A test of the cumulative effect of river weirs on downstream migration success, speed and mortality of Atlantic salmon (*Salmo salar*) smolts: an empirical study

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Running Title: Downstream migration success of Atlantic salmon smolts

Abstract

This study investigated the cumulative impact of weirs on the downstream migration of wild Atlantic salmon *(Salmo salar)* smolts in the River Foyle, Northern Ireland. In spring of 2013 fish were released in two tributaries of similar length; one tributary (impacted) had seven low head weirs along the migration pathway and the other was devoid of such structures (un-impacted). Salmon smolts fitted with acoustic transmitters were monitored via a passive acoustic telemetry array during downstream migration. In 2014 the study was repeated only in the impacted tributary. Overall freshwater survival rates were high (>94%). There was no significant difference in mortality, movement pattern, delay or travel speeds between rivers or between years at any phase of migration. Escapement of salmon smolts through Lough Foyle (a marine sea lough) to the open ocean was low, approximately 18% in each year. Escapement did not differ between impacted and un-impacted rivers. This study showed no post-passage effects of weirs on mortality, migration speed or escapement of downstream migrating smolts. This suggests that the elevated mortality at low head obstacles described 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. Causes of apparent high mortality in the early part of marine migration in this study, are unknown; however similar studies have highlighted the impact of fish predators on smolts.

Key Words: *Salmo salar*, Habitat fragmentation, River barriers, Downstream migration, Survival

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, Kehler, Bourne, & Wiersma, 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 migrate 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 that in England and Wales alone there are 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 because of the numerous environmental and biological variables that may influence passage. The 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's biology. Passage at small scale barriers is likely to be highly temporal and defined by 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 a few 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 the 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 during passage through hydropower turbines is regularly reported (Hvidsten & Johnsen 1997; Thorstad et al., 2012a). It is also possible that physical damage of fish occurs from downstream passage of over-spill weirs, through contact with the weir face or stream bed due to hydraulic forces present at such structures. This impact, not necessarily causing instant mortality, may result in a delayed response, affecting individuals during the later 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 have been shown in downstream migrating anadromous trout *(Salmo trutta)* smolts over a single low head weir of 3m in height (Gauld et al., 2013). This study showed mortality rates of between 9% and 44% of tagged fish associated with a single weir and that the mortality rate was highly dependent upon flow rate. Even mortality rates from the lower end of the range recorded by Gauld et al., (2013), point towards a potentially high cumulative loss over several low-head obstacles 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 commonly expressed (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 upon survival through increased exposure to predation risks (Jepsen et al. 1998; Koed et al. 2002). A number of studies on salmonids indicate a positive 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. 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. The study presented here, used acoustic telemetry and a comparative approach to compare seaward migration of Atlantic salmon smolts in adjacent tributaries: one with no man-made obstacles; the second with seven, low head, man-made obstacles in series.

It was hypothesised that the cumulative effect of low-head, but passable, barriers would be to reduce travel speed, increase mortality rate and lower escapement success of seaward migrating Atlantic salmon smolts, by comparison to those in a neighbouring river without such obstacles.

Methods

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 4450 km^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 single fish counting weir (between F4 and F5), the form of which has been shown to have no impact on upstream fish movement (Smith, Johnstone, & Smith, 1997). In contrast, the second major tributary, the River Mourne, has seven man-made low-head overspill weirs along its length (Fig. 1, Table 1). All barriers span the complete river width and had water flowing over them continuously during the study period (albeit the depth varied with time). Here the Rivers Finn

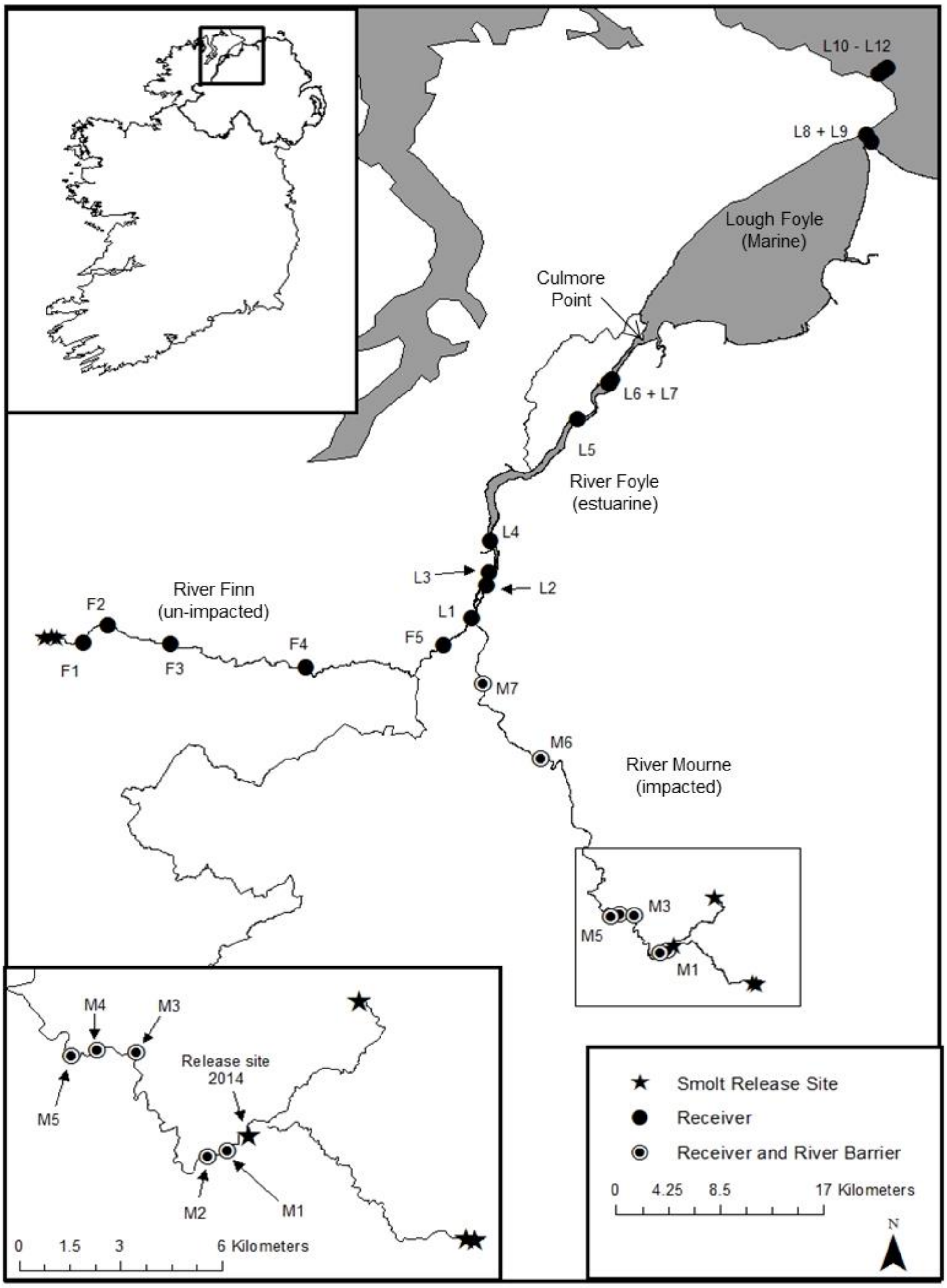

Figure 1: Location of the Foyle catchment in Ireland, on the border between Northern Ireland and the Republic of Ireland (top left). Automatic listening station (ALS) deployment throughout the catchment is presented in the main map. Bottom left is a larger version of the headwater of the impacted river 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).

and Mourne will be referred to as ‘un-impacted’ and ‘impacted’ rivers, respectively. 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.

Smolt capture and tagging

This study was conducted across two years. In 2013 fish were tagged in both the impacted and un-impacted rivers. Unexpectedly (*cf* literature, see above), in 2013, freshwater survival was high in the impacted river and there was no significant difference in travel speeds in freshwater between the impacted and un-impacted rivers. Therefore, in 2014, to determine if the same pattern held, the study was repeated in the impacted river. Due to resource limitations, tagged fish were released only in the impacted river.

In 2013, salmon smolts were captured by electro-fishing in the upper reaches of both rivers between the 14^{th} and 15^{th} April. Due to technical problems, salmon smolts were captured by rod and line in April 2014. Smolts were placed into a holding tank filled with aerated river water. Fish large enough for tagging (>15g) and which were also clearly smolting, were anaesthetised with clove oil (0.5mg per litre); mass (g) and fork length (FL, 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 weight in air, Thelma Biotel AS, Trondheim, Norway [2013], or Model V7-2x, 7 mm diameter, 18 mm length, 1.4 g weight 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. 1).

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 July of each year, after the migration period and the expected tag life had been reached. Six ALS were positioned in the impacted river (M1 – M7), each located slightly upstream from a river obstacle (Fig. 1). All such structures were over-spill sloping weirs, apart from M1 which comprised a degraded historic weir and a series of rapids and M6, a vertical weir. Barriers ranged from 0.75-4.3m head height (Table 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. 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 receiver coverage at each location, providing a detection gate through which tagged individuals had to pass. More specifically at ALS L8 and L9 (Fig.1), to ensure detection coverage was adequate to detect passing tags, 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 for 1500m by a drifting boat (engine off) to test for acoustic breaches, this was repeated four times. Data from this exercise identified an effective acoustic range of 450m and thus receivers were deployed to create overlap in the detection ranges of ALS L8 and L9. Tag failure rate reported by manufacturers (Vemco, Thelma) is low (<2%). For Thelma tags of the same model used here Gauld et al. (2013) reported control tag failure rates of 0% in field tests. 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. 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 or 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, Hansen, Quinn, & Saunders, 1998). Successful estuarine migration is defined here as 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 (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 (early marine mortality).

Freshwater travel time of smolts was calculated as the time between the last detection at receiver M1 or F1, and first detection at the estuarine receiver L4 (M7 in 2014). Estuarine travel time was calculated as the time from 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 was thus conducted both spatially, within one year (impacted vs un-impacted, 2013) and temporally (impacted 2013 vs impacted 2014).

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 kilometre by kilometre basis and migration speed in km.d^{-1} to reflect this variation.

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 (Fig. 3).

Statistical Analysis

All analysis was performed using R statistical software programming. Welch-t-tests were used to test for differences in fork length between populations. Normality of data was confirmed using a Shapiro Wilks test. Where normality was not confirmed or assumptions of t-tests not met, Wilcoxon Mann-Whitney rank sum tests were performed. Wilcoxon Mann-Whitney rank sum tests were also performed on differences in delay times between rivers and speed of travel due to some observations highly skewing the mean observation. Fisher's exact tests were used to determine if the observed frequencies of mortalities was different from expected frequencies between years, rivers and phases of migration. Analysis of variance (ANOVA) was used to determine differences in delay by fish between each of the barriers, data were log transformed to meet assumptions of normality, confirmed by Shapiro Wilks test. A Levene's test was used to determine the differences in variances of freshwater migration speed between impacted and un-impacted rivers.

Results

Sixty eight fish were tagged during the study period: impacted 2013, n = 20, (mean fork length [FL] = 144.3 ± SD 9.1, mean mass [M] = 31.3 ± SD 4.9g) un-impacted 2013, n = 19, (mean FL = 132.2 ± SD 10.8, mean M = 24.8 ± SD 6.3g), impacted 2014, n = 29, (mean FL = 135.2 ± SD 27.3, mean 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,) but no difference in length between years (t = 1.49, p= 0.14, d.f. = 46.9) (Table 1). Data from the ALS receiver array was used to estimate survival for all fish over multiple sections along their migration. Data from ALS M5 were removed from the analysis because acoustic noise severely reduced 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 2013 (85%, n = 17) in 2013. There was no difference in fork length or tag mass to body mass ratios between fish detected within the array and those not detected. The exact fate of undetected fish cannot be directly determined. No smolt was detected at a downstream receiver which was not previously detected at an upstream receiver

Total escapement (survivorship of fish from first upstream detection zone [M1, F1] to the lough exit to the open coast at either L8/L9) of tagged fish in 2013 was 18% (n = 3), and 19% (n = 3) from the impacted and un-impacted river respectively (Fig. 2). In 2014, loss of ALS L8 prevented total coverage of the lough exit and thus full 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 (100% per km, n = 17) was not statistically different (p=0.53, *Fisher's Exact Test)* from the impacted system (99.9% per km) 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 were marginally lower during estuarine migration for tagged fish from both rivers (impacted 2013 = 99.4% per km, un-impacted 2013 = 99% per km) in 2013 (Fig. 2). Significantly lower survival ($p < 0.01$, *Fisher's Exact Test*) occurred in the early marine phase of migration (L6 + L7 to L9) in both rivers (impacted 2013 = 97.4% per km, un-impacted 2013 = 97.5% per km) and years (impacted 2014 = 97.3% per km), than in the freshwater and estuarine phase (L1/F1 to L6 + L7 [Fig. 2]).

Migration Delay

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. Mean delay per fish in 2013 was not significantly different 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) (Wilcoxon-Mann-Whitney, $W = 159$, $p = 0.86$). Mean delay in 2014 in the impacted river (n = 12, median = 0.5hr, range = 0-72.5hr) was not significantly different than in 2013 ($W = 84$, $p = 0.44$). Total Delay (sum of delays at individual receivers, per fish) at some individual obstacles (Table 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 between 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, creating outliers that exaggerated the mean delay time from that measured for other fish (Table 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).

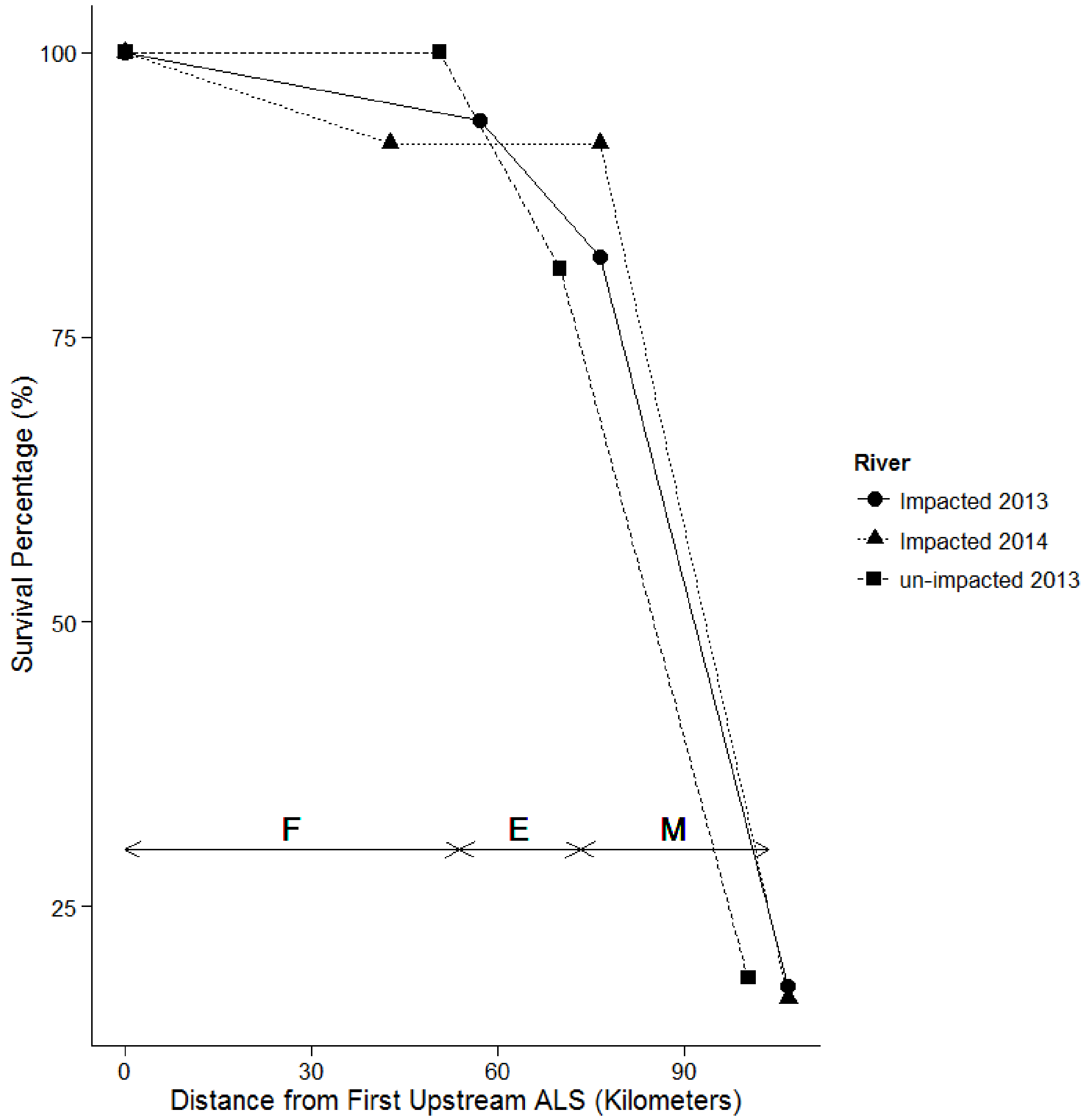

Figure 2: Survivorship curve of tagged salmon smolts from the three release groups. Survivorship is calculated for freshwater (F), estuarine (E), and early marine (M) elements of the migration. Distance 0 is the most upstream ALS with distances calculated downstream from this point.

Table 1: Summary of obstacle type with mean and median time of fish detected at ALS deployments across the study period. Time is not calculated at M5 due to receiver being compromised by excess noise.

Station name	**Obstacle type**	**Head height (meters)**	**Mean (Median) delay (Hours)**	
			2013	**2014**
F1	N/A	N/A	0.06 (0.02)	NA
F2	N/A	N/A	0.17 (0)	NA
F3	N/A	N/A	0.18 (0.008)	NA
F4	N/A	N/A	0.08 (0.08)	NA
F5	N/A	N/A	1.97 (0.38)	NA
M1	Broken weir above rapids	4.3	1.18 (0.05)	6.17 (0.06)
M2	Sloping Weir	0.75	18.86 (0.07)	5.48 (0.16)
M3	Sloping Weir	1.89	0.18 (0.14)	0.56 (0.31)
M4	Two sloping weirs approx. 30 meters apart	1.5+ 0.75	0.15 (0.11)	6.21 (0.97)
M5	Over spill weir	0.75	NA	NA
M6	Vertical weir	1.2	0.07 (0.07)	0.04 (0)
M7	Sloping weir	3.4	0.86 (0.22)	0.06 (0.03)

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 in the impacted river (mean ± SD, 17.2 ± 22.6, median = 10.6 km.d^{-1}) was not significantly different (Wilcoxon rank sum, W = 145, p = 0.34) to that of the un-impacted river (mean ± SD 6.4 ± 4.4, median = 4.6 km.d^{-1}). One fish travelling at 41.8 km.d^{-1} skewed the mean in the impacted river but was included within the Wilcoxon test. Freshwater ground speed in 2014 was not significantly different to 2013 (Wilcox rank sum, W = 179.5, p = 0.37). A Levene's test indicated no significant difference in variances of ground speed between impacted and un-impacted rivers (F = 3.46, p = 0.07) or between years in the impacted rivers (F = 0.53, p = 0.47).

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 significant 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}.

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. 3).

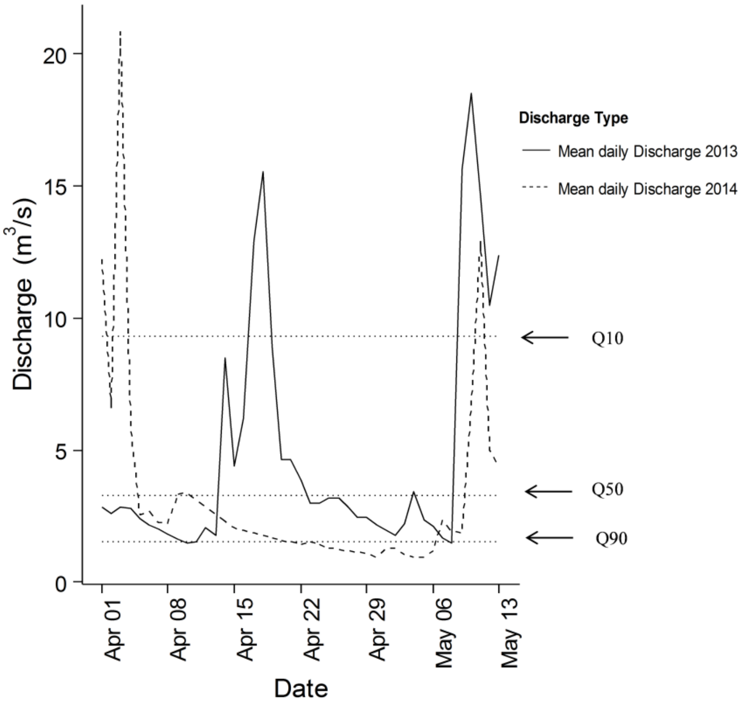

Figure 3: Mean daily flow taken from flow gauging station on the impacted river for 2013 and 2014. Also drawn are flow exceedance percentiles, Q90, Q50 and Q10 flows calculated from mean daily flows of the previous ten years of data during the study period.

Discussion

This study is the first to compare directly downstream wild Atlantic salmon smolt migration in a river impacted by multiple low head obstacles, with a river un-impacted by such structures 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%). There was no evidence of differential survival rates between impacted and un-impacted rivers in the one year where this comparison was possible (2013). Whilst acknowledging the modest sample size, this finding contrasts significantly with a number of other studies that indicate that in-stream obstructions, including low head ones, contribute to smolt mortality and ultimately reduce smolt escapement (Aarestrup & Koed 2003; Thorstad et al., 2012a; Gauld et al., 2013). Similarly, it has been shown recently that survival rates for Pacific salmon (*Oncorhynchus* species) smolts is higher in rivers which lack large hydro-electric dams (Welch et al., 2008). There are a number of environmental conditions that have the potential to impact upon, migrating salmon and it is highly likely that these differ between catchments. Similarly it is highly likely that 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. For example a study in the River Conway, UK, reported survival of 99.4% km^{-1} (Moore et al., 1995); in the River Test, UK, 95% km^{-1} was reported (Moore et al., 1998) and in a meta-study (Thorstad et al., 2012) found survivorship in the range 93% - 99.7% km^{-1}. The barriers in this study appear similar in format (1-3m head height, overspill weirs) to those described by Gauld et al., (2013) yet mortality rates between the two studies contrasts considerably. It is likely local pressures, such as predation, influence survival differentially across catchments. Salmon populations exhibit both ecological and genetic differences between rivers; it is possible that populations might exhibit local adaptations to their the natal water body (Taylor 1991; Heinimaa et al., 1998; Garcia de Leaniz et al., 2007). In this study there were no differences in mortality between smolts migrating from contrasting rivers during the estuarine migration phase. Thus at least in this study there is no evidence of delayed 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. For example in the River Tweed, UK between 19 and 45% was recorded (Gauld et al., 2013); in Nova Scotia, Canada, similar escapement was 39-74% in one study (Halfyard et al., 2012); in the River Lærdalselva, Norway, this was 85% (Urke et al., 2013) and in the Romsdalsfjord System, Norway 35% , (Thorstad et al., 2007). Lough Foyle contains a number 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). Similarly cod and saithe (*Gadus virens*) populations combined were 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 other predator species, such as birds or mammals, or on population numbers of potential predators and their diet. Thus it is difficult to directly quantify the effect of predators on smolt emigration, particularly in areas such as sea loughs and river mouths where predator density is likely to be high and sea migrating smolts may be constrained by geography (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) apparently did not impact on mortality, migration speeds or delay in freshwater migration 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 findings. Slack waters above weirs and dams likely create suitable habitat for predatory behaviour that does not normally occur in fast flowing river stretches. Any delay caused by barriers potentially expose fish to predators for a greater period of time thus increasing exposure to potential predators. Although telemetry tagging effects on fish behaviour can occur (Wilson et al., 2017), in this study if any such effect occurred, it was likely to be expressed equally between impacted and un-impacted rivers as the same method was used. The main findings of this study, that survival was high and not different across sites, suggests no obvious tagging effect. Tag effects from the same study system have been explored in a previous paper (Newton et al., 2016). Taken together and in the context to relevant contemporary literature (Cooke et al., 2011; Jepsen et al., 2008; Larsen et al., 2013; Wagner et al., 2011; Brown et al., 1999; Rechiskey and Welch 2010) we conclude that there was no obvious tagging effect resulting in bias in our study.

Delay and mortality at riverine barriers is regularly reported, however the direct simultaneous comparison of delay in an impacted river to that of a natural system is rare (Thorstad et al. 2012a; 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. Given that the findings presented here run contrary to several other studies, we tested the magnitude of the effect for its proximity to statistical significance. Thus we simulated a sequential increasing differential in the median travel speed between fish from the two groups (in the impacted and un-impacted rivers) to identify the point where the differential is large enough in magnitude to exhibit a statistically significant difference for $P = 0.05$. The result shows that the differential in modified travel speed would need to increase from 0.07 ms^{-1}, almost two fold to 0.12 ms^{-1} to become statistically significantly different. This points to the finding presented here and the conclusions drawn from this as being robust.

Site specific delays can differ significantly between years even when delay throughout the whole system does not. Surprisingly, delay was not different between individual barriers within years despite significant physical differences in barrier construction (Table 1). 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 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 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 kilometre is not dissimilar to that reported in other studies of estuarine and marine migration (Thorstad et al., 2007a). However there is an ever present need for similar telemetry studies with larger sample size and longer time series. In reality, to accurately represent a significant proportion of any smolt population may require thousands of individuals to be tagged due to the vast numbers of downstream migrating juveniles. Although sampling strategies differed between years, the low mortality observed in year 1 (2013) differs substantially from that reported elsewhere and requires some interpretation (Lucas & Frear 1997; Ovidio & Philippart 2002; O'Connor et al., 2006; Gauld et al., 2013). Variation in river flow between years has previously been reported to affect smolt survival (Gauld et al., 2013). Repeating this study in the impacted river, across years, enabled the effect of river flow to be eliminated as the cause of high survival. Resource constraints however did not allow for a complete repetition (by virtue of a lack of a full control group in the un-impacted river) of the previous year (2013), yet the similarities between the data (high survival) suggest that survival within the system was generally high and riverine barriers did not elevate mortality.

Our study raises important questions regarding the migration of Atlantic salmon smolts, in that not all systems with multiple obstacles, although expected to have cumulative effects, may in fact result in elevated mortality. The evidence of this study is 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 wild 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.

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References

Aarestrup, K., & Koed, A. (2003). Survival of migrating sea trout (Salmo trutta) and Atlantic salmon (Salmo salar) smolts negotiating weirs in small Danish rivers. *Ecology of Freshwater Fish*, *12*(3), 169–176. https://doi.org/http://dx.doi.org/10.1034/j.1600-0633.2003.00027.x

Antonio, R. R., Agostinho, A. A., Pelicice, F. M., Bailly, D., Okada, E. K., Henrique, J., & Dias, P. (2007). Blockage of migration routes by dam construction : can migratory fish find alternative routes ? *Neotropical Icthyology*, *5*(2), 177–184. https://doi.org/http://dx.doi.org/10.1590/S1679-62252007000200012.

Baguette, M., Blanchet, S., Legrand, D., Stevens, V. M., & Turlure, C. (2013). Individual dispersal, landscape connectivity and ecological networks. *Biological Reviews*, *88*(2), 310–26. https://doi.org/http://dx.doi.org/10.1111/brv.12000

Baras, E., Lambert, H., & Philippart, J. (1994). A comprehensive assessment of the failure of Barbus barbus spawning migrations through a fish pass in the canalized River Meuse (Belgiurn). *Aquatic Living Resources*, *7*, 181–189. https://doi.org/http://dx.doi.org/10.1051/alr:1994020

Baras, E., & Lucas, M. C. (2001). Impacts of man’s modification of river hydrology on freshwater fish migration: a mechanistic perspective. *Ecohydrology and Hydrobiology*, *1*, 291–304.

Beamish, R. J., Thomson, B. L., & Mcfarlane, G. A. (1992). Spiny dogfish predation on Chinook and Coho salmon and the potential effects on hatchery-produced salmon. *Transactions of the American Fisheries Society*, *121*(Figure 1), 444–455. https://doi.org/http://dx.doi.org/10.1577/1548-8659

Beier, P., & Noss, R. F. (1998). Do habitat corridors provide connectivity? *Conservation*

Biology, *12*(6), 1241–1252. https://doi.org/http://dx. doi.org/10.1046/j.1523-1739.1998.98036.x

Branco, P., Segurado, P., Santos, J. M., Pinheiro, P., & Ferreira, M. T. (2012). Does longitudinal connectivity loss affect the distribution of freshwater fish ? *Ecological Engineering*, *48*, 70–78. https://doi.org/10.1016/j.ecoleng.2011.05.008

Brown, R. S., Cooke, S. J., Anderson, W. G., & Mckinley, R. S. (1999) Evidence to challenge the "2% rule" for biotelemetry. *North Amercian journal of Fisheries Management*, 19, 867 - 871

Caudill, C. C., Daigle, W. R., Keefer, M. L., Boggs, C. T., Jepson, M. A., Burke, B. J., … Peery, C. A. (2007). Slow dam passage in adult Columbia River salmonids associated with unsuccessful migration: delayed negative effects of passage obstacles or condition-dependent mortality ? *Canadian Journal of Fisheries and Aquatic Sciences*, *64*, 979–995. https://doi.org/http://dx.doi.org/10.1139/F07-065

Ceballos, G., & Ehrlich, P. R. (2002). Mammal Population Losses and the Extinction Crisis. *SCIENCE*, *296*(5569), 904–907. https://doi.org/http://dx.doi.org/10.1126/science.1069349

Chanseau, M., & Larinier, M. (1999). The behaviour of returning adult Atlantic salmon (Salmo salar L.) in the vicinity of a hydroelectric plant on the Gave de Pau river (France) as determined by radiotelemetry. In A. Moore & I. Russell (Eds.), *Advances in Fish Telemetry* (pp. 257–264).

Cooke, S. J., & Hinch, S. G. (2013). Improving the reliability of fishway attraction and passage efficiency estimates to inform fishway engineering, science, and practice. *Ecological Engineering*, *58*, 123–132. https://doi.org/10.1016/j.ecoleng.2013.06.005

Cooke, S. J., Woodley, C. M., Eppard, M. B., Brown, R. S., & Nielsen, J. L. (2011) Advnacing the surgical implantation of electronic tags in fish: a gap analysis and research agenda based on review of trends in intracoelomic tagging effects studies.

Reviews in Fish Biology and Fisheries. **21:** 127-151

Cote, D., Kehler, D. G., Bourne, C., & Wiersma, Y. F. (2009). A new measure of longitudinal connectivity for stream networks. *Landscape Ecology*, *24*(1), 101–113. https://doi.org/http://dx.doi.org/10.1007/s10980-008-9283-y

Dall, S. R. X., Bell, A. M., Bolnick, D. I., & Ratneiks, F. L. W. (2012). An evolutionary ecology of individual differences. *Ecology Letters,* 15(10): 1189 - 1198. doi:10.1111/j.1461-0248.2012.01846.x.

Dieperink, C. (2002). Predation on Atlantic salmon and sea trout during their first days as postsmolts. *Journal of Fish Biology*, *61*(3), 848–852. https://doi.org/10.1006/jfbi.2002.2090

Elosegi, A., Díez, J., & Mutz, M. (2010). Effects of hydromorphological integrity on biodiversity and functioning of river ecosystems. *Hydrobiologia*, *657*(1), 199–215. https://doi.org/10.1007/s10750-009-0083-4

Environment Agency. (2009). *Response to DEFRA consultation: Modernisation of salmon and freshwater fisheries legislation; new regulatory order to address the passage of fish (for WFD and EU eel regulation).*

Friedland, K. D., Manning, J. P., Link, J. S., Gilbert, J. R., Gilbert, a. T., O'Connell, a. F., & O'Connell-JR, A. F. (2012). Variation in wind and piscivorous predator fields affecting the survival of Atlantic salmon, Salmo salar, in the Gulf of Maine. *Fisheries Management and Ecology*, *19*(1), 22–35. https://doi.org/10.1111/j.1365-2400.2011.00814.x

Garcia de Leaniz, C., Fleming, I. A., Einum, S., Verspoor, E., Jordan, W. C., Consuegra, S., … Quinn, T. P. (2007). A critical review of adaptive genetic variation in Atlantic salmon: implications for conservation. *Biological Reviews of the Cambridge*

Philosophical Society, *82*(2), 173–211. https://doi.org/10.1111/j.1469-185X.2006.00004.x

Gauld, N. R., Campbell, R. N. B., & Lucas, M. C. (2013). Reduced flow impacts salmonid smolt emigration in a river with low-head weirs. *The Science of the Total Environment*, *458–460*, 435–443. https://doi.org/http://dx.doi.org/10.1016/j.scitotenv.2013.04.063

Gowans, A. R. D., Armstrong, J. D., & Priede, I. G. (1999). Movements of adult Atlantic salmon in relation to a hydroelectric dam and fish ladder. *Journal of Fish Biology*, *44*, 713–726. https://doi.org/10.1006/jfbi.1998.0910

Greenstreet, S. P. R., Morgan, R. I. G., Barnett, S., & Redhead, P. (1993). Variation in the numbers of shags *Phalacrocorax aristotelis* and common seals *Phoca vitulina* near the mouth of an Atlantic salmon *Salmo salar* river at the time of the smolt run. *Journal of Animal Ecology*, *62*(3), 565–576. https://doi.org/http://dx.doi.org/10.2307/5205

Halfyard, E. a, Gibson, A. J. F., Ruzzante, D. E., Stokesbury, M. J. W., & Whoriskey, F. G. (2012). Estuarine survival and migratory behaviour of Atlantic salmon Salmo salar smolts. *Journal of Fish Biology*, *81*(5), 1626–1645. https://doi.org/10.1111/j.1095-8649.2012.03419.x

Haro, A., Odeh, M., Noreika, J., & Castro-santos, T. (1997). Effect of Water Acceleration on Downstream Migratory Behavior and Passage of Atlantic Salmon Smolts and Juvenile American Shad at Surface Bypasses. *Transactions of the American Fisheries Society*, *127*(1), 118–127. https://doi.org/http://dx.doi.org/10.1577/1548-8659

Heinimaa, S., Erkinaro, J., & Soivio, A. (1998). Differences in the physiological status of Atlantic salmon smolts in three tributaries of the River Teno. *Aquaculture*, *168*(1–4), 85–94. https://doi.org/10.1016/S0044-8486(98)00341-X

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

https://doi.org/http://dx.doi.org/10.1080/00028487.2011.618356

Hvidsten, N. A., & Johnsen, B. O. (1997). Screening of descending Atlantic salmon (*Salmo salar* L.) smolts from a hydropower intake in the River Orkla, Norway. *Nordic Journal of Freshwater Research*, *73*, 44–49.

Hvidsten, N. A., & Lund, R. A. (1988). Predation on hatchery-reared and wild smolts of Atlantic salmon,. *Journal of Fish Biology*, *33*, 121–126.

Hvidsten, N. A., & Møkkelgjerd, P. I. I. (1987). Predation on salmon smolts , Salmo salar L ., in the estuary of the River Surna , Norway. *Journal of Fish Biology*, *30*, 273–280. https://doi.org/http://dx.doi.org/10.1111/j.1095-8649.1987.tb05752.x

Jager, H. I., Chandler, J. A., Lepla, K. B., & Winkle, W. Van. (2001). A theoretical study of river fragmentation by dams and its effects on white sturgeon populations. *Environmental Biology of Fishes*, *60*, 347–361. https://doi.org/http://dx.doi.org/10.1023/A:1011036127663

Jepsen, N., Christoffersen, M., & Munksgaard, T. (2008) The level of predation used as an indicator of tagging/handling effects. *Fisheries management and ecology*. 15: 365-368

Jepsen, N., Aarestrup, K., Økland, F., & Rasmussen, G. (1998). Survival of radio-tagged Atlantic salmon (Salmo salar L .) and trout (Salmo trutta L .) smolts passing a reservoir during seaward migration. *Hydrobiologia*, 347–353.

Kemp, P. S., & O’Hanley, J. R. (2010). Procedures for evaluating and prioritising the removal of fish passage barriers: a synthesis. *Fisheries Management and Ecology*, *17*, 297–322. https://doi.org/http://dx.doi.org/10.1111/j.1365-2400.2010.00751.x

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

Kjelson, M. A. A., & Brandes, P. L. (1989). The Use of Smolt Survival Estimates To Quantify the Effects of Habitat Changes On Salmonid Stocks in the Sacramento-San Joaquin Rivers, California. In C. D. Levings, L. B. Holtby, & M. A. Henderson (Eds.), *Proceedings of the National Workshop on Effects of Habitat Alteration on Salmonid Stocks* (pp. 100–115). Canadian Special Publication of Fisheries and Aquatic Sciences 105.

Koed, A., Jepsen, N., Aarestrup, K., & Nielsen, C. (2002). Initial mortality of radio-tagged Atlantic salmon (*Salmo salar* L .) smolts following release downstream of a hydropower station. *Hydrobiologia*, *483*, 31–37. https://doi.org/http://dx.doi.org/10.1023/A:1021390403703

Larsen, M. H., Thorn, A. N., Skov, C., & Aarestrup, K. (2013) Effects of passive integrated tansponder tags on survival and growth of juvenile Atlantic salmon *Salmo salar*. Animal Biotelemtry 1:19.

Larsson, P. (1985). Predation on migrating smolt as a regulating factor in Baltic salmon , Sulmo suluv L ., populations, 391–397.

Lucas, M. C., & Baras, E. (2001). *Migration of freshwater fishes*. Oxford, UK: Blackwell.

Lucas, M. C., Bubb, D. H., Jang, M. H., Ha, K., & Masters, J. E. G. (2009). Availability of and access to critical habitats in regulated rivers: Effects of low-head barriers on threatened lampreys. *Freshwater Biology*, *54*, 621–634. https://doi.org/http://dx.doi.org/10.1111/j.1365-2427.2008.02136.x

Lucas, M. C., & Frear, P. A. (1997). Effects of a flow-gauging weir on the migratory behaviour of adult barbel, a riverine cyprinid. *Journal of Fish Biology*, *50*, 382–396. https://doi.org/http://dx.doi.org/10.1111/j.1095-8649.1997.tb01366.

McCormick, S. D., Hansen, L. P., Quinn, T. P., & Saunders, R. L. (1998). Movement, migration, and smolting of Atlantic salmon (Salmo salar). *Canadian Journal of Fisheries* *and Aquatic Sciences*, *55*(S1), 77–92. https://doi.org/10.1139/cjfas-55-S1-77

McGonigle, C., McLean, S. & Santiago, R. (2011). *Lough Foyle Status Report 2011*. Retrieved from http://www.loughs-agency.org/fs/doc/publications/2011-status-report-foyle-160712.pdf

Meixler, M. S., Bain, M. B., & Walter, M. T. (2009). Predicting barrier passage and habitat suitability for migratory fish species. *Journal of Ecological Modelling*, *220*, 2782–2791. https://doi.org/10.1016/j.ecolmodel.2009.07.014

Moore, A., Ives, S., Mead, T. A., & Talks, L. (1998). The migratory behaviour of wild Atlantic salmon (Salmo salar L.) smolts in the River Test and Southampton Water, southern England. *Hydrobiologia*, *371/372*, 295–304. https://doi.org/http://dx.doi.org/10.1023/A:1017087524694

Moore, A., Potter, E. C. E., Milner, N. J., & Bamber, S. (1995). The Migratory behaviour of Atlantic salmon (*Salmo salar*) smolts estuary of the River Conwy, North Wales. *Canadian Journal of Fisheries and Aquatic Sciences*, *52*, 1923–1935. https://doi.org/http://dx.doi.org/10.1139/f95-784

Naughton, G. P., Caudill, C. C., Keefer, M. L., Bjornn, T. C., Stuehrenberg, L. C., & Peery, C. A. (2005). Late-season mortality during migration of radio-tagged adult sockeye salmon (*Oncorhynchus nerka*) in the Columbia River. *Canadian Journal of Fisheries and Aquatic Sciences*, *62*, 30–47. https://doi.org/http://dx.doi.org/10.1139/F04-147

Newton, M., Barry, J., Dodd, J. A., Lucas, M. C., Boylan, P., & Adams, C. E. (2016). Does size matter? A test of size-specific mortality in Atlantic salmon Salmo salar smolts tagged with acoustic transmitters. *Journal of Fish Biology*, 1–10. https://doi.org/10.1111/jfb.13066

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

https://doi.org/http://dx.doi.org/10.1111/j.1600-0633.2006.00162.x

O'Hanley, J. R., & Tomberlin, D. (2005). Optimizing the removal of small fish passage barriers. *Environmental Modeling & Assessment*, *10*(2), 85–98. https://doi.org/http://dx.doi.org/10.1007/s10666-004-4268-y

Ovidio, M., & Philippart, J. (2002). The impact of small physical obstacles on upstream movements of six species of fish. *Hydrobiologia*, *483*, 55–69. https://doi.org/http://dx.doi.org/10.1023/A:1021398605520

Rechisky, E. L., & Welch, D. W. (2010) Surgical implantation of acoustic tags: Influence of tag loss and tag-induced mortality on free-ranging and hatchery-held spring chinook salmon (*Oncorhynchus tshawytscha*) smolts. *PNAMP Special Publication*: *Tagging, Telemetry and Marking Measures for Monitoring Fish Populations,* 2, 71-96

Roscoe, D. W., Hinch, S. G., Cooke, S. J., & Patterson, D. A. (2011). Fishway Passage and Post-Passage Mortality of up-River migrating Sockeye Salmon in the Seton River, British Columbia. *River Research and Applications,* (27), 693–705. https://doi.org/10.1002/rra

Serrano, I., Rivinoja, P., Karlsson, L., & Larsson, S. (2009). Riverine and early marine survival of stocked salmon smolts, *Salmo salar* L., descending the Testebo River, Sweden. *Fisheries Management and Ecology*, *16*(5), 386–394. https://doi.org/10.1111/j.1365-2400.2009.00688.x

Smith, I. P., Johnstone, A. D. F., & Smith, G. W. (1997). Upstream migration of adult Atlantic salmon past a fish counter weir in the Aberdeenshire Dee , Scotland. *Journal of Fish Biology*, *51*, 266–274. https://doi.org/http://dx.doi.org/10.1111/j.1095-8649.1997.tb01664.x

Taylor, E. B. B. (1991). A review of local adaptation in Salmonidae, with particular reference to Pacific and Atlantic salmon. *Aquaculture*, *98*, 185–207. https://doi.org/http://dx.doi.org/10.1016/0044-8486(91)90383-I

Thorstad, E. B., Økland, F., Aarestrup, K., & Heggberget, T. G. (2007a). Factors affecting the within-river spawning migration of Atlantic salmon, with emphasis on human impacts. *Reviews in Fish Biology and Fisheries*, *18*(4), 345–371. https://doi.org/http://dx.doi.org/10.1007/s11160-007-9076-4

Thorstad, E. B., Økland, F., Finstad, B., Sivertsga, R., Plantalech, N., Bjørn, P. A. A., & Mckinley, R. S. S. (2007). Fjord migration and survival of wild and hatchery-reared Atlantic salmon and wild brown trout post-smolts. *Hydrobiologia*, *582*, 99–107. https://doi.org/http://dx.doi.org/10.1007/s10750-006-0548-7

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

Thorstad, E. B., Whoriskey, F., Uglem, I., Moore, A., Rikardsen, A. H. . H., & Finstad, B. (2012b). A critical life stage of the Atlantic salmon *Salmo salar*: behaviour and survival during the smolt and initial post-smolt migration. *Journal of Fish Biology*, *81*(2), 500–542. https://doi.org/http://dx.doi.org/10.1111/j.1095-8649.2012.03370.x

Urke, H. A., Kristensen, T., Ulvund, J. B., & Alfredsen, J. A. (2013). Riverine and fjord migration of wild and hatchery-reared Atlantic salmon smolts. *Fisheries Management and Ecology*, *20*(6), 544–552. https://doi.org/10.1111/fme.12042

Wagner, G. N., Cooke, S. J., Brown, R. S., & Deters, K. A., (2011) Surgical implantation techniques for electronic tags in fish. *Reviews in Fish Biology and Fisheries.* 21: 71-81

Welch, D. W., Rechisky, E. L., Melnychuk, M. C., Porter, A. D., Walters, C. J., Clements, S., & Schreck, C. (2008). Survival of migrating salmon smolts in large rivers with and without dams. *PLoS Biology*, *6*(10), e265. https://doi.org/http://dx.doi.org/10.1371/journal.pbio.0060265

Wilson, A.D.M., Hayden, T.A., Vandergoot, C.S., Kraus, R.T., Dettmers, J.M., Coke, S.J., Krueger, C.C. (2017) Do intracoelomic telemetry transmitters alter the post-release behaviour of migratory fish. Ecology of Freshwater Fish, 26: 292-300.

Woody, C. A., Nelson, J., & Ramstad, K. (2002). Clove oil as an anaesthetic for adult sockeye salmon: field trials. *Journal of Fish Biology*, *60*(60), 340–347. https://doi.org/10.1006/jfbi.2001.1842