of the 40 which successfully ascended the weir. Four fish were removed from the analysis. Three of these fish were detected upstream by manual tracking however their passage route at the weir could not be determined and were removed from any subsequent analysis. It is possible these fish ascended the weir under flood conditions where routes not normally available for passage and not covered by the telemetry array, were accessible for a brief period of time when high water conditions allowed, however their exact behaviour cannot be determined. One fish was not detected at the weir but was routinely tracked to a location downstream of the weir (approx. 9km), and was subsequently detected upstream of the study site via an aerial tracking survey (17 January 2014), is likely this fish ascended the weir after the array ceased to operate.

4.3.1. Fish Presence in the Vicinity of the weir.

Time to first detection at the weir from release was highly variable (mean ± S.D. = 48.7 ± 33.7 days), two fish reached the weir in under five hours after release, conversely the maximum time to detection at the weir was 130 days. Mean *total delay* at the weir per fish was 47.8 hrs (± S.D. 132.0hrs) range (15 minutes to 31 days) with no significant difference in *total delay* between years (Wilcox-Rank-Sum, W= 138, p = 0.44).

The majority of fish were successful in passing the weir on either their first (46%) or second (43%) *attempt*. However, four fish required 3,5,7 and 11 *attempts* respectively to ascend the weir. Mean *passage attempt time* per fish was 561 ± 1707 S.D. minutes (median = 132 minutes, range 8 minutes to 10 days). Mean *passage attempt time* on a successful attempt was 755 ± 2370 S.D. minutes (median = 125 minutes, range 10 minutes to 10 days) but this was not significantly different (Wilcox-Rank-Sum, W = 79, p = 0.7) from first unsuccessful attempts (*passage attempt time* mean ± S.D. = 378 ± 611 minutes, range 8 to 2760 minutes). Mean *passage attempt time* for successful first attempts was 198 ± 213 S.D. minutes (range 23 to 867 minutes) but not significantly different (Wilcox-Rank-Sum, W = 86, p = 0.2) from fish which passed on their second *passage attempt* (mean = 1343.267 ± S.D. 3567 minutes, median = 240 minutes, range 10 minutes to 10 days).

A greater number of *passage attempts* were initiated during daylight hours compared with darkness hours (χ^2 = 20.1, p = < 0.001), however there was no significant difference between the number of successful *passage attempts* in either the day or night (χ^2 = 0.04, p = 0.8).

Analysis indicated significant channel preference during all *passage attempts* ($\chi^2 = 164.8$, $p < 0.001$), successful *passage attempts* ($\chi^2 = 97.2$, $p < 0.001$) and unsuccessful *passage attempts* ($\chi^2 = 97.2$, $p < 0.001$). Out of all successful *passage attempts* 34 of the 36 attempts occurred at zone 4. For unsuccessful *passage attempts*, 31 of 37 occurred at zone 4 with five individuals making attempts at zone 3 and one individual at zone 2.

4.3.2. Fish Pass use

The total number of observations of fish on weir face aerials (Zone 1 to 5) was 22460, of these 1831 (8.2%) were at the entrance to the constructed fish pass channels (Zone 2 and Zone 5), however 1665 (91%) of these detections came from a single individual, indicating only 166 detections (0.74 %) came from other fish. Of the 45 fish detected at the weir, 20 had at least one detection in zone 2 or zone 5, however 12 of these fish had less than 8 detections at the foot of fish pass channels. A significantly greater ($\chi^2 = 1050.7$, $p = < 0.001$) number of detections occurred in zone 2 than in zone 5. Three fish (8%), of those making a successful passage attempt, were deemed to have utilised the fish pass as a successful passage route, all three fish passed through the Denil fish pass (Fig. 4, Zone 2 and Zone 1). No fish ascended through the Larinier fish pass. Fish tagged in 2012, which were initially caught within the pass did not re-ascend through this channel, instead re-ascending over the weir face.

4.3.3. Statistical Modelling

The binary response of a fish's success or failure at ascending the obstacle on its first attempt was modelled using logistic regression (glmer) with explanatory variables (outlined in Table 4.1). From 2,100 models the best model indicated by AIC scores was that which included; zone per unit time (χ^2 (1) = 4.99, p = 0.03), length (χ^2 (1) = 10.09, p = 0.002) and fat content (χ^2 (1) = 4.71, p = 0.03). A fish was more likely to have a successful first *passage attempt* if it was smaller (fork length) with a low fat content and exerted a greater effort in searching for a passage channel. Although this model was ranked best by AIC, a number of competing models (11) were also identified within two AIC units of the best model. Further examination of akaike weights ratios suggest there is low support for the best model, the evidence ratio for the best model, versus the model two AIC units worse is only 2.67. The variable akaike weight for the three variables indicated in the best model were in excess of 0.9 and thus strong evidence that these variables are components of the actual ‘best’ model (Fig 4.5).

To examine the factors (Table 4.1) influencing the *passage attempt time* on successful obstacle passage, the *passage attempt time* on each successful *passage attempt*, for attempts one and two (due to highly unbalanced data across all attempts; only four fish had more than two attempts) is modelled on predictor variables (outlined in Table 4.1) with the addition of the passage attempt number (one or two). Following model validation the dependent variable was log transformed log10(y). The model was re-run with the transformed data and the assumptions of homogeneity of variance and normality were confirmed. Out of 1,050 models, the model of lowest AIC was that which included only the ‘mean search flow’ (Table 4.1) as an independent variable (χ^2 (1) = 25.26, p = <0.001). *Passage attempt time* increases with *mean search flow* during an *attempt*. Although this model was ranked best by AIC, a number of competing models (56) were also identified within two AIC units of the best model. Further examination of Akaike weights ratios suggest there is low support for the best model, the evidence ratio for the best model, versus the model two AIC units worse is only 2.7. The variable weight for “mean search flow” was in excess of 0.9 and thus strong evidence that this variable is a component of the ‘best’ model (Fig 4.6).

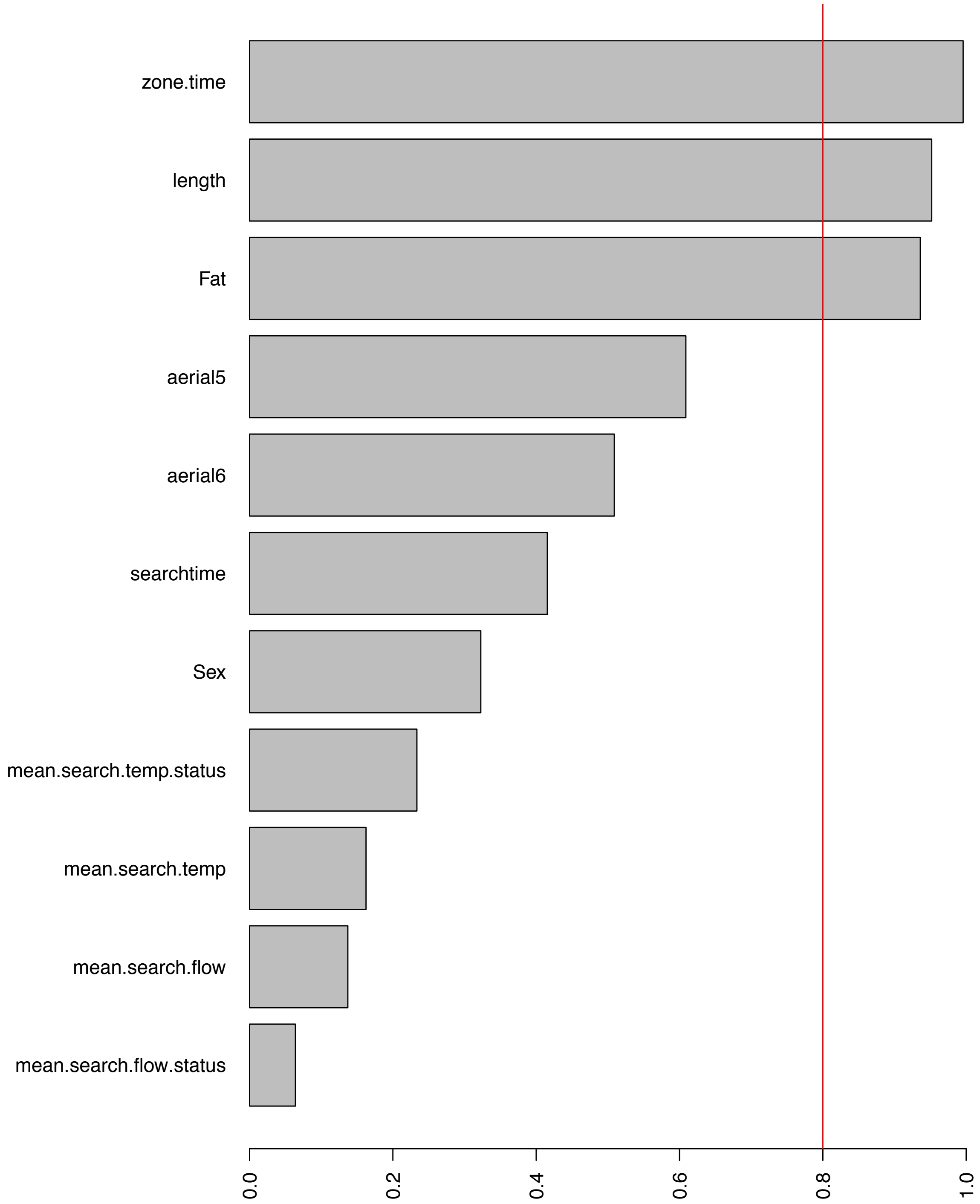

Figure 4.5 Sum of weights for each variable across all models of glmulti output in model 1. Vertical redline is drawn at 0.8.

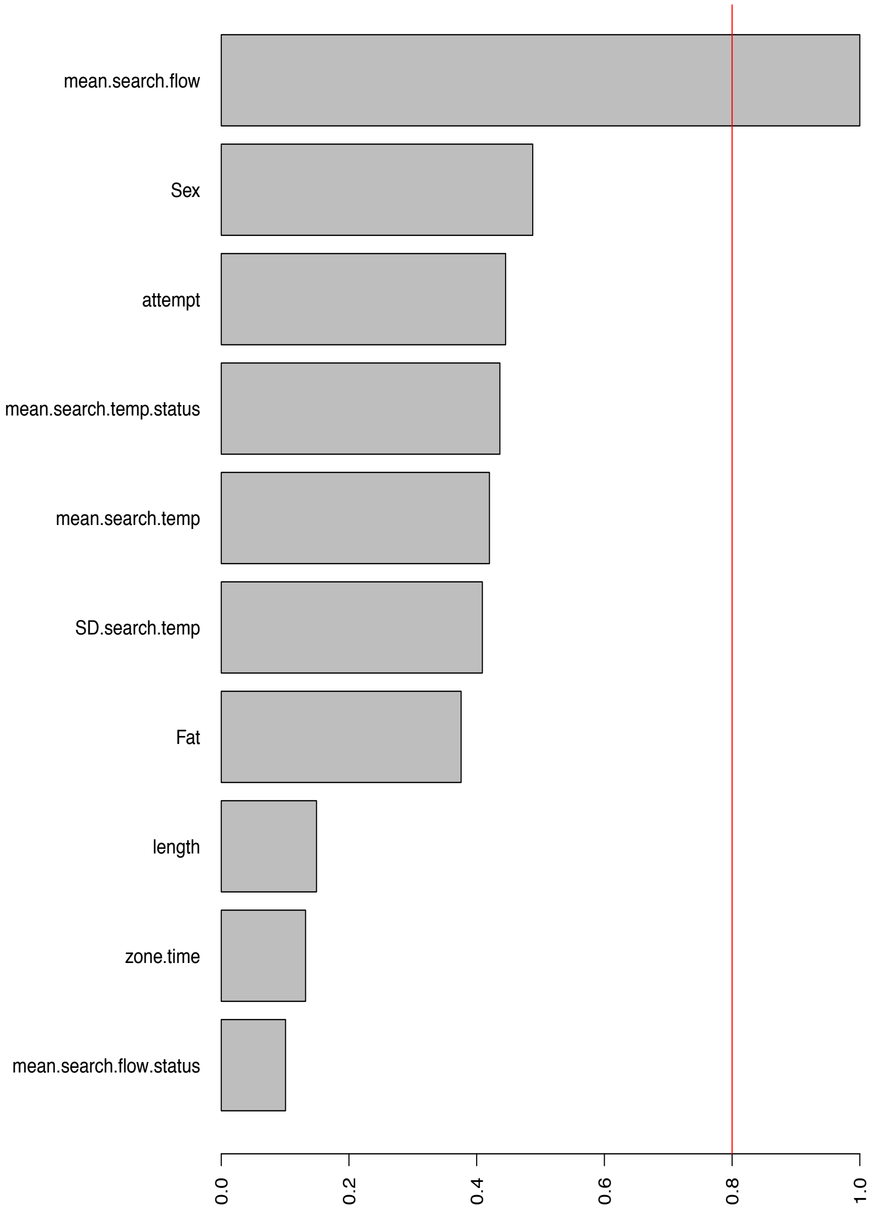

Figure 4.6 Sum of weights for each variable across all models of glmulti output in model 2. Vertical redline is drawn at 0.8.

indicating that higher discharge during a *passage attempt* had a significant, positive effect on the *passage attempt time*.

4.3.4. Fall-back

Following a failed passage attempt, the distance to which fish moved downstream was highly variable, one individual fell back downstream 3.4km following an unsuccessful *passage attempt*, but did eventually ascend the weir. Another individual, despite being detected at the weir and registering a *passage attempt*, fell back downstream and was later recorded 45 km away in a neighbouring river system and did not ascend the weir.

4.4. Discussion

This is the first study to identify the behaviour of returning adult Atlantic salmon on approach to a low-head complex river obstacle over small spatial scales. It has highlighted their ability to surmount such a structure but also the variability in behaviour which is required to do so. Of the 41 tagged fish which were detected at the weir, 40 were successful in ascending the obstacle enabling them to reach suitable spawning grounds. Time to first detection was highly variable, some fish were detected at the weir within a few hours of release, with the longest time between release and first detection at the weir being 130 days. The time spent at the weir was highly variable; however there was no significant difference in *passage attempt time* between *successful* or *unsuccessful passage attempts*. The wide variation of behaviours recorded likely impact on the low support, based on Akaike evidence ratios. However the high importance value, indicated by the sum of weights of the variables suggest that they are influencing the dependent variable for both models presented. The *passage attempt time* on *successful attempts* was positively related to discharge, with fish taking longer to ascend under higher flow regimes. Upstream migrating salmon tend to follow the strongest current (Banks 1969, Karppinen *et al.* 2002). Despite deep channels carved into the river bed (Fig. 4.3), increasing flow and thus a greater attraction toward the entrance of the fish passes, there was still significant preference for the zones immediately downstream of the weir face. Attraction efficiency of channels is highly dependent on the hydraulic conditions (Larinier 2008). At obstacles such as this, where numerous passage channels are present, flow dynamics are likely to alter significantly with discharge, thus as discharge increases, competing flows mask suitable channels for passage and hence longer time is required to identify suitable passage channels. The ability of salmon to identify and utilise small scale variations in flow conditions is relatively unknown but thought to play an essential role in their ability to ascend river barriers. Only with further fine spatial resolution movement data combined with hydrodynamic modelling will it be possible to study such behaviour.

Significant preference for passage at zone 4 (Fig. 4.3) was shown throughout the study, yet this is potentially the most physically challenging passage route available. It is the shortest channel in length (upstream to downstream distance) of the weir (Fig. 4.4.A), however it requires a leap onto the weir face removing any potential momentum gain, followed by a swim up a steep gradient on the weir for 13 meters to gain passage. Following guidelines on available obstacle porosity measurements outlined by a water framework barrier classification tool (SNIFFER 2010), such a channel would be deemed impassable to adult Atlantic salmon. This evidence suggests that barrier classification tools need re-fining or that further work similar to presented here is explored across a variety of locations to more rigorously test such tools.

Surprisingly fish in 2012 which were sampled from within the fish pass and subsequently released downstream did not attempt to re-ascend through the pass a second time, instead ascending across the weir face. It is possible the initial passage attempt which ultimately resulted in failure due to capture and release downstream was a learning event which influenced subsequent passage attempts through a secondary route, the same phenomena was reported by Karpinnen *et al.* (2002).

A greater number of attempts were initiated during daylight as opposed to during the night however there was no difference in light conditions between successful and unsuccessful attempts, suggesting a greater success in attempts under darkness. In salmonids, the relationship between light intensity and passage attempts at obstacles is not clearly defined, at large complex obstacles, where fish are delayed and their migration thwarted, passage occurs primarily during daylight (Chanseau and Larinier 1999, Chanseau *et al.* 1999, Gowans *et al.* 1999, 2003, Null and Niemela 2011), whilst at less complex structures and natural by-pass channels passage occurs at night (Dunkley and Shearer 1989, Chanseau *et al.* 1999). Light intensity preference for passage requirements appears to be site specific and related to the visual orientation needs at each given obstacle (Banks 1969, Thorstad *et al.* 2008). The timing of passage (in either day or night) maybe an early indicator of passage difficulty for salmon, daytime passage potentially indicating higher levels of passage difficulty. Indeed there is likely to be an interaction between the light required to successfully ascend obstacles and the preference of turbid water or darkness as an anti-predator mechanism (Banks 1969, Thorstad *et al.* 2008).

Delay at the obstacle in this study was relatively low compared to other studies (Chanseau *et al.* 1999, Gowans *et al.* 1999, Thorstad *et al.* 2003), and more similar to delay identified at a natural obstacle (Kristinsson *et al.* 2015), however there are few studies on anthropogenic structures of comparable head height (Gerlier and Roche 1998, Croze 2008). Small scale obstacles (<1.5m) in the Pau river, France, tended not to cause a delay in migration, however the effect of larger structures (>2.5m) was variable and depended on local factors such as passage facilities (Chanseau *et al.* 1999). Prolonged delays which prevent fish reaching spawning locations may obviously diminish their reproductive ability, whether a temporary delay, such as seen here, has any reasonable effect on the reproductive success of a fish which ultimately reaches spawning grounds, remains unclear (Lucas and Frear 1997, Thorstad *et al.* 2008).

Indeed the cumulative effects of such delay at multiple obstacles maybe substantial, the obstacle in this study is the first of seven similar structures along the river length, however the consequences to the population of such a delay remains unknown (Thorstad *et al.* 2008). Mesa and Magie (2006) identified Chinook salmon *Oncorhynchus tshawytscha* migrating slowly between dams in the Columbia river basin utilised 5-8% more energy from muscle than faster migrants. Over an average of 29 days fish lost between 6 and 17% of muscle energy density depending on their travel time (Mesa and Magie 2006), a cumulative delay of such magnitude may not be uncommon along a river length with multiple low-head obstacles. Energy expenditure is also likely to increase with the number of passage attempts a fish makes to ascend an obstacle and the distance to which an individual may fall-back downstream following a failed attempt. In this study, when a fish failed in its passage attempt, the fish moved back downstream to suitable resting locations (fall back), although fall-back distance is not significant in determining a subsequent successful passage attempt, it does emphasize the cost of delay. A failed attempt and subsequent fall back (downstream movement), increases energy use, which, if a successful passage had occurred would otherwise be used to migrate upstream towards spawning grounds. The greater number of failures and fall back attempts which occur, the more energy is utilised. In this study one fish made 10 passage attempts prior to a successful passage occurring (11 passage attempts in total), including a fall back of 3.4km downstream, such behaviour results in significantly increased energy expenditure compared to fish which successfully ascended the obstacle in a short period of time. Fall back also re-exposes fish to pressures, such as angling, pollution, poaching and predation which it has already experienced and successfully circumvented downstream; pressures it would not be re-exposed to should a successful passage attempt have occurred.

The fact that higher search rates (zone per unit time) at the weir face and a lower fish fat content were significant factors in predicting fish passage on an initial attempt, implies fish with lower energy reserves cannot afford to be delayed at an obstacle and thus may increase energy expended in a single passage attempt. Obstacles directly increase energy consumption, thus fish with low energy reserves may need to reach spawning locations rapidly so as to rest and preserve remaining reserves for spawning. Although the effect of increased energy expenditure on reproductive success remains unknown, it would not be un-reasonable to hypothesise that reduced energy reserves will ultimately have a negative impact on reproductive success (Thorstad *et al.* 2008).

The variability in delay and also the number of attempts prior to successful passage maybe linked with physiological characteristics of individuals. A significant predictor in an initial passage attempt was fish length, with larger fish less likely to be successful in their initial passage attempt. Similarly, Kristinsson *et al.* (2015) observed a small but significant positive relationship between delay at an obstacle and fish length. For high average thrust, fish need large caudal fins (Weihs 1973), and as Webb (1973) suggests, a deep caudal fin is required to generate high acceleration. Conditions which prevent a fish utilising its caudal fin at maximum efficiency, such as shallow water where part of the fin is exposed to air, ultimately reduces a fishes thrust. Hence, shallow water flowing over a weir face will reduce the ability of larger fish with deeper caudal fins to ascend them. Laboratory experiments have shown maximum swimming speeds vary substantially between physiological capabilities (Fisher and Hogan 2007) and populations of the same species (Webb *et al.* 1984, Ralph *et al.* 2012). Thus it maybe unsurprising that some individuals take longer to ascend the obstacle than others, this is particularly true when passage relies heavily on the swimming ability of an individual which is pre-determined by its physical characteristics and genetic make-up (Fisher and Hogan 2007). It is thus possible that river barriers, such as this are creating a selection pressure against larger individuals. Recent evidence of selection based on size and passage ability was presented by Sigourney *et al.* (2015) where larger fish were less likely to ascend hydroelectric dams. With larger fish being delayed for greater period of time, increasing energy consumption, their overall fitness is likely to be reduced negatively impacting reproductive success. Along with flow, temperature has a significant effect on the swimming abilities of fish since it directly effects muscle activity. Although no such relationship was identified in this study, Gerlier and Roche (1998) identified obstacles that were passable by early migrants, became impassable to migrants later in the year due to low water temperatures reducing fish swimming ability, similarly fish failed to ascend a fish ladder at Pitlochry dam (Scotland) when water temperature dropped below 5.5°C and only few doing so below 8.5°C (Gowans *et al.* 1999).

Sample size in telemetry studies is regularly a constraining factor. In the statistical modelling presented here both models, although significant, had numerous similar competing models with evidence ratios suggesting little support for the best model. It is likely that the amount of variability within the data set prevents stronger relationships being identified. Despite a relatively large sample size of fish tagged only a small proportion of these fish were available for analysis. The resource constraints associated with telemetry combined with natural variations in behaviours across populations creates a challenge for such work. None-the-less telemetry has the ability to shed light on the behaviour of migrating fish in the wild.

For any given obstacle there is a highly variable temporal window within which environmental variables such as flow and water temperature combine with fish characteristics to enable passage for an individual, this passage window fluctuates significantly from one individual to the next depending on their own physical features. There is a need to understand the costs associated and potential selection pressure with delay and passage success at an obstacle, and especially how a delay may impact the reproductive ability of an individual either through fewer egg numbers, or smaller less eggs with lower nutrient availability.

Chapter 5

An estimate of the rate of illegal net fishing for sea-migrant Atlantic Salmon, *Salmo salar*, in a dendritic river system in the western Atlantic

5.1. Introduction

Sustainable exploitation of renewable resources depends on the existence of a reproductive surplus, which is determined by the balance between births and deaths. The reproductive surplus differs spatially and temporally as environmental conditions vary even in the absence of exploitation. The current approach to managing anadromous Atlantic salmon (*Salmo salar*) population exploitation is primarily focussed on management at the single catchment level. One of the main difficulties in adequately managing exploitation by recreational (and/or other fisheries) is the largely unpredictable change in population sizes of returning sea migrants over a short period of time (Jonsson and Jonsson 2009). The difficulties of managing exploitation are compounded by illegal exploitation which has the potential to modify the population size of returning migrants downwards (Agnew *et al.* 2009). Attempts to estimate illegal exploitation (to include its effects on population size estimates) are hampered by the fact that it is, by definition hidden, hence illegal catch rates are very difficult to determine.

What evidence there is however, suggests that such effects maybe high and growing. Incidents of fish poaching (defined as the removal or destruction, or an attempt to do so, of any fish in water which is private property or in which there is a private right in fishery) are increasing. Statistics from the National Wildlife Crime Unit (NWCU) show that fish poaching incidents in Scotland increased by 75% between 2008 and 2009 (Scottish Government, 2009). A report by the NWCU (covering the period September 2008 to August 2010) indicated that of the 9518 wildlife crime incidents reported in the UK, 484 (5%) were related directly to fish poaching (National Wildlife Crime Unit, 2011). Of the 1473 wildlife crimes recorded by police in Scotland between 2008- 2012, 439 (30%) were recorded within the offence category ‘Salmon, freshwater and fisheries offences.’ Similarly fish poaching was directly responsible for 14-17% of NWCU intelligence logs each year between 2008 and 2012 (Scottish Government, 2012). A more recent strategic assessment by the NWCU (2011 to 2013) identified fish poaching as specifically accounting for 11% (545) of all intelligence, with no significant progress in prevention across the period (National Wildlife Crime Unit (NWCU) 2013).

The use of gill nets to capture salmon or migratory trout has been prohibited in the UK since 1975 under the Salmon and Migratory Trout (Prohibition of Fishing) Amendment Order 1975. 'Gill net' means any length of net, being a net designed for the purpose of catching fish by enmeshing them. The Loughs Agency, the body responsible for the conservation and protection of the Foyle catchment, has reported an increase of 27% in the number of illegal nets (gill nets) seized between 2009 (127) and 2011 (161) (Loughs Agency 2011b). On average 114 nets are seized per year (data available 2004 – 2011 inclusive), this is equivalent to a quarter of all reported poaching incidents across England and Wales between 2008 and 2010 (National Wildlife Crime Unit, 2011). Nets are seized along all major tributaries on the Foyle (Fig 5.1B), with the highest number of seizures occurring below the confluence of the Rivers Finn and Mourne. Here fish are continually moving both up and downstream with the tidal cycle, and are thus subjected to multiple exposures of any illegal nets. It is in this small section of the tidal river, approximately 20km in length, where 48% of all net seizures within the entire Foyle catchment occurred between 2000 and 2009. Clearly a considerably amount of illegal netting does take place within the Foyle area, it is likely that to some degree illegal nets are successful in catching salmon, however figures of seizures do not necessarily help in quantifying the impact of illegal fishing

Here, as one component part of a larger study on Atlantic salmon behaviour we were able to make an estimate of the rate of illegal salmon poaching in the River Foyle, a large dendritic river in Ireland.

5.2. Methods

5.2.1. Study Site

The Foyle (55°00'N; 07°20'W) is a large dendritic river system with a catchment area of 4450km^2. It forms part of the border between Northern Ireland and the Republic of Ireland (Fig. 5.1). The Foyle system as a whole is a designated European Union Special Area of Conservation (SAC) for Atlantic salmon. The main tributaries of the Foyle are the River Mourne and River Finn, which form the tidal River Foyle at their confluence. The Loughs Agency is the governmental cross border body responsible for the conservation and protection of inland fisheries within the Foyle catchment.

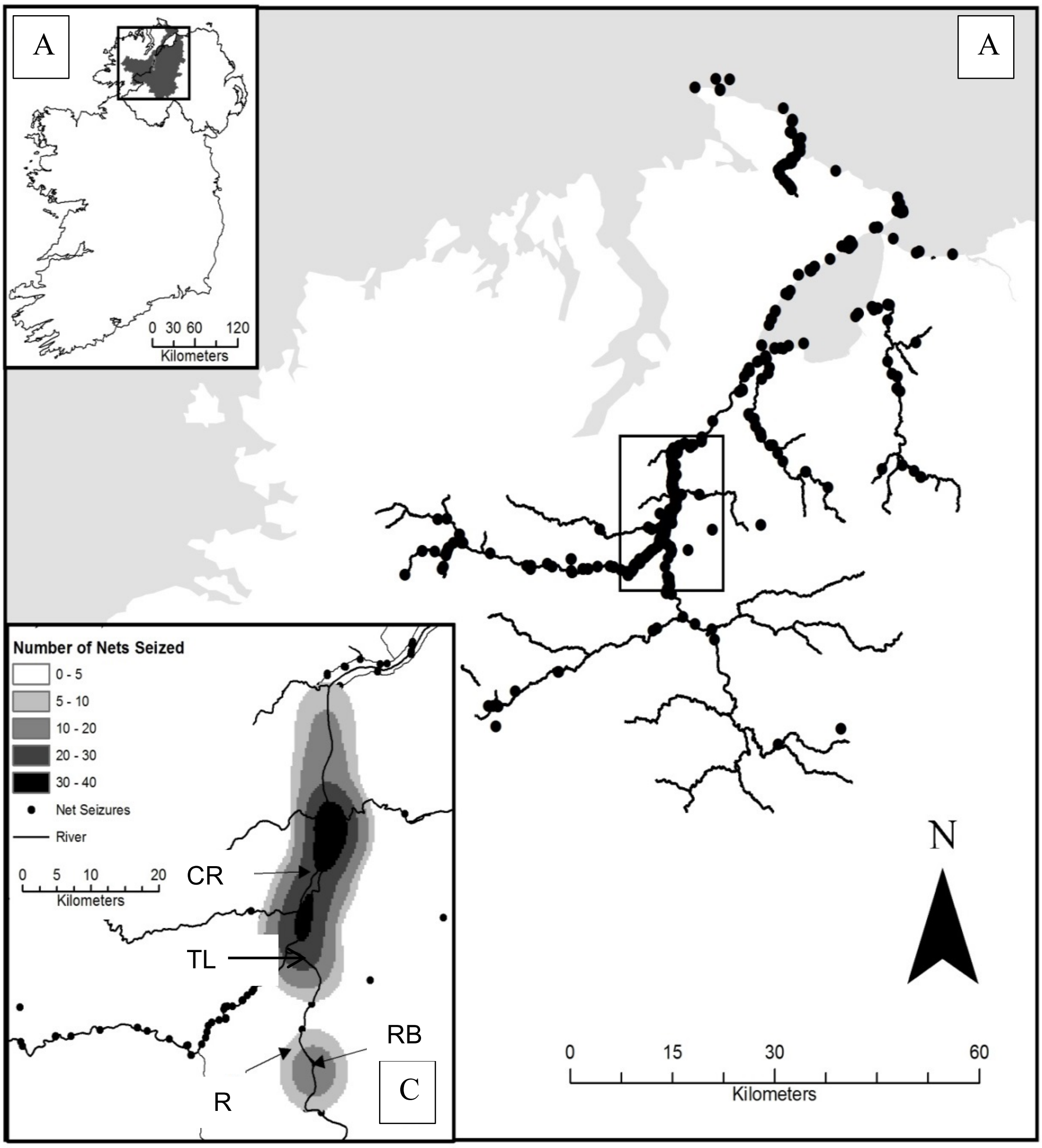

Figure 5.1 The Foyle catchment and study area. A) The geographic location of the catchment on the island of Ireland. B) showing the major tributaries of the catchment. Black dots indicate individual illegal net seizures by poaching enforcement staff of the Loughs Agency between 2000 and 2009. C) The core study area indicating the location of the river barrier (RB) the capture location of fish for this study in 2012 (RB), the site of release for tagged fish in 2012 (RS) and the capture and release site of fish in 2013 (CRS). Shaded area is a kernel density plot showing the density of illegal net poaching seizures between 2000 and 2009 around the main study area. The river flow is in a Northerly direction, and the River Foyle is tidal up to the confluence of the rivers (TL)

5.2.2. Fish Tagging

In a two year study, 132 upstream migrating adult Atlantic salmon were tagged with radio telemetry tags (Model: F1835, Advanced Telemetry Systems) and tracked throughout the catchment (Fig 5.1). In 2012, fish (n = 12, Mean fork length [L_F] =655.9 ± SD 46.9mm , mean mass [M] = 3.0 ± SD 0.6kg) were captured between 30th August and 20th September in a fish trap installed within a denil fish pass on a river barrier on the River Mourne (Fig 5.1). In 2013 fish (n = 120, mean L_F = 593.0 ± SD 30.7mm, M = 2.6 ± SD 0.5kg) were captured between 7th July and 13th August using a draft net within the river Foyle (Fig 5.1). Fish were rejected from the study if they indicated any signs of disease or physical damage. Once anaesthetised a radio tag was inserted via the oesophagus in to the stomach of the fish. A panjet was used to mark each fish with alcian blue dye between the pectoral fins on the ventral surface to enable easy identification and subsequent release of tagged individuals by anglers. In 2012 fish were released downstream of the capture site (Fig 5.1B). Fish in 2013 were released at the capture site after completion of a tagging session (Fig 5.1).

5.2.3. Telemetry Fate Identification

A fixed automatic listening station (ALS) was installed in the main study area at a migration barrier (Fig 5.1A). The telemetry array was operational throughout the study period in each year (May to the following January). Out with the array, from 8 km downstream to 14 km upstream, locations of tagged fish were recorded daily by manual bankside tracking. Wider area searches across the catchment and neighbouring tributaries were undertaken every two days to try and locate fish which had moved out with the local search area. Bankside mobile tracking utilised a GPS positioned R4520C receiver (Advanced Telemetry Systems), in combination with a car mounted dipole antenna, fixed to the roof of the vehicle. Tracking surveys were undertaken along roads running parallel to the river, upon detection of a tag, a 6-element yagi antenna was then used to more accurately position the tag location. An aerial survey was undertaken across the catchment and neighbouring catchments, five hours flying time in a helicopter traced all large tributaries within the Foyle catchment which were not covered by the ALS in January 2013 with fish expected to be on spawning grounds.

The ultimate fate of tagged individuals was assigned based on the final location of the tag as determined by signal triangulation or tag recovery. The fate of a tagged fish was determined as a successful migrant if it was detected passing the river barrier (Fig 5.1A), or located upstream of spawning grounds in a neighbouring tributary.

It was possible to determine the fate of some un-successful migrants directly, and others by inference. Anglers were encouraged to report captures of tagged fish and return tags of these killed in the fishery. Posters were placed around the catchment providing information about tagged fish and how to identify them (blue dye between pectoral fins). Radio tags were printed with a name and contact details of researchers to enable their return. There was no reward for recovering a tag so as to prevent study fish from being targeted specifically. Triangulation and recovery of a number of tags allowed their fate to be determined by the recovery location. Some tags which were located after fish were released and known to be operating normally were subsequently not detected in the study area, the wider river catchment or elsewhere. The fate of the fish carrying these tags can only be inferred.

5.3. Results

In 2012, 9 (75%) individuals were detected successfully moving upstream to spawn, whilst three individuals (25%) moved downstream out of the study area. In 2012 there was no evidence to suggest that these fish had been predated upon or removed from the study area by poaching or angling activities.

Of fish tagged in 2013, 62 (60%) fish were categorised as successful migrants, ascending to spawning grounds within the catchment. In addition a number of radio tags were recovered and thus the fate of the fish determined. A single tag (0.8%) was returned by an angler, either anglers did not report catching tagged fish, or no other tagged fish were caught. One tag (0.8%) was located in a water course with no direct connection to the main river system, adjacent to a probable otter (*Lutra lutra*) holt. This fish was categorised as having been subject to predation. During the study researchers were notified of a tag which had been discarded in a specific location by poachers and was thus recovered. In addition two tags were detected in fish which had been recovered from poaching nets seized by fishery officers. A further 11 tags were tracked to land within the catchment at a substantial (>200m) distance from the watercourse. Lack of bite marks on these tags and the absence of any fish carcass strongly indicated that the tagged fish had been removed by poachers and the tag discarded. Thus of 120 tagged fish in 2013, 12% were killed directly by poaching activities. However the fate an additional 42 tagged individuals is less certain. Daily radio tracking downstream of the release site identified a decrease in the number of tags present overtime, a comprehensive aerial and bankside radio tracking survey in January 2014 failed to locate any fish in the study area downstream from release site B (Fig 5.1C). The aerial tracking survey did not detect any tags which had not already been detected by bankside tracking or within the ALS. No tags were identified as moving downstream out of the study area in 2013. No tags were recovered from the release site as regurgitations; the majority of individuals were identified as actively moving away from the tagging location by bankside radio tracking. A logical parsimonious inference is that a significant proportion of these fish were removed from the river, most likely, by illegal netting practices.

5.4. Discussion

Implantation of radio tags into the stomach via the oesophagus for adult migratory salmonids is the preferred tagging approach for Atlantic salmon as it is generally accepted as having negligible impact on behaviour or migration ability (Eiler 1990). The process does not require surgery, and requires little fish handling time with faster recovery periods (Ramstad and Woody 2003, Keefer *et al.* 2004). A weakness of gastric implantation is the ability of fish to occasionally regurgitate tags, the rate of regurgitation is difficult to measure (Keefer *et al.* 2004), but where regurgitation rates have been assessed in salmonids, tag retention is high, regularly exceeding 90% as summarised in Table 1.

Table 5.1. Literature derived tag retention rates of salmonids with oesophageal implanted radio tags in both laboratory and field studies.

Species	Number of fish in study	Retention rate (%)	Trial Duration (d)	Study Site	Reference
Sockeye Salmon	89	98	15 – 33	Net pens	(Ramstad and Woody 2003)
Sockeye Salmon	33	100	1	Holding pen	(Canada *et al.* 2005)
Spring - Summer Chinook Salmon	838	97	NA	Field (Columbia River)	(Keefer *et al.* 2004)
Atlantic Salmon	20	100	23 - 139	Field (Upper Rhine)	(Gerlier and Roche 1998)
Atlantic Salmon	27	85.2	21-90	Field (River Tweed)	(Smith *et al.* 1998)
Atlantic Salmon	127	91	105	Field (River Umeälven)	(Rivinoja *et al.* 2006)
Atlantic Salmon	243	93	133	Field (River Umeälven)	(Lundqvist *et al.* 2008)

Extrapolating the data in this study, and utilising a cautious estimation of tag loss by regurgitation, it is possible to make some inference about the fate of tagged fish where this is not certain. Using a conservative estimation of 10% tag loss by regurgitation, 12 of the 42 fish, where fate was uncertain, may have regurgitated tags (although no regurgitated tags where detected). Poaching within the Foyle catchment is known to be relatively high; the number of nets seized in 2011 alone equates to one third of the two year total of fish poaching incidents reported to NWCU for the whole of the UK (National Wildlife Crime Unit (NWCU) 2013). In addition, illegal net seizures appear to be geographically clustered around the release location of fish in 2013 (Fig. 5.1C). Given the evidence of the lack of predation and angling pressure, combined with heightened poaching pressure around the release location (Fig 5.1C), it would not be unreasonable to attribute the fate of the 30 remaining unknown tags to removal from the system via illegal means. In doing so this would give an upper estimation of the exploitation as a result of illegal poaching at 37%.

5.4.1. The consequences of illegal poaching for management

Non-compliance in fisheries management is un-avoidable and is likely to occur at varying extents across all fisheries. Quantifying this exploitation through illegal methods is essential in creating greater accuracy and robustness to fisheries management models. Until now there has been little, if any, quantification of the numbers of fish removed by illegal netting activities. It has been shown here that a minimum of 12% of fish are lost to illegal netting activities, but the evidence suggests that this figure may in fact be as high as 37%.

Using historical fish counts, combined with rates of illegal exploitation it is possible to estimate the number of fish removed from the population of returning migrants illegally. Two logie resistivity fish counters installed at a river barrier (Fig 5.1C [RB]), count returning adult fish entering the Mourne system. These counts are used as a major component part of an adaptive fisheries management protocol for the Foyle. Combining these counts with known exploitation rates it is possible to estimate the numbers of fish being removed by illegal netting practices.

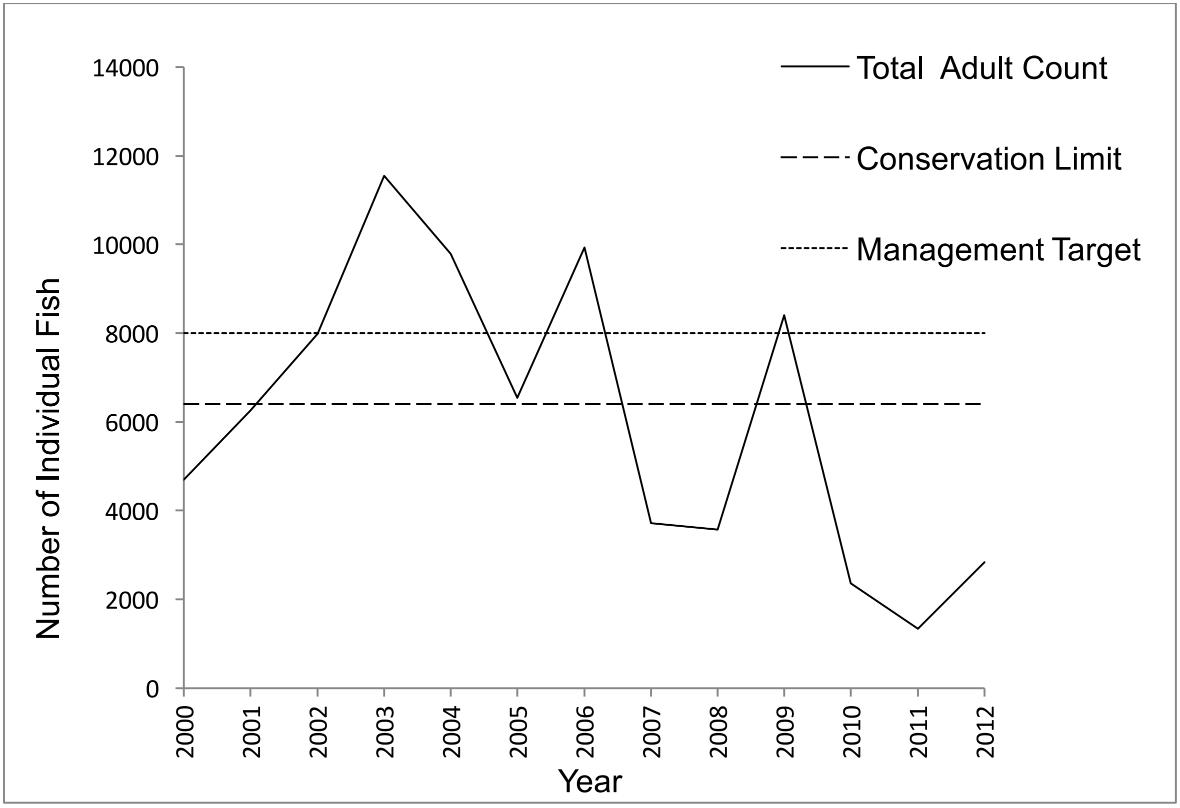

Figure 5.2 Numbers of returning adult Atlantic salmon recorded by logie resistivity fish counters sited at a weir on the River Mourne (Fig. 5.1C[RB]). Data from Loughs Agency (Loughs Agency 2016)

Due to the vast majority of illegal netting taking place downstream from the fish counters, and little evidence of fish removal occurring upstream (although it is likely to occur) it is reasonable to assume that the number of fish being counted is actually a reduced number of the initial population entering the Foyle due to the illegal netting pressure (hence removal of fish) taking place prior to these fish being counted.

In 2013, 12% of fish were removed from the system as a direct determined effect of illegal netting, with the remaining 88% of the initial salmon population entering the Foyle available for counting at the fish counters. Using past fish counts, and a conservative assumption of a 12% illegal exploitation rate within each year, an average of 850 (range = 187 – 1611) salmon per annum (2000-2012) are being lost prior to fish reaching fish counters where management targets are calculated (Fig 5.2). This number may be much higher, if the actual rate of poaching is closer to the inferred 37%, would results in an average of 3,500 (range = 788 – 6782) fish lost per annum.

The ecosystem services provided by Atlantic salmon has overwhelming economic benefits, salmon and sea trout (*Salmo trutta*) angling in Scotland is estimated to contribute £87m per annum in expenditure to the economy (The Scottish Government 2013). There is a lack of literature available concerning the value of an individual salmon to a river system; however Butler *et al*, (2009) calculated that each rod caught salmon within the Spey catchment (Scotland), on average, contributed £970 to household incomes. Using this value, combined with the number of fish removed from the returning population through poaching (12%) equates to a loss of £866,000 per annum to the economy of the Foyle catchment, worryingly this figure may be as high as £3.4 million (37% poaching rate) depending on the exact poaching rate and numbers of returning wild Atlantic salmon (Fig. 5.2). Although the monetary value of a fish within each system is likely to vary considerably, these figures emphasize the wider impact illegal exploitation has on wild fisheries and how it may indirectly effect the wider economy. The ability to track radio transmitters both in aquatic and terrestrial environments enables a potential method by which illegal exploitation can be measured, aiding fishery managers and policy makers in protecting valuable wild fish stocks.

Chapter 6

General discussion

The main focus of work presented in this thesis has been to study the impacts of small scale riverine barriers on the migration, both downstream (Chapter 2) and upstream (Chapter 4), of Atlantic salmon. Whilst the impact of large scale barriers, such as hydropower dams and impoundments, is relatively well known and studied, the impact of smaller structures, which by far outnumber their larger counterparts, is lacking. This thesis has begun to fill this knowledge gap and has subsequently challenged the conventional view of the impact of barriers on migrating salmon.

6.1. Observing the unseen

Biotelemetry, the remote collection of data of the physiology, behaviour and energetic status of animals enables researchers to document how undisturbed organisms interact with each other and their environment in real time (Bridger and Booth 2003, Cooke *et al.* 2004). The development of biotelemetry within fishes, specifically the use of electronic transmitters, has provided one of, if not, the most important advances for studying fish migration and behaviour (Lucas and Baras 2000). Electronic tags enable rapid, long-term positioning and identification of fishes in high spatial and temporal resolutions in environments which are in general, in-accessible to human observers (Lucas and Baras 2000). Cooke *et al.* (2013) hypothesise that:

> *"Many meaningful gains in conservation and management will likely be ascribed to electronic tagging innovations in freshwater in the next 10 to 20 years, and we expect novel discoveries relating to fundamental animal and environmental biology."*

Results of telemetry studies often produce dramatic results exposing previously unseen behaviour or outcomes which challenge the popular train of thought (Lucas and Baras 2000, Bridger and Booth 2003, Jonsson and Jonsson 2009, Cooke *et al.* 2013). Using telemetry we can observe that which was previously unseen.

The behaviour of salmon as they arrive at a barrier is not consistent, a single barriers' effect on delay, mortality and even behavioural response invoked in a fish, varies from one structure to the next (Lundqvist *et al.* 2008, Lucas *et al.* 2009, Gauld *et al.* 2013). Riverine barriers are consistently correlated with mortality of downstream migrating fish (Thorstad, *et al.* 2012, Gauld *et al.* 2013). In this thesis however, I have shown that, in contrast to previous literature, cumulative small scale barriers have negligible impact on the downstream migration of smolts (Chapter 1). It is evident that some barriers have a far greater effect (Thorstad *et al.* 2012, Gauld *et al.* 2013, Moore *et al.* 2013) than others (Chapter 2), leading to the general conclusion that there is considerable variability in the effect of barriers on fish movements and thus one conclusion of the study presented here is that we should approach each one individually in terms of its impact on migration. It is possible that the presence of, and density of predators is a key factor which, combined with the local effect of the barrier (in terms of delay) will ultimately determine mortality at the structure itself.

Previously, the behaviour of returning adult Atlantic salmon on approach to, and below, small low head structures was unknown. The study presented here has shown that adult salmon exhibit a great amount of searching at riverine obstacles, chapter 4 indicates that numerous up and downstream movements occur prior to a successful passage and that these occur despite apparently viable passage routes being available. Thus a conclusion of this study may be that barriers or passage routes which initially seem passable are in fact not. As reported in chapter 4, salmon may not always take, what appears to be, the easiest option for passage, indeed the majority of fish in chapter 4 ascended across what was considered the toughest passage route as assessed by a barrier assessment methodology (SNIFFER 2010). When barriers are assessed for their passability, the 'easiest' route option is used to determine passability. In reality, the effect of any given barrier is far more complex than a simple passage efficiency score. There are still many unknowns as to the effect of barriers on upstream migrating fish, such as delay and increased energy expenditure.

Until now there has been a general lack of comparison of results from empirical studies on fish passage at barriers with natural un-impeded or un-impacted migration. Indeed chapter 2 is the first study to recognise that migration, in river sections with barriers, should not rely on comparisons with river sections without barriers to test for the impact of such structures. I argue here that migration along the river length as whole should be investigated to test the true effect of instream structures. A scientific control enables researchers to identify a baseline against which a treatment may be tested, in river barrier studies the treatment (e.g. the presence of river barriers) should be tested against a control (e.g. no river barriers).Since fish migrating in natural, un-impacted systems appear to reduce migration speed within pools and impoundments created by riffle pool sequences equivalent to the delay recorded above instream barriers (Chapter 2), it is only by comparing migration across the river length as a whole that a true effect can be determined. This is supported by the data presented in chapter 2, which demonstrate that there was no difference in travel speeds, mortality or delay across the entire river length, between the impacted (seven barriers over 50km) or un-impacted (absent of river barriers) systems. To sufficiently appreciate the effects of small scale river barriers on fish migration there is a requirement to first understand the effects of natural impediments, only then is it possible to identify the impacts such structures have on migrating fish.

In chapter 4 I showed that upstream migrating salmon were delayed at a low-head river barrier for on average 48 hours, this is a relatively short period of time in terms of the entire migration duration. Despite this, we still do not understand what the effect of the delay might be (Thorstad *et al.* 2008). There are a number of very specific questions that we still do not know the answer to: Firstly, if this is an irregular length of delay, do fish in rivers without barriers rest in pools for short periods of time before continuing their upstream migration? Karpinen *et al.* (2004) report that rapids may delay migration within the River Tana. Secondly, is there a consequence of such a delay in terms of reproduction? A fish may have multiple attempts to ascend a barrier and search for a passage route, expending energy which cannot be recovered and used in reproduction, or is this delay negligible, having no effect what-so-ever on the overall fitness of fish?

An interesting question is: Is it possible that barriers are creating a contemporary selection pressure on salmon? As is eluded to in Chapter 2 and 4, the generation time of salmonids is likely to enable a relatively fast evolutionary response, for example some riverine barriers which cause a velocity impediment may be, over time, selecting for larger fish which have greater swimming ability and as such are able to swim through the high velocity current.

Similarly a depth barrier may select for smaller fish, which are able to transcend through shallow water due to their smaller body depth and caudal fin size. There is evidence to suggest alterations in selective regimes may occur within 6-15 generations in salmonids following implementation of hydroelectric dams or fish ladders (Haugen *et al.* 2008, Fraser *et al.* 2011). It has previously been reported that successful fish passage has a significant negative size-selective influence on upstream migrating Atlantic salmon with larger fish consistently less likely to successfully ascend hydro-electric dams (Sigourney *et al.* 2015). Data presented in chapter 4 supports this position and suggests that selection may be occurring at much smaller riverine obstacles, and not those which are at the upper limits of salmon swimming ability. The river barrier (in chapter 4), which in general presented a swim obstacle to fish, delayed larger fish for a significantly longer period of time than smaller fish. Kinnison *et al.* (2016) demonstrate that the cost of migration is not only at the expense of tissue energy reserve, but also a cost in ovarian investment expressed through reduced egg size. Greater delay exposes fish to predation/angling pressure and increased energetic expenditure. This may ultimately reduce their reproductive fitness or remove them from the gene pool all together. Sockeye salmon have been shown to be predisposed at the beginning of their migration to their fate (success or failure), statistical analysis revealed that in successful fish, 88 genes were expressed at greater levels than those which perished on their migration (Cooke *et al.* 2008). Genetic profiling indicated survivors expressed 88 genes at a higher level than mortalities, suggesting individuals die due to a variety of physiological reasons, whereas those which survive have a common physiology (Cooke *et al.* 2008). It can be hypothesised that successful passage may partly be a result of their genetic make-up, again providing evidence for the anthropogenic selection of salmon which are able to ascend barriers.

Due to the variation in behaviour, survival, passage success, and delay shown across weir structures, the implications for fish passage are complex. Evidence within this thesis suggests that passage itself should be assessed independently on a site by site basis. If fish are delayed slightly, and there is very little predation, there is, potentially, little cause for concern. Similarly, because a fish pass is present, it does not mean that fish will utilise it, the easiest route may not be the one always preferred by the fish. A complex web of variables such as flow, fish species, habitat types interact temporally, combinations of which vary across sites thus creating barrier impact variability.

One additional insight that emerges from this thesis, is that of the illegal exploitation of fisheries. The ability to estimate illegal exploitation is highly problematic due to, by its definition, being hidden. The added advantage of radio telemetry is its ability to work both in and out of water, hence it is possible to accurately locate a tag either within the aquatic or terrestrial environment. Manual, bankside tracking enabled us to locate tags which had been placed inside, in fields, and sometimes hedgerows alongside roadways strongly suggesting that these had been discarded by illegal activities, the ability to identify the extent of illegal exploitation is rare but invaluable for fishery managers. By releasing a known population of tagged fish into the wild and being able to directly identify their fate through location of the tag has, for the first time, given an insight into the extent of illegal exploitation in the River Foyle. Here I show that the illegal exploitation has potential to negatively impact stocks and ultimately the wider economy. One outcome of the work presented here is that radio telemetry may ultimately be an effective way of determining illegal exploitation rates and aid in prosecution of illegal activities. That fact that a tag can tracked continuously, and relatively easily, justifies its use as a method which, although costly, has the potential to aid in the protection of a highly valuable species.

6.2. Effect of telemetry

A limiting factor in telemetry studies, for fishes, is the fish size relative to transmitter size which currently limits use of the technique on small species and very early life stages. There are three key elements which must be considered when selecting a transmitter for any study; the ping rate of the signal, the transmitter size and battery life required. Each of these elements directly impacts the other, for example a high ping rate uses more power than a low ping rate thus battery life is reduced. To increase battery life more batteries must be added to the transmitter, increasing transmitter size. Ultimately there is a trade-off between the three elements which determine the transmitter suitable for any given study. The primary driver of this selection process is the size of fish which the transmitter is destined for. Although transmitters have been miniaturised there remains a minimum size limit to the fish which can be utilised in telemetry studies. In fishes, the '2% rule' proposed by Winter (1996) has been frequently accepted as a 'rule of thumb' for maximum tag mass to body mass ratios in fish telemetry. The impact of tagging and handling of fish for telemetry studies is regularly questioned (Jepsen *et al.* 2015). A major assumption of telemetry studies is that tagged fish behave and respond in the same way as untagged fish (Zale *et al.* 2005, Drenner *et al.* 2012). It is virtually impossible to test this in the wild since it is not possible to monitor an untagged fish with the same frequency or accuracy as a tagged individual. Currently there is a bias in smolt migration studies to utilise larger individuals which reduces tag mass to body mass ratios, ultimately in these kinds of studies, the tagged population is thus not representative of the study population as a whole (Chapter 3). As shown in chapter 3, it is possible to tag smaller smolts representative of the whole population with acoustic transmitters. If telemetry studies are to accurately represent wild fish behaviour there is a requirement to move away from the 2% rule of thumb towards a more practical and species specific criteria. For example, it may be more important to investigate the effects of buoyancy on tagged individuals or the relative volume of the tag. A fish maybe required to work harder to maintain the desired swimming depth with a high density tag compared to that of a lower density. Tag volume may also limit the efficiency of the swim bladder due to reduced space within the body cavity. With the interpretation of result of telemetry studies there must be an acceptance of the relative unknown effect of the tag on behaviour, however the value of data from such telemetry studies, in general, far outweighs the arguably minimal effect of the tag and its attachment method. In chapter 4, fish which initially ascended through the fish pass, were tagged and subsequently released downstream did not ascend through the pass a second time. Have these fish associated the tagging and release downstream as an impassable passage route? Although not previously reported, this response may highlight a learned effect, where an impassable route was identified by the fish and thus attempted passage via a different route choice. This may have severe consequences for studies where fish are recruited from fish passes. If a fish associates this return downstream following tagging as a failed attempt its subsequent behaviour may not be representative of natural behaviour. Telemetry studies investigating barriers and fish passage should use barrier/pass naïve fish so that their behaviour at the obstacle in question is not compromised.

6.3. The need for small scale barriers

Energy security and a developing understanding of environmental awareness continue to enhance the diversification and development of energy supplies (Johnson *et al.* 2014). The department of Energy and Climate change indicate that there is ample opportunity for the development of small scale hydropower schemes (Department of Energy and Climate Change 2013). Small scale hydro is in most cases 'run-of-river' where channel obstructions such as weirs stabilise water levels enabling a proportion of the flow to be diverted away from the river channel into turbines before it is returned back to the main channel further downstream. With an estimated 20 – 30 thousand weirs in UK alone there is significant potential for small scale hydropower developments (Driscoll 2008, Johnson *et al.* 2014).

Although chapter 2 and to a certain extent chapter 4 indicate a relatively low, direct impact on salmonid migration, this does not suggest such structures are suitable for use within hydropower schemes or in water abstraction systems. In river structures also prevent the downstream movement of: sediment, organic matter, nutrients aquatic species and plant propagules as reviewed in detail by Anderson *et al.* (2015). Indeed there are extensive regulations available regarding the placement and development of small scale hydropower facilities (SEPA 2015). The change in use of a structure will likely alter the flow dynamics and thus the behaviour of fish at that obstacle. Legislation aims to increase passage ability of barriers when hydropower projects are designed and consented (SEPA 2015), however, as shown in chapter 4, the presence of a fish pass, or suitable passage channel does not indicate fish's desire to use it successfully. Considering the evidence suggesting that a long term selection pressure of barriers on fish exists, it is likely that all riverine barriers, even those with fish passes have a negative impact on fish populations. The need for 'green' energy is ever increasing, as such hydropower development will continue at the cost of ecology. There is a clear need for further research on small scale barriers which may enable more suitable hydropower development with minimal impact to ecology. There are still many unanswered questions regarding the effects of 'run-of-river' hydro schemes on fish populations, although research is being conducted, it is at a far reduced rate compared to the development of hydropower schemes.

6.4.Future Research

Physiology and energetics are fundamental to migrations, the understanding of these through non-lethal biopsies and conditional assessments, whilst combined with telemetry will allow for an understanding in the failure and success of populations (Cooke *et al.* 2008). These techniques do not allow for real time analysis of data, however they do provide insight into the condition of the fish at the time of release, coupling this data with positional behaviour and movement will allow for hypothesis to be tested in relation to condition, behaviour and fate (Cooke *et al.* 2008). Adult Atlantic salmon rely on energy reserves built up within the marine environment, highlighting a potential for fitness costs to be acquired through slow passage. The hypothesis, that delay at river barriers influences individual fitness remains unanswered. By determining how migration behaviour below river barriers relates to the overall fate of an individual is imperative to understanding how widespread and how cumulative these effects maybe on/in the ecology of adult anadromous fish.

In order to provide successful management tools to aid in the migration of Atlantic salmon there is a clear requirement for mechanistic understanding of how initial traits, condition, behaviour and environmental conditions interact and ultimately determine migration success and reproductive ability (Caudill *et al.* 2007). The possibility of telemetry studies following biopsied fish is simple, with the insight into links between fate and physiology being invaluable (Cooke *et al.* 2008).

> "*The coupling of telemetry and genomics is going to yield unprecedented information on migration biology of fish*"
>
> (Cooke *et al.* 2008)

As with most studies, there are frequently as many questions generated as are answered. Here I try to define what I think are the main unanswered questions related to salmon migration around low head barriers.

1. What is the post migration effect of delay?
    - We know delayed fish have increased exposure to predation, disease and angling, however we do not know how increased energy expenditure impacts on migration and/or reproductive success.
2. The effect of (more) small scale riverine barriers on the migration of Salmonids
    - Chapter 4 is the first study to identify, in detail, the behaviour of returning adult Atlantic salmon to a complex weir structure, Chapter 2 challenges previous work on downstream migration and presents data that contradicts previous theory. Given the diversity of barriers, fish passes, fish physiology the results of many studies are often difficult to apply on a broader scale. A wider understanding at a greater number of obstacles will help in identifying potential behaviour of migrating species.
3. The effect of riverine barriers on non salmonid species
    - Salmonids, due to their economic value, attract greater research than other fish. However many other fish species migrate, if only over a small scale, however their ability to ascend structures or need for longitudinal connectivity remains unknown.
4. The use of more specific, genetic markers, to determine if migration success and the ability to pass obstacles is indeed related to genomic and physiological make-up
    - Are fish pre-disposed to passage failure or success at riverine barriers.

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Chapter 7 Appendix

R – code used in model forumaltion of chapter 5

Model 1: Passage success on first attempt

```
library (glmulti)

library (lme4)


# create a function for glmulti to act as a wrapper for glmer:


glmer.glmulti <- function (formula, data, random = "", ...) {

  glmer(paste(deparse(formula), random), data = data, REML=F, ...)

}


# run exhaustive screening with glmulti:

# ‘level’ - If 1, only main effects (terms of order 1) are used to build the candidate set. If 2, pairwise interactions are also used (higher order interactions are currently ignored).

bab <- glmulti(Pass~searchtime * mean.search.flow * zone.time *

mean.search.temp * length * Fat * mean.search.temp.status * Sex *

mean.search.flow.status * aerial5 * aerial6, data=DF1, family = binomial, level = 1, fitfunc = glmer.glmulti,

random = "+(1|Year)")


# After 2100 models:

# Best model: Pass~1+searchtime+zone.time+length+Fat+aerial5+aerial6

# Crit= 36.0014333715536

# Mean crit= 42.0187026373684

# Completed.
```

```
# plot relative importance of model terms

# The importance value for a particular predictor is equal to the sum of the weights/probabilities for the models in which the variable appears.

# This generates figure 4.5


par(mfrow=c(1,1))

par(mar=c(4,8,2,1))

plot(bab, type = "s")


# Get model weights from all models within 2 AIC units of the ‘best’ model

# and identify competing models


tmp <- weightable(bab)

tmp <- tmp[tmp$aic <= min(tmp$aic) + 2,]

tmp


# Calculate evidence ratio

head(tmp$weights,1)/tail(tmp$weights,1)


# Construct the ‘best’ model and determine significant terms using (drop 1)

M1 <- glmer(Pass ~ searchtime+zone.time + length + Fat + aerial5 + aerial6 + (1 | Year),

        data = DF1,

        na.action = na.omit,

        family = "binomial")


drop1(M1, test = "Chi")
```

```
# confirm drop1 results using anova and single term deletions. Also obtain P- values


# construct final model with only significant terms
M2 <- glmer(Pass ~ zone.time + length + Fat + (1|Year),
     data = DF1,
     na.action = na.omit,
     family=binomial)


# Construct a 'NULL' model
M2a <- glmer(Pass ~ 1 + (1|Year),
      data = DF1,
      na.action = na.omit,
      family=binomial)


# Construct models with single term deletions
M2b <- glmer(Pass ~  length + Fat + (1|Year),
      data = DF1,
      na.action = na.omit,
      family=binomial)
M2c <- glmer(Pass ~  zone.time + Fat + (1|Year),
      data = DF1,
      na.action = na.omit,
      family=binomial)
M2d <- glmer(Pass ~  zone.time + length + (1|Year),
      data = DF1,
      na.action = na.omit,
      family=binomial)
```

```
# Likelihood ratio tests using anova
anova(M2a,M2)
anova(M2b,M2)
anova(M2c,M2)
anova(M2d,M2)
```

Model 2: Search time at the weir

```
library (glmulti)
livrary (lme4)

# Create a function for glmulti to act as a wrapper for lmer:

lmer.glmulti <- function (formula, data, random = "", ...) {
  lmer(paste(deparse(formula), random), data = data, REML=F, ...)
}

# Run model selection through glmulti

bab <- glmulti(log10(searchtime) ~ zone.time * length *Sex* Fat * mean.search.flow
        * mean.search.temp * attempt * mean.search.temp.status * SD.search.temp*
        mean.search.flow.status,data=pass, level = 1, fitfunc = lmer.glmulti,
        random = "+(1|Year)")

summary(bab)

# After 1050 models:
```

```
#   Best model: log10(searchtime)~1+mean.search.flow
# Crit= 30.0987641663189
# Mean crit= 32.5728518667363
# Completed.


# Get model weights from all models within 2 AIC units of the ‘best’ model
# and identify competing models


tmp <- weightable(bab)
tmp <- tmp[tmp$aic <= min(tmp$aic) + 2,]
tmp


# Calculate evidence ratio
head(tmp$weights,1)/tail(tmp$weights,1)


# Plot relative importance of model terms
# The importance value for a particular predictor is equal to the sum of the
weights/probabilities for the models in which the variable appears.
# This generates figure 4.6


par(mar=c(4,8,2,1))
plot(bab, type = "s")




# Likelihood ratio tests to determine significance of final model.
# test against a ‘NULL’ model
```

```
M1 <- lmer(log10(searchtime) ~ mean.search.flow + ( 1 | Year),
        data = pass,
        na.action = na.omit)

M1a <- lmer(log10(searchtime) ~ 1 + (1 | Year),
        data = pass,
        na.action = na.omit)

anova(M1a, M1)
```