Are we designing fishways for diversity? Potential selection on alternative phenotypes resulting from differential passage in brown trout

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Angus J Lothian[1] (Corresponding author) angus.j.lothian@durham.ac.uk, phone: 01913341260

Michael Schwinn[2] schwinn.michael@gmail.com

A Harrison Anton[1] harrison.anton@mac.com

Colin E Adams[3] Colin.Adams@glasgow.ac.uk

Matthew Newton[3] Matthew.Newton@glasgow.ac.uk

Anders Koed[2] ak@aqua.dtu.dk

Martyn C Lucas[1] m.c.lucas@durham.ac.uk

[1] Department of Biosciences, Durham University, South Road, Durham, DH1 3LE, England, United Kingdom.

[2] Section for Freshwater Fisheries Ecology, National Institute of Aquatic Resources, Technical University of Denmark, Vejlovej 39, Silkeborg, Denmark.

[3] Scottish Centre for Ecology and the Natural Environment, Institute of Biodiversity, Animal Health and Comparative Medicine, University of Glasgow, Glasgow, G63 0AW, Scotland, United Kingdom.

Declarations of interest: none

Abstract

Fishways are commonly employed to improve river connectivity for fishes, but the extent to which they cater for natural phenotypic diversity has been insufficiently addressed. We measured differential upstream passage success of three wild brown trout (*Salmo trutta*) phenotypes (anadromous, freshwater-resident adult and parr-marked), encompassing a range of sizes and both sexes, at a Larinier superactive baffle fishway adjacent to a flow-gauging weir, using PIT telemetry (*n*=160) and radio telemetry (*n*=53, double tagged with PIT tags). Fish were captured and tagged downstream of the weir in the autumn pre-spawning period, 2017, in a tributary of the River Wear, England, where over 95% of tributary spawning habitat was available upstream of the weir. Of 57 trout that approached the weir-fishway complex, freshwater-resident adult and parr-marked phenotypes were less successful in passing than anadromous trout (25%, 36%, and 63% passage efficiency, respectively). Seventy-one percent of anadromous trout that passed upstream traversed the weir directly. Although the fishway facilitated upstream passage, it was poor in attracting fish of all phenotypes (overall attraction efficiency, 22.8%). A higher proportion (68.2%) of parr-marked trout that approached the weir were male and included sexually mature individuals, compared with that of freshwater-resident (37.8%) and anadromous trout (37.0%). The greater passage success of anadromous trout was likely due to their greater size and locomotory performance compared to the other phenotypes. Barriers and fishways can act as selection filters, likely the case in this study, and greater consideration needs to be given to supporting natural diversity in populations when proposing fishway designs to mitigate river connectivity problems.

Keywords: migration, fishway performance, river connectivity, telemetry, river restoration, precocious parr

1. Introduction

The anthropogenic modification of rivers through the building of structures such as dams and weirs negatively impacts many aquatic species (Lucas and Baras, 2001; Reidy Liermann et al., 2012). Due to the linear nature of rivers they become easily fragmented, partitioning habitats which differ in availability and quality (Peter, 1998; Rosenberg et al., 2000; Birnie-Gauvin et al., 2017a). Furthermore, these structures often restrict the movement of aquatic fauna, especially fishes (Silva et al., 2018). For many fish species, natural movement within a river is a vital element of their life-history allowing them to make use of the spatially-separated resources required at different life stages (Lennox et al., 2019). Thus for most temperate riverine fishes, summer feeding habitat is likely different in nature and location from spawning habitat, which in turn is likely different from overwintering habitat, all of which are essential for survival, growth and successful reproduction (Lucas and Baras, 2001). Impeded passage between these habitat types is highly likely to impact on ultimate fitness for affected individuals (Thorstad et al., 2008; Lennox et al., 2019; Tamario et al., 2019).

Where anthropogenic barriers exist, a key river rehabilitation tool is the improvement of longitudinal connectivity between habitat patches (Wohl et al., 2015) to facilitate restoration of hydromorphic and ecological processes, including animal dispersal and migration (Radinger and Wolter, 2015; Tummers et al., 2016). Ideally this is done by barrier removal, but a range of societal constraints mean that this is often not feasible (Birnie-Gauvin et al., 2017b). For fish, the most common mitigation to support passage past obstacles, especially in an upstream direction, is the provision of fishways (Dodd et al., 2017; Silva et al., 2018). While several fishway designs may work well for target species, it is increasingly apparent that they work poorly for others (Bunt et al., 2012; Foulds and Lucas, 2013), or fail to provide adequate community-level migration and dispersal solutions (Hall et al., 2012). Human actions such as fisheries can act as natural selection filters, resulting in anthropogenic induced evolutionary change (Edeline et al., 2007; Tillotson and Quinn, 2018); dams and fishways can also operate in this way (Haugen et al., 2008; Volpato et al., 2009). There is evidence that shows genetic changes within, and divergence between, populations that are partially or wholly split by barriers (Stamford and Talyor, 2005; Gouskov et al., 2016; Wilkes et al., 2018; Van Leeuwen et al., 2018). The extent to which small anthropogenic obstacles and fishways may exert a selection pressure on naturally existing phenotypic diversity within fish populations has, however, been insufficiently addressed (Haugen et al., 2008; Tamario et al., 2019).

Many anthropogenic river barriers are 'low-head' obstacles (Jones et al., 2019) and leaping fish such as salmonids may pass them, in some conditions, in the same way as at small, natural waterfalls (Stuart, 1962). Pool-and-weir fishways, and pre-barrages (small weirs built downstream of the main obstacle), are designed to operate by breaking the main obstacle into a series of smaller vertical obstacles more easily leapt (Armstrong et al., 2010). By contrast, baffle-type fishways require no leaping and slow the flow using baffles on the floor and/or walls of the fishway channel (Larinier, 2008; Armstrong et al., 2010). Baffle fishways are usually characterised by high water velocities and turbulence (the magnitude dependent on slope and baffle size), thereby tending to provide a greater chance of passage success for larger fish with a strong swimming ability and high endurance (Larinier, 2001). Nevertheless, lower-velocity routes occur along wall edges, and close to baffles, that may be exploited by smaller fish able to utilise the turbulent conditions (Nikora et al., 2003; Wang and Chanson, 2018). The degree to which the fishway type and the specifics of its design impact on fish passage success is very poorly understood, and yet has considerable management consequences.

Salmonid fishes often exhibit a variety of discrete phenotypes and life histories within a single population (Campbell, 1977; Leider et al., 1986; Bekkevold et al., 2004; Seamons et al., 2004). In any brown trout (*Salmo trutta*) population, for example, multiple phenotypic groups associated with alternative life histories strategies are frequently expressed (Jonsson and Jonsson, 2011). Three of the most common life history patterns exhibited in brown trout populations are: anadromy, freshwater residence, and precocious maturation.

The anadromous (*An*) phenotype ('sea trout') is characterised by migration between freshwater and the sea, with individuals carrying out most body growth at sea (McDowall, 1992). This migration provides access to nutrient-rich habitats in order to grow in size, and thereby increasing potential fitness, before returning to freshwater to reproduce (Klemetsen et al., 2003; Jonsson and Jonsson, 2011; Aarestrup et al., 2017). As a result, *An* individuals tend to be larger in size than those that remain in freshwater. *An* trout may travel entire river lengths during their movement between river and sea, and therefore require a high degree of river connectivity. Although larger body sizes generally result in greater burst and sustained swimming speeds that might confer advantages in passing small anthropogenic barriers over other phenotypic groups, the added energy expenditure in attempting passage is an additional cost that could have fitness consequences later on in the migration (Thorstad et al., 2008).

Freshwater-resident (*FR*) brown trout do not migrate to sea, but instead remain in the freshwater environment. At adulthood this phenotype (*FRA*) is typically smaller than *An* trout, and can take many behavioural forms, including: remaining near the site where they hatched, movements to other areas containing refuge habitat, or longer potamodromous migrations (those wholly within freshwater; McDowall, 1992) along rivers or between rivers and lakes (Ferguson et al., 2019; Tamario et al., 2019). The drivers of this complex life history in the *FR* brown trout are unknown, but the knowledge of each strategy in a river requires adequate river management to sustain each strategy in a given population.

Some brown trout individuals become sexually mature at a relatively small size whilst retaining their markings typical of the juvenile parr-marked (*PM*) stage, exhibiting a cryptic mating strategy. Becoming “precocious parr” is a trait commonly observed in brown trout and other salmonids (Klemetsen et al., 2003). Precocious parr are also important to the population, with Saura et al., (2008) reporting that up to 60% of an Atlantic salmon (*Salmo salar*) population could be sired by mature *PM* males. Historically there was a tendency to regard sexually mature *PM* individuals as remaining resident in habitat suitable for foraging close to spawning areas, but there is increasing evidence of distinct but short-distance migrations made by precocious parr at or close to spawning time (Buck and Youngson, 1982; Forty et al., 2016). Although upstream migrations of *PM* trout are short distance, the smaller size of mature *PM* trout, compared to conventional adult phenotypes might put them at a disadvantage in passing upstream of barriers to movement.

These different phenotypes are frequently expressed in trout from the same catchment, and as such are drawn from a common gene pool (Archer et al., 2019). Thus phenotypes are not determined solely by genetics (Ferguson et al., 2019). The initiation of the processes leading to anadromy appears to be regulated by a quantitative genetic threshold system based on an individual’s rate of energy accumulation. If the threshold is reached this results in differential gene switching, and initiation of the physiological processes leading to anadromy. The threshold value is known to be heritable (Pulido, 2011; Ferguson et al., 2019). A consequence of this is that selection for certain threshold values may occur at partial barriers to migration as a result of size-selectivity, resulting in shifts in size at first maturity (Haugen et al., 2008; Ferguson et al., 2019). Thus we would predict that the upstream passage filter effect of semi-permeable low-head barriers on individual fitness of trout would be phenotype, particularly size, dependent. Irrespective of the direction in which selection effects might be observed, diversity in life histories exhibited in salmonids is fundamental for supporting the widest natural gene pools for local and adaptive responses, including climate change (King et al., 2007).

One aim of this study was to examine the potential for anthropogenic selection effects of a low-head riverine barrier on a brown trout population consisting of three expressed phenotypic groups: *An*, *FRA*, and *PM*. This was quantified by assessing the upstream passage success of the three phenotypes at a barrier using telemetry. We hypothesised that any passage filter effect of such a barrier would be greatest on the small body size *PM*, least on larger *An* and intermediate for *FRA* phenotypes. A second aim was to examine if the installation of a baffle fishway affected differential passage success and associated selection potential of phenotypes. We determined this by quantifying the route choice and relative effectiveness of the fishway compared to the adjacent weir. Specifically we hypothesised that greater proportions of each phenotype would pass upstream by using the baffle fishway than by passage over the weir directly.

2. Materials and Methods

2.1 Study Site

The River Browney, a tributary of the middle reaches of the River Wear, northeast England, is 45 km long and has a mean daily discharge of ~1.6 m^3s^{-1}. The tributary has plentiful spawning habitat for salmonids and is an important nursery stream for trout (Winter et al., 2016). Its spawning population comprises of *An*, *FRA* and *PM* adult phenotypes. An Environment Agency flow-gauging weir, Burnhall weir (Latitude: 54.742552; Longitude: -1.599043), 2.7 km upstream of the Browney-Wear confluence, is the first obstacle encountered during upstream migration in the Browney (Figure 1). This has been demonstrated by radio tracking to be an obstacle to upstream passage of *An* phenotype trout at low to moderate flows (Tummers et al., 2016). More than 95% of salmonid spawning and nursery habitat in the Browney occurs upstream of Burnhall weir.

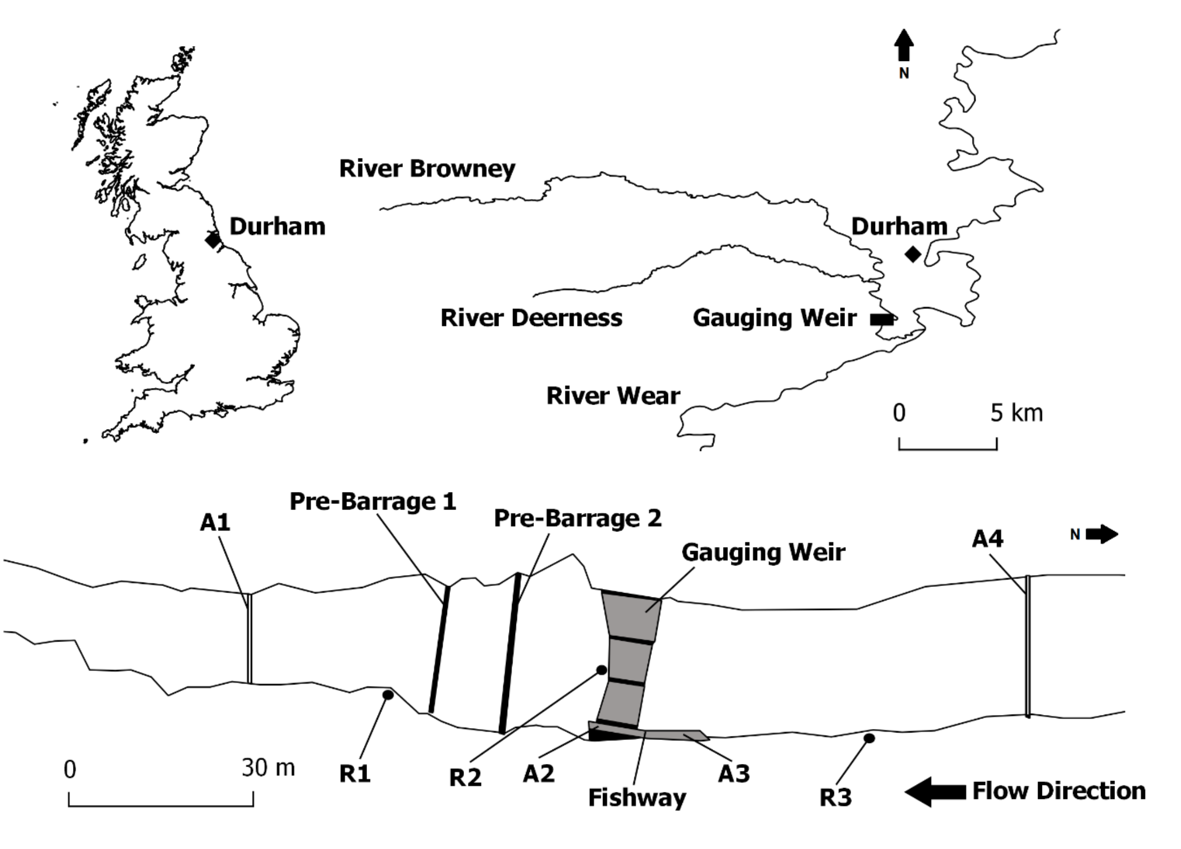

Figure 1. Map of the River Wear with its tributary the River Browney, and its tributary the River Deerness. Lower panel, overview of the immediate study area around Burnhall gauging weir with PIT antennas (A1, A2, A3, and A4) and stationary radio antennas (R1, R2, and R3) shown.

Burnhall weir was built in 1954 on an existing bedrock cascade. It is an 18-m wide compound, broad-crested weir, with a 3-m gently sloping (~3%) apron and a vertical truncation at the downstream end, with current overall head difference of 0.7 m at Q59 (0.50 m^3 s^{-1}; Q value derived from gauged data over the period 2000-2017). Two full-channel-width pre-barrages (29-m and 16-m downstream of the weir) with step heights of ~0.25 m were built in their current form in 1996 to facilitate passage of jumping fish. The first pre-barrage has four equidistant notches, and the second five notches, each 2.2-m wide and 0.1-m deep, formed from stacked timbers in slots, with a greater notch depth (0.2 m) on the left-most notch, creating attraction flow (especially on the left side) and jumping points at low to moderate river flows (Figure S1). Velocity (measured with a Valeport 801 EM flow meter) and depth profiles (18-19 February 2019 at Q59) of the immediate area surrounding the weir are given in Figure S2.

For societal reasons Burnhall weir cannot be removed. Following the observations of restricted passage of adult *An* trout (Tummers et al., 2016) a 17-m long, 0.6-m wide, 12.5% slope, Larinier superactive baffle fishway was installed in 2017 (Figure 1, Figure S3) aimed at facilitating upstream passage of salmonids. The downstream opening of the fishway is parallel to the weir face, on the left side. The fishway incorporates two baffle sections; a 7-m long downstream section, and a 3-m long upstream section, each utilising 0.1 m high baffles. A 3.6-m long resting pool sits between the baffled sections (Figure S3a). Fishway velocity profiles at 10% depth and 50% depth are provided in Figure S3. The proportion of flow through the fishway at Q59 was 14.2% of main channel flow, meeting United Kingdom fishway design recommendations (Armstrong et al., 2010).

2.2 Fish Capture and Tagging

Fish were captured in the Browney, 440-2240 m downstream of the weir, on eight days between 22 September and 31 October 2017 (Table 1), prior to spawning (normally mid-November to late- December in this stream), using pulsed DC electrofishing. We assume that adult trout captured were either resident to, or had originated from, the tributary and expected that this would maximise the likelihood that tagged fish would migrate upstream and encounter the study weir, as reproductive homing in brown trout is well-known (Lucas and Baras, 2001). During later sampling dates, we avoided localities in the fishing zone where radio-tagged fish were, to minimise disturbance; any Passive Integrated Transponder (PIT) tagged fish recaptured were returned to the capture site immediately after fishing.

All trout captured in a sampling session in a given zone (Table 1) and exceeding 120 mm in length were tagged and released in the same capture zone on the same day. We assumed that sexually mature individuals from all phenotypes tagged downstream of the obstacle would exhibit upstream migratory behaviour. Numbers of each phenotype tagged were dictated by their availability. *An* and *FRA* phenotypes had no parr-marks, and were distinguished from each other by colouration and size (Jonsson and Jonsson, 2011; Figure S4). These fish were assumed to be reproductively mature. Secondary sexual characteristics were used to determine sex (possible for all *An* and some *FRA* phenotypes). *PM* fish were identified by parr marks (Figure S4) on the flanks but this group could be juvenile (reproductively immature parr) or adult (reproductively mature 'precocious parr'). The abdomens of all *PM* fish (lightly sedated, tricaine methanesulphonate, 100 mg l^{-1}) were gently stripped to release gametes to determine sex and maturation status; this was only possible for those fish of advanced sexual maturity. Following sedation, each fish was measured (fork length; mm) and weighed (g). A small incision (~4 mm) was made anterior to the pelvic girdle on the ventral surface before a PIT tag (for fish with fork length <160mm: half-duplex [HDX], 23x3.4 mm, 0.6 g in air, Oregon RFID, Oregon; for fish with fork length >160mm: HDX, 32x3.7 mm, 0.8 g in air, Oregon RFID) was inserted into the body cavity.

TABLE 1. The number of fish PIT tagged and Radio+PIT tagged, the range of fish lengths (mm), distance of release site downstream of the weir (m) and sex (Male/Female/Unknown) based on molecular sexing for each day of tagging split by phenotype (*PM*: Parr-marked; *FRA*: Freshwater Resident Adult; *An*: Anadromous).

Date	Phenotype	No. PIT tagged	Length (mm; range)	No. radio + PIT tagged	Length (mm; range)	Distance downstream of weir (m)	Sex (M/F/Un)
22/09/2017	*PM*	18	143-201	-	-	1115	1/1/16
22/09/2017	*FRA*	12	147-295	-	-	1115	2/1/9
29/09/2017	*PM*	10	162-198	-	-	440	0/1/9
29/09/2017	*FRA*	1	264	1	322	440	2/0/0
29/09/2017	*An*	-	-	8	428-700	440	1/7/0
10/10/2017	*PM*	19	143-198	-	-	1315	4/1/14
10/10/2017	*FRA*	1	206	-	-	1315	0/0/1
11/10/2017	*PM*	8	145-210	1	229	2000	1/2/6

11/10/2017	*FRA*	2	194-210	2	271-294	2000	1/1/2
11/10/2017	*An*	-	-	3	520-570	2000	1/2/0
17/10/2017	*PM*	10	174-205	3	189-238	2000	4/0/9
17/10/2017	*FRA*	3	221-226	-	-	2000	0/1/2
17/10/2017	*An*	-	-	12	490-770	2000	9/3/0
24/10/2017	*PM*	24	121-201	1	190	2000	3/2/20
24/10/2017	*An*	-	-	11	490-640	2000	3/8/0
26/10/2017	*PM*	5	154-177	-	-	2000	0/0/5
26/10/2017	*PM*	20	142-194	2	172-197	1900	6/0/16
26/10/2017	*FRA*	1	198	-	-	2000	0/0/1
26/10/2017	*FRA*	8	178-218	4	184-294	1900	4/4/4
26/10/2017	*An*	-	-	3	480-575	2000	2/1/0
26/10/2017	*An*	-	-	2	570-585	1900	1/1/0
31/10/2017	*PM*	7	164-214	-	-	440	1/1/5
31/10/2017	*FRA*	6	185-214	-	-	440	2/1/3
31/10/2017	*An*	5	440-590	-	-	440	0/4/1
Total	*PM*	121	121-214	7	172-238	n/a	20/8/100
Total	*FRA*	34	147-312	7	184-322	n/a	11/8/22
Total	*An*	5	440-590	39	428-770	n/a	17/26/1

Samples of *An*, *FRA* and spermiating male *PM* trout (and one female *PM*), greater than 170 mm in length, were double-tagged with a radio tag and a PIT tag. An incision, slightly longer than the radio tag width, was made on the ventral surface of the fish anterior to the pelvic girdle. Either an F1740 coded radio transmitter with a whip antenna (3.4 g in air, 11.54 pulses per minute, ATS, Minnesota) or an F1210 coded transmitter with an internal coil antenna (11 g in air, 35 pulses per minute, ATS, Minnesota) was inserted into the body cavity of *An* trout.

FRA trout were tagged with F1740 tags and *PM* trout were tagged with F1430 non-coded transmitters (whip antenna, 1.7 g in air, 33 pulses per minute, ATS, Minnesota). Two to three independent sutures (3–0/4–0 Vicryl) were used to close the incision. Aerated river water was passed over the fish's gills during the entire tagging procedure.

A fin clip (5x3 mm) of the posterior section of the dorsal fin from each fish was taken and stored in 95% ethanol for molecular sexing of fish. DNA was extracted using the HOTSHOT method of DNA precipitation before the sex was validated by PCR to detect the presence of two *sdY* gene exons (Eisbrenner et al., 2014; Ayllon et al., 2015). Male fish were classified as having both exons, whereas females either lacked an exon or exhibited a very weak single exon. Genetic sexing gave 94.5% agreement with observations from primary and secondary sexual characteristics. A total of 89 trout (42 *An*, 19 *FRA*, 28 *PM*), comprising all radio tagged fish, all fish that approached the weir and all spermiating males (as a molecular sexing quality control) were genetically sexed. One FRA trout could not be genetically sexed, but due to its lack of male secondary sexual characteristics, it was assumed to be female.

After recovery (1.5-3 h) in aerated tanks at the river bank, fish were returned to the river section they were captured from (Table 1). All procedures were conducted in accordance with the UK Animals (Scientific Procedures) Act 1986.

2.3 PIT Logging Station Network

Four PIT antennas were installed around the weir and fishway to monitor trout upstream migration between 22 September and 14 December 2017 (Figure 1). To avoid damage by large woody debris during high flows, antennas in the main channel were flatbed designs attached to anchors drilled into the bedrock. A flatbed antenna (A1), with a vertical detection range of ~0.2 m and Q59 depth of ~0.1 m was placed 64 m downstream of the fishway entrance, to record fish approaching the weir. Two PIT antennas were placed in the fishway: one at the downstream entrance (A2) and one at the upstream exit (A3). Both A2 and A3 were of loop form, set within recesses in the fishway walls, encompassing the width and height of the fishway and had horizontal detection ranges of ~0.5 m either side of the antenna. Another flatbed antenna (A4) was positioned 65 m upstream of the fishway exit. The vertical detection range of A4 was ~0.2 m and water depth over the antenna was 0.2-0.3 m at Q59. Detection ranges were tested with a 23 mm PIT tag to provide the smallest possible detection range.

A1 and A4 were operated as described by Bolland et al. (2009). A2 and A3 were operated as described by Lothian et al. (2019). Data (date, time, antenna number, PIT tag ID) were downloaded on each site visit. Antenna functionality and range were checked manually on each visit (every 3-4 days); all readers and antennas were operational for >94% of the study period. Field detection efficiencies of PIT antennas over the study period were estimated from the proportions of tagged fish known to have moved upstream of a given antenna based on records from passive PIT and radio stations upstream. Efficiency measurement of A4 was based on detections of double-tagged fish on radio antenna R3 and manual radio tracking upstream of A4 (Figure 1). Detection efficiency of PIT stations over the study period were: A1, 87.3%; A2, 100%; A3, 100%; A4, 96.3%.

2.4 Automated Radio Receiver Network and Manual Tracking

An automated radio receiver system was used to determine fish movement around the weir complex (Figure 1). A dipole antenna (R1, range radius ~30 m) was positioned 38 m downstream of the fishway entrance to record fish approaching the pre-barrages from downstream. A monopole (R2, range radius ~15 m) was positioned immediately downstream of the weir. R2 recorded radio tags in the weir pool but due to the weir structure itself, tags upstream of the weir were not detected. A dipole antenna (R3, range radius ~40 m) was placed 45 m upstream of the fishway exit to detect fish completing passage of the weir-fishway complex. R1 and R2 were controlled by a receiver (ATS R4500C) with a multiplexer that alternated between R1 and R2 combined, R1 only and R2 only every 24 seconds. This time interval was a result of the receiver being set to a fixed cycle rate of six seconds for each of four radio frequency bands. R3 was controlled by a single receiver that operated at a cycle rate of six seconds per frequency. If a coded radio tag was detected, the detection cycle halted for 30 seconds to decode and record the tag, along with the date, time and the radio antenna number. R1 and R2 were operational for 100% of the study period, and R3 was operational for 94.7% as a result of battery failure between two consecutive visits. Field detection efficiencies of passive radio stations and antennas over the study period were estimated from the proportions of tagged fish known to have moved upstream of a given antenna based on records from passive PIT and radio stations upstream. Efficiency measurement of R3 was based on detections of double-tagged fish on PIT A4 and manual tracking upstream of R3. Detection efficiency of radio stations over the study period were: R1 and R2 combined (as a consequence of alternating listening cycle), 96%; R3, 64.3%. The proportions of phenotypes passing the weir-fishway complex were calculated as those approaching (i.e. detected on A1 and/or R1/R2) that were subsequently detected on A4 and/or R3. The passage route was determined by whether or not a fish was detected exiting the fishway (on the condition that the fish had entered the fishway, i.e. detected on both A2 and A3), with failure to be detected exiting the fishway as evidence for traversing the weir directly.

In addition to detection by stationary radio receivers, manual tracking was carried out during daylight hours four to six times per week between 29 September and 14 December to identify fish locations in the catchment in relation to their release points, as well as the weir. Three to 18 km sections of the Wear, Browney and Deerness were surveyed on foot during each tracking session using a Yagi antenna and portable radio receiver (ATS, R4520C) to locate the fish. The GPS position, time and the radio tag ID were recorded when fish were located, as well as the habitat characteristics in the immediate vicinity of the tagged fish. Detailed statistical approach and results of manual tracking can be found in Supplementary Material S1.1.

2.5 Statistical Approach

To assess which variables might influence overall passage success, a binary Generalised Linear Model (GLM) was created including those fish that approached the weir (i.e. were detected on A1 or R1/R2). Overall passage success, either "1" for successful or "0" for failed approach, was modelled against: phenotype, sex of fish, river temperature at time of first detection on A1, mean daily river discharge at time of first detection on A1, and whether the approach was initiated during the day or night. A step-down method was used for model selection, with removal of the most insignificant variable at each step based on a Likelihood Ratio Test (LRT) between nested models. Although length of fish was not included in the overall multiple factor passage success model, as length was implicit in the phenotype variable of the model (as lengths of phenotypes differed), a second GLM with a binomial distribution was created to examine the significance of length on passage success of those fish approaching the weir. Further to these two models, several Welch two sample *t*-tests were carried out to compare: length of fish and route choice, and mean daily flow and route choice. Chi-squared tests were also carried out to examine the number of fish in each phenotype that were attracted to the fishway entrance, comparative fishway passage success (i.e. those that enter the fishway to those that exit it) between phenotypes, and to compare frequencies of each phenotype that passed via the weir directly or via the fishway. All analyses and data interrogation was performed in RStudio (v1.1.463) using R (v3.5.1; R Core Team, 2014).

Approach duration was also investigated. For successful fish, approach duration was defined as the time difference between the first detection on A1 until the first detection on A4, and defined as the time taken between first detection on A1 until the last detection on A1 for failed attempts. Passage duration was calculated for successful fish only, and defined as difference in time between the last detection on A1 and the first detection on A4. Passage duration was compared between fish that took the weir route or the fishway route.

3. Results

3.1 Passage Performance

A total of 213 trout (*An*, 44; *FRA*, 41; *PM*, 128) were tagged and released (Table 1). These comprised 39 double-tagged and five PIT-tagged *An* phenotype; seven double-tagged and 34 PIT-tagged *FRA*; seven double-tagged and 121 PIT-tagged *PM*. Fifty seven of the 213 trout approached the weir, comprising 22 *PM* (17.2% of *PM* released), 8 *FRA* (19.5% of *FRA* released) and 27 *An* (61.4% of *An* released; Table 2; Figure 2). Of the 57 fish that approached, 27 were subsequently detected upstream of the weir, equating to an overall passage success of 47.7% (Figure 2). Phenotype was a significant variable in the overall passage success model (LRT: χ^2_2 =6.76, p =0.03; Table S3; S4), where *An* trout were the most successful at passing the weir with 63.0% (n =17) of those approaching successfully passing, followed by *PM* trout (36.4% of those that approached; n =8), and then *FRA* trout (25.0% of those that approached; n =2).

Thirteen fish were detected entering the fishway, equating to 22.8% (n =13/57) attraction efficiency of all those approaching the weir (attraction efficiencies per phenotype: *PM* [5/22] =22.7%; *FRA* [2/8] =25.0%; *An* [6/27] =22.2%). Significantly fewer fish than expected were attracted to the fishway entrance (Chi squared test with Yates correction: χ^2_2 =6.94, p <0.05), but there was no difference between the phenotypes (Chi squared test with Yates correction: χ^2_2 =1.01, p >0.50). Of those that entered the fishway, 10 were successfully detected at the upstream exit, a combined passage efficiency for the fishway route of 76.9% (n

=10/13; passage efficiencies per phenotype: *PM* =80.0% [5/6]; *FRA* =50.0% [1/2]; *An* =83.3% [4/5]). There was no difference in fishway passage success between each phenotype (Chi squared test with Yates correction: χ^2_2 =1.43, p >0.25). One of the three fish that was unsuccessful in passing via the fishway (*An* phenotype) subsequently traversed the obstacle by the weir route, whereas the other two unsuccessful fishway fish (*PM* and *FRA*) failed to pass the weir-fishway complex entirely.

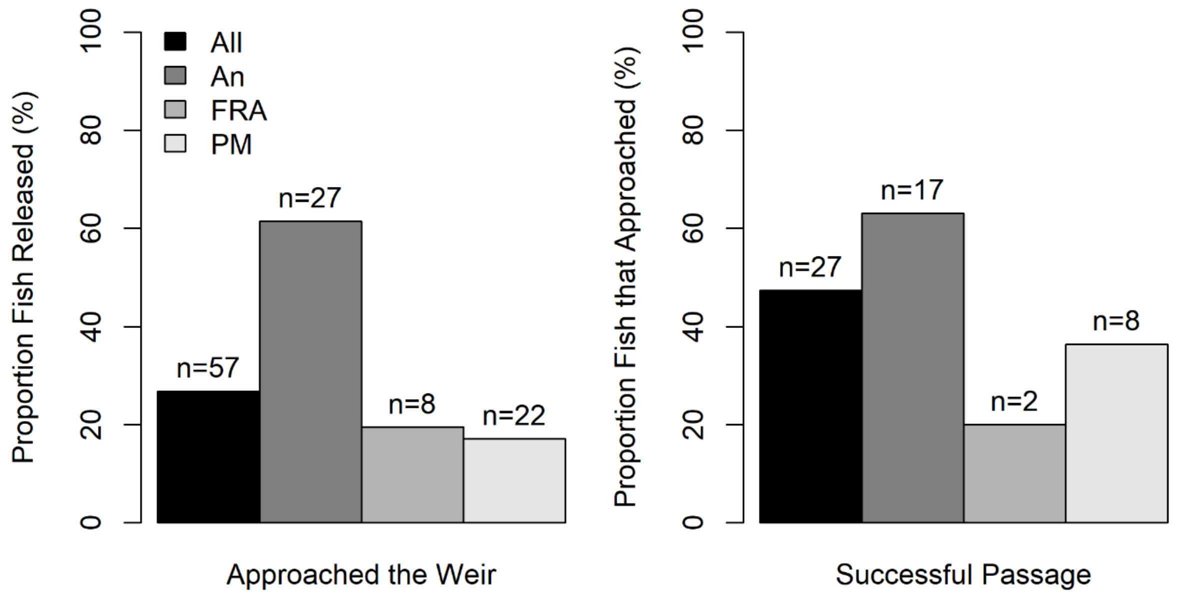

Figure 2. The proportion of each brown trout phenotype (*An*: Anadromous; *FRA*: Freshwater Resident Adult; *PM*: Parr-Marked) released that approached the weir (left) and the proportion of each phenotype that approached the weir that ultimately succeeded in passing the weir-fishway complex.

More fish traversed the weir (n =17) than ascended the fishway (n =10; Table 2) but this was not significantly different (Chi-square test: χ^2_1 =1.82, p >0.10). Equal numbers of *PM* and *FRA* phenotype trout traversed the weir and ascended the fishway. More *An* trout traversed the weir (n =12) than ascended the fishway (n =5) but this was not significant (Chi-square test: χ^2_1 =2.88, p >0.05). Similar numbers of male and female fish approached the weir (n_{male} =28; n_{female} =29) but the proportions varied by phenotype with greater proportions of male *PM* and smaller proportions of male *An* and *FRA* (Table 3) though none differed greatly. Overall, sex of fish was not an important predictor variable in the overall passage success model (LRT: χ^2_2

=0.72, p =0.40). Twelve male and 15 female trout succeeded in passage of the weir (Table 3). Environmental variables (temperature and river height) were not found to be significant in the overall passage success model (more information on environmental variables can be found in Supplementary S1.2).

Overall, length of fish was found to be a significant factor in determining passage success (GLM: z_1 =1.9, p =0.05; Table S5; Figure S6), driven by differences in size between the phenotypes. Lengths of successful and unsuccessful fish by phenotype are supplied in Table S2. Of all fish that were successful, there was no significant difference in length between those that traversed the weir (mean ±S.D. =446 ±181 mm) and those that used the fishway (368 ±199 mm; Welch two sample t-test: $t_{17.6}$ =1.0, p =0.32).

3.2 Passage Duration

Fish that did not pass the weir had a greater approach duration (median [25th percentile, 75th percentile] =13.1 [0.9, 50.0] hrs) compared to those that passed (2.1 [1.2, 7.2] hrs). Fish that successfully passed upstream of the weir that used the fishway route had a significantly greater passage duration (5.2 [3.5, 8.5] hrs) than those that traversed the weir (1.3 [1.0, 1.6] hrs; Wilcoxon rank sum test: W =18, p =0.001). This was seen in all phenotypes (Table 4), but the difference was most apparent for *An*. *FRA* and *PM* phenotypes ascending the weir took longer to do so than *An* fish (Table 4).

TABLE 2. The number of tagged fish that approached the weir, and the number of fish that either traversed the weir or utilised the fishway (*FRA*: Freshwater Resident Adult).

Phenotype	Tag type	No. tagged	No. approached (proportion of tagged fish)	No. successful (proportion of fish that approached)	No. traversed weir (proportion of successful fish)	No. used fishway (proportion of successful fish)
Parr-marked	PIT	121	20 (16.5%)	8 (40.0%)	4 (50.0%)	4 (50.0%)
Parr-marked	PIT and Radio	7	2 (28.6%)	0 (0.0%)	0 (0.0%)	0 (0.0%)
FRA	PIT	34	7 (20.0%)	2 (28.6%)	1 (50.0%)	1 (50.0%)
FRA	PIT and Radio	7	1 (14.3%)	0 (0.0%)	0 (0.0%)	0 (0.0%)
Anadromous	PIT	5	3 (60.0%)	3 (100.0%)	2 (66.7%)	1 (33.3%)
Anadromous	PIT and Radio	39	24 (61.5%)	14 (58.3%)	10 (71.4%)	4 (28.6%)
Total		213	57 (26.8%)	27 (47.4%)	17 (63.0%)	10 (37.0%)

TABLE 3. The number of male and female fish in each phenotype category that approached the weir, succeeded in passage, and the route taken to succeed in passage of the weir (i.e. traversing the weir or using the fishway; *FRA*: Freshwater Resident Adult). [a] One FRA individual (that attempted but subsequently failed in its passage attempt) could not be molecularly sexed, but was assumed to be female due to it not showing male secondary sexual characteristics.

Phenotype	Approached the weir		Successful Passage (proportion of fish that approached)		Traversed Weir		Fishway	
	No. male	No. female	No. male	No. female	No. male	No. female	No. male	No. female
Parr-marked	15	7	5 (33.3%)	3 (42.9%)	2	2	3	1
FRA	3	4 (5[a])	0 (0.0%)	2 (40.0%)	0	1	0	1
Anadromous	10	17	7 (70.0%)	10 (58.8%)	5	7	2	3
Total	28	28	12 (42.9%)	15 (53.6%)	7	10	5	4

TABLE 4. Passage duration (determined from last detection on A1 to first detection on A4; in hours) per phenotype. Passage duration of those fish that traversed the weir and those that used the fishway are also provided (*FRA*: Freshwater Resident Adult).

Phenotype	**Overall Passage Duration (hrs; 25th,75th)**	**Weir Route Passage Duration (hrs; 25th,75th)**	**Fishway Route Passage Duration (hrs; 25th,75th)**
Parr-marked	4.2 (3.4, 4.3)	3.4 (3.4, 3.4)	4.3 (3.6, 5.3)
FRA	2.3 (1.9, 2.8)	1.4 (1.4, 1.4)	3.2 (3.2, 3.2)
Anadromous	1.4 (,1.0, 3.3)	1.2 (1.0, 1.6)	8.6 (6.1, 9.4)
Total	**1.8 (1.1, 4.2)**	**1.3 (1.0, 0.6)**	**5.2 (3.5, 8.5)**

4. Discussion

To be effective, environmental mitigation measures for biota need to support life cycle completion, productivity and genetic diversity over the long term – if such mitigations support only a subset of diversity they are likely to promote evolutionary change. Anthropogenic changes to the environment can drive evolutionary change in aquatic animal populations (Alberti, 2015). One of the best documented is fisheries-induced evolution (Law, 2007; Heino et al., 2015), where changes to fish size, spatial distribution, and life history strategy have been recorded as a result of harvesting particular sizes from specific regions (Sinclair et al., 2002a; Sinclair et al., 2002b). Similarly, damming and the creation of reservoirs caused shifts in morphology in red shiner (*Cyprinella lutrensis*) to deeper body and smaller heads as the habitat changed from lotic to lentic (Franssen, 2011). Volpato et al. (2009) observed a selective filter effect on physiological traits for population components successfully passing a tropical dam fishway, compared to those attempting passage, although the long-term evolutionary responses were not recorded, as they have not been in this study.

4.1 Passage Performance

As predicted in this study, passage success was not equal across the three phenotypes. Significantly more *An* trout passed the weir than *PM* or *FRA*, suggesting potential selective pressures exerted on the trout population by the weir in favour of the larger *An* phenotype over *PM* or *FRA*. The ranking of passage efficiency, *An*>*PM*>*FRA*, differed from that hypothesised, but passage efficiency of *PM* and *FRA* did not differ statistically, and sample sizes of both phenotypes were small.

In our study, twice as many *An* trout traversed the weir than used the fishway, and equal numbers of *PM* and *FRA* each traversed the weir or used the fishway, indicating that the fishway has not mitigated the weir as an obstacle to movement, nor alleviated the selection pressures of the weir on the population as a whole. This was principally due to poor attraction efficiency rather than passage efficiency (22.8% vs 76.9%, respectively). A similar study on ascending adult Atlantic salmon on the River Mourne, Ireland, showed that fish preferred to traverse the weir than use a fishway (Newton et al., 2018). Variable attraction efficiencies have also been reported for fishways of all types, with a meta-analysis indicating attraction efficiency of 0%-100% (mean =62.3%) across the design spectrum (Bunt et al., 2012). In this study, in addition to poor attraction efficiency of the fishway, individuals that used the fishway took longer to pass upstream of the weir than those that traversed the weir itself; further highlighting that the fishway does have the potential to act as a selection pressure on the population. Those fish that spend more time attempting to find a fishway entrance are likely to expend more energy and have increased exposure to predation risk, potentially reducing their reproductive fitness (Thorstad et al., 2008).

Although few fish were attracted to and entered the fishway in this study, similar proportions of each phenotype were attracted to the fishway and succeeded in passing it, indicating that the fishway did not select for a phenotype, but was simply inefficient for all phenotypes. Although *An* trout passage success was not very different between the weir route and fishway route (once they had found and entered the fishway), the passage success for *PM* and *FRA* trout for the fishway route (once they had entered the fishway) was greater than for the weir route. Furthermore, there was no significant difference in fishway passage between *An*, *FRA* and *PM* trout. This suggests that the fishway does have the potential to remove the selective pressure imposed on the trout population by the weir.

The failing of fishways to attract fish to their entrance is one of the more difficult hurdles to overcome in fishway engineering. There is evidence to suggest that upstream migrating salmonids are attracted to areas of higher flow and discharge (Thorstad et al., 2008), and further evidence that fishways co-located with areas of high flow (i.e. next to turbine outlets, in the main channel, etc.) have a far greater attraction efficiency for a range of species migrating upstream (Dodd et al., 2018; Tummers et al., 2018). This should perhaps be considered more carefully when designing fishways and identifying installation locations to minimise the barrier effect on movements and thus minimising resultant selective pressures. The greatest proportion of flow at the weir in this study was directly over the weir (as indicated by the velocity in Figure S2b,c) and although the fishway entrance was close, evidently the relatively lower flow emerging from, or near to it, made it unattractive.

4.2 Potential Evolutionary Consequences

Differential passage between phenotypes, and within phenotypes, can lead to changes in the population structure. Haugen et al., (2008) showed that the construction of a fishway altered the upstream assemblage of brown trout in a Norwegian river above a dam from larger to smaller fish as the fishway worked most efficiently for medium-sized fish. The weir in our study has been present since 1954, and was built on a series of natural cascades which may have acted as a natural selection agent for larger (i.e. *An*) trout, although the complex hydraulics of sloping cascades can facilitate passage of small as well as larger trout (Forty et al., 2016). If the fishway in the current study on the Browney functioned effectively for sexually mature trout of all three phenotypes, a shift in population structure, and possibly genetic structure, might be seen in the future as more *FRA* and *PM* trout gain access to the mid- and upper-Browney. Given that an abundant trout population exists upstream of the weir, there may only be a limited impact on the trout population upstream as a result of the redistribution of phenotypes across the weir. However, it is important to ensure sufficient bidirectional gene mixing across partial barriers to ensure adequate diversity is maintained in a population (Wilkes et al., 2018). Population isolation as a result of barriers can cause changes in genetic structure, resulting in genetically distinct populations either side of the barriers (Stamford and Taylor, 2005; Gouskov et al., 2016; Van Leeuwen et al., 2018).

Anadromy in salmonids is often female biased (brown trout: Campbell, 1977; Bekkevold et al., 2004, steelhead [*Oncorhynchus mykiss*]: Leider et al., 1986; Seamons et al., 2004), presumably due to the greater energy requirement for producing eggs (cf. sperm), along with the greater number of larger eggs that a larger female can produce. In this study, the sex ratio of *An* trout captured and tagged was 26F:17M and the sex ratio of *An* trout approaching the weir was near equality, as was the case for *FRA* trout, unlike for *PM* trout where over twice the number of males attempted upstream migration as females, putatively "precocious parr". Although only 6.3% of all *PM* trout were recorded as spermiating at tagging in September and October, this is a conservative estimate of the proportion becoming sexually mature as many do not begin to spermiate until November in this stream (A. Lothian, unpublished data). It is unknown whether the female *PM* fish approaching the weir in this study were juvenile or reproductively mature (female brown trout can mature at 11 cm in small Norwegian streams [Jonsson and Jonsson, 2011]). Nevertheless, the overall proportion of PM tagged fish that approached the weir and were migrating upstream was low (17.2%) and may reflect either a relatively low rate of precocious maturation within the parr form and/or that a large proportion of sexually mature parr morphotypes spawned locally, downstream of the weir.

Genetic, and phenotypic, diversity within a population is important for resilience to changing environments (i.e. climate change, anthropogenic structure construction, pollution events, etc.; King et al., 2007). For example, this study experienced what might be considered to be unusual environmental conditions (an extended low-flow period, see Supplementary S1.2), but which are also becoming more frequent. Unlike in many other studies (Jensen and Aass, 1995; Lucas and Frear, 1997; Newton et al., 2018; Tummers et al., 2018), environmental variables had almost no influence on the probability of passage success in this study (Supplementary S1.2; Figure S5). An extended dry summer in 2017 led to flows being lower than in most years and resulted in the tagging period coinciding with very low flows (Q90 or lower flow for 45.5% of the period 22 September to 15 November). Although upstream movements did correlate with elevated flows, these happened much later in the study period, after spawning had already commenced (A. Lothian, pers. obs.). Most *An* fish moved out of the Browney and into the Wear initially post-release, although over 60% of these returned back upstream later and approached the weir. This 'drop-back' is a documented response behaviour of captured, tagged and released salmonids (Thorstad et al., 2003; Havn et al., 2015), but, due to the low flows, may also have been a response to perceived predation/disturbance risk in what is a small stream channel. At least four tagged *An* trout are known to have been predated by otter (*Lutra lutra*) within a week of release. Similarly, radio tracked *FRA* and *PM* trout largely remained within a localised area for the majority of the study. This may be a result of tracking only during the day, as brown trout can be most active at dawn and dusk (Bunnell Jr. and Isely, 1998). Indeed, *FRA* trout approaching the weir did so more regularly at night. However, overall relatively few *FRA* and *PM* trout successfully migrated upstream where the majority of spawning and rearing habitat was. Therefore, genetic and phenotypic diversity is a necessity in a population to accommodate yearly environmental fluctuations.

4.3 Conclusion

In conclusion, this study illustrates that in natural populations of salmonids in spawning tributaries, multiple phenotypes may take part in migration, and environmental mitigation should provide for all phenotypes in order to support the widest gene pool for adaptive responses. Although fish were able to pass the obstacle in our study over a range of environmental conditions, weir passage was highest in the *An* phenotype and the construction of the fishway has not strongly mitigated the effect of the weir as a partial barrier to fish migration for *An*, *FRA*, or *PM* brown trout. Fishways have the capability to reduce the selective pressures on a population, but only if they are constructed in a way that enables them to work to their full capacity. Attraction to fishway entrances need to be improved either through allowing a greater volume of water through the fishway or by co-locating the entrance with areas of high discharge to greatly reduce the time spent searching by fish and increase permeability of the barrier.

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Supplementary Material

S1.1 Manual Tracking

For manually-tracked fish the relationship between direction of fish movement and river flow was compared using a Welch two sample *t*-test. Mean river flow was calculated for the time between two subsequent detections of a radio tagged fish, and associated with that fish's direction of movement (i.e. upstream or downstream between subsequent detections).

Of 53 radio-tagged trout, 51 were relocated at least once, comprising 7 *FRA* (2 female, 5 male), 6 *PM* (1 female, 5 male), and 38 *An* (21 female, 17 male) trout. Post-release, 34 trout (33 *An* and 1 *FRA*) dropped downstream into the River Wear. Many anadromous trout (n =21) re-entered the Browney, principally during the periods of flow elevation, especially the major flow peak in the third week of November (Figure S5) and approached the weir. Overall, fish tended to move upstream after periods of higher flows (upstream: 0.77 ±1.4 m^3s^{-1} [mean ±S.D.]; downstream: 0.49 ±0.6 m^3s^{-1}; Welch two sample t-test: t_{283} =-2.7, p =0.008). Of those radio tagged fish that successfully passed the weir (n =14; all of which were anadromous trout), 13 were fish that had initially dropped back into the Wear. Tagged trout were observed spawning in suitable habitat patches downstream as well as upstream of the weir, as well as in the River Wear itself, including around the Browney confluence. Over the study duration, radio-tagged *An* trout travelled a significantly greater mean distance (mean =8.2 km) than *FRA* (mean =1.9 km; *t*-test: $t_{19.1}$ =-4.9, p <0.001) and *PM* trout (mean =0.6 km; *t*-test: $t_{40.7}$ =-8.3, p <0.001; Table S2). Amongst all phenotypes, males tended to travel greater mean distances (Table S2), but this was not significant among phenotypes.

S1.2 Abiotic Variables Influencing Passage Performance

River temperatures ranged from 0.1°C to 14.0°C (Figure S5). River temperature at time of first detection on A1 did not have an influence on passage success (median [25th percentile, 75th percentile), successful attempts =9.4 °C [7.0°C, 11.9°C], unsuccessful attempts =8.1°C [6.1°C, 11.5°C], LRT: χ^2_2 =2.27, p =0.13). A large range of flows (Q3.4-Q98.1) occurred over the study period, but flow distribution was dominated by long periods of low flow during the pre-spawning period. Nevertheless, fish were detected throughout this range in approaching (Q3.4-Q96.9) and passing the weir (Q3.4-Q96.4; Figure S5). Mean daily flow at the time of first attempt was not significant in the passage success model (LRT: χ^2_2 =0.69, p =0.41). Anadromous trout were observed passing the weir on the greatest range of flows (Q3.4-Q94.4), followed by *PM* (Q40.3-Q96.4), and then *FRA* (Q54.5-Q94.4). Although the fishway route was used under a narrower range of flow conditions (Q29.1-Q96.4) than when fish traversed the weir (Q3.4-Q94.4), there was no difference in mean daily river discharge between passage routes (Welch two sample t-test: $t_{9.5}$ =-1.2, p =0.28). Passage was not influenced by whether a fish attempted during the daytime or night-time (LRT: χ^2_2 =1.53, p =0.22).

TABLE S1. The mean and range of distances travelled by male and females of each phenotype (*FRA*: Freshwater Resident Adult).

Phenotype	Distance (km; mean (range))		
	Male	Female	Overall
Parr-marked	0.7 (0.1-1.5)	0.03 (0.03-0.03)	0.6 (0.03-1.5)
FRA	2.4 (0.1-7.3)	0.6 (0.2-1.0)	1.9 (0.1-7.3)
Anadromous	9.2 (1.2-18.5)	7.5 (0.4-18.3)	8.2 (0.4-18.5)

TABLE S2. Length (mm; mean (±S.D.)) of fish that approached the weir by phenotype that successfully or unsuccessfully passed the weir (*FRA*: Freshwater Resident Adult).

Phenotype	Successful Passage		Unsuccessful Passage	
	No.	Length (mm)	No.	Length (mm)
Parr-marked	8	171 (±12)	14	174 (±13)
FRA	2	221 (±5)	6	238 (±56)
Anadromous	17	559 (±58)	10	562 (±105)
Total	27	447 (±182)	30	316 (±190)

TABLE S3. Output of Likelihood Ratio Test (LRT) carried out on the final overall passage success model, indicating that Phenotype should not be removed from the model.

Variable	Degrees of Freedom	Deviance	AIC	LRT	P value
Empty model		69.03	75.03	-	-
Phenotype	2	75.79	77.79	6.76	0.03

TABLE S4. Output of final Generalised Linear Model (GLM) with binomial distribution (based on model selection by Likelihood Ratio Test) describing overall passage success.

Variable	Confidence Intervals (2.5%, 97.5%)	Estimate	Std. Error	Z value	P value
Intercept	-3.02, 0.37	-1.10	0.82	-1.35	0.18
Phenotype Parr-Marked	-1.53, 2.35	0.25	0.95	0.26	0.79
Phenotype Anadromous	-0.04, 3.68	1.63	0.91	1.79	0.07

TABLE S5. Output of Generalised Linear Model (GLM) with binomial distribution comparing passage success to length.

Variable	Confidence Intervals (2.5%, 97.5%)	Estimate	Std. Error	Z value	P value
Intercept	-2.35, 0.01	-1.13	0.60	-1.90	0.05
Length	0.00, 0.01	0.002	0.001	1.94	0.05

Figure S1. View from downstream to upstream, of Burnhall flow-gauging weir, and the notched pre-barrages installed to break the weir height into a series of smaller steps more easily passable by trout. The fishway entrance is out of sight on the right-side of the image (left bank).

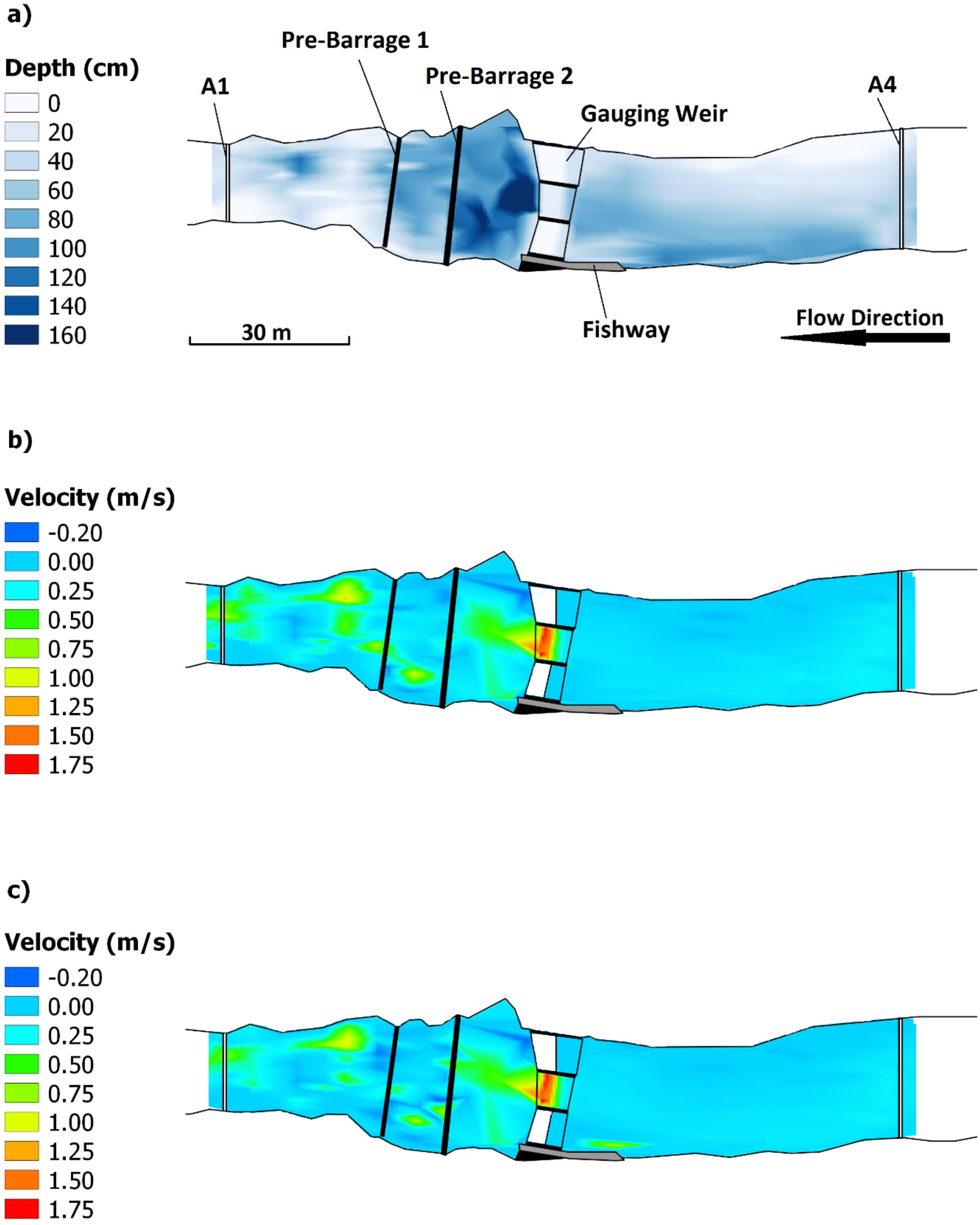

Figure S2. a) the depth (cm) of water flowing from A1 to A4, b) the flow velocity (m s^{-1}) at 10% depth between A1 and A4, and c) the flow velocity (m s^{-1}) at 50% depth between A1 and A4. River flow is from right to left. Measurements taken on 18th and 19th February 2019 at Q59.

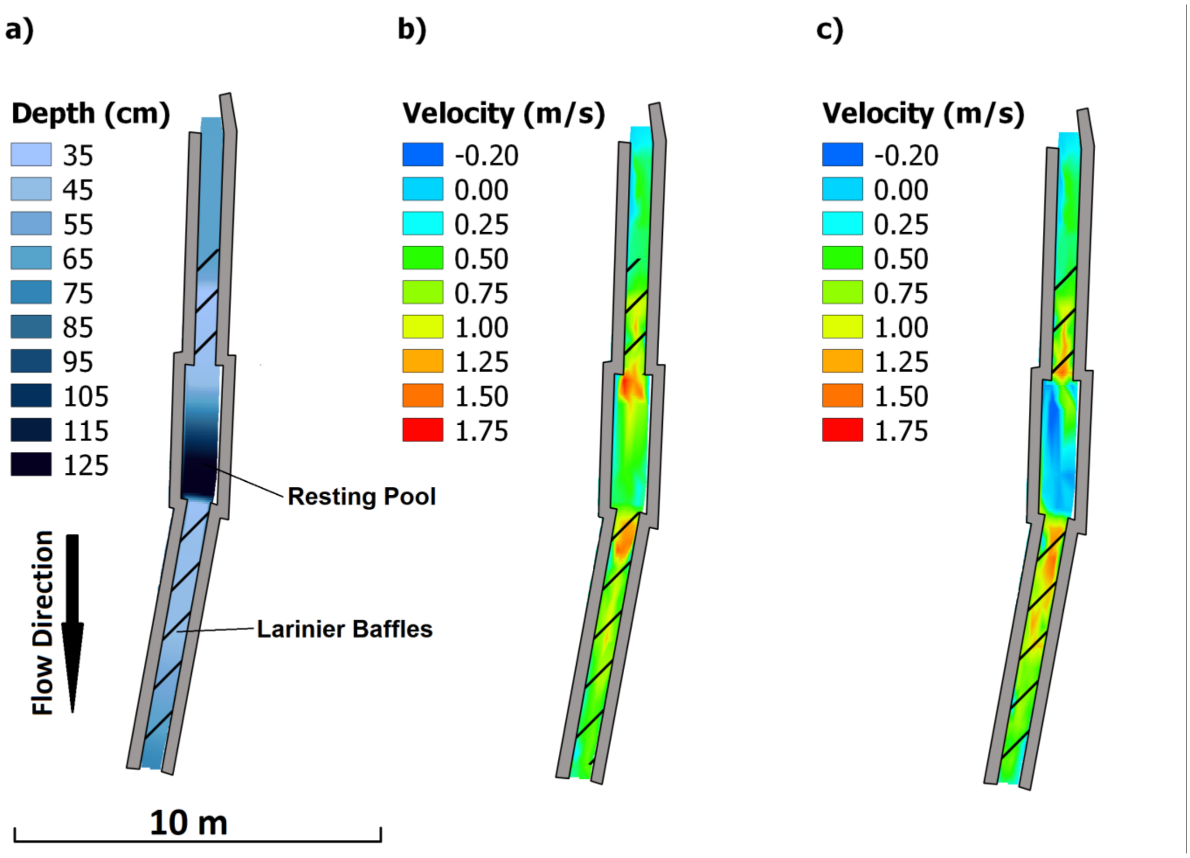

Figure S3. a) the depth (cm) of water flowing through the fishway, b) the flow velocity (m s^{-1}) of water at 10% depth through the fishway, and c) the flow velocity (m s^{-1}) at 50% depth through the fishway. Measurements taken on 18th and 19th February 2019 at Q59.

Figure S4. Examples of Anadromous (*An*; top), Freshwater Resident Adult (*FRA*; middle), and Parr-Marked (*PM*; bottom) trout from the study.

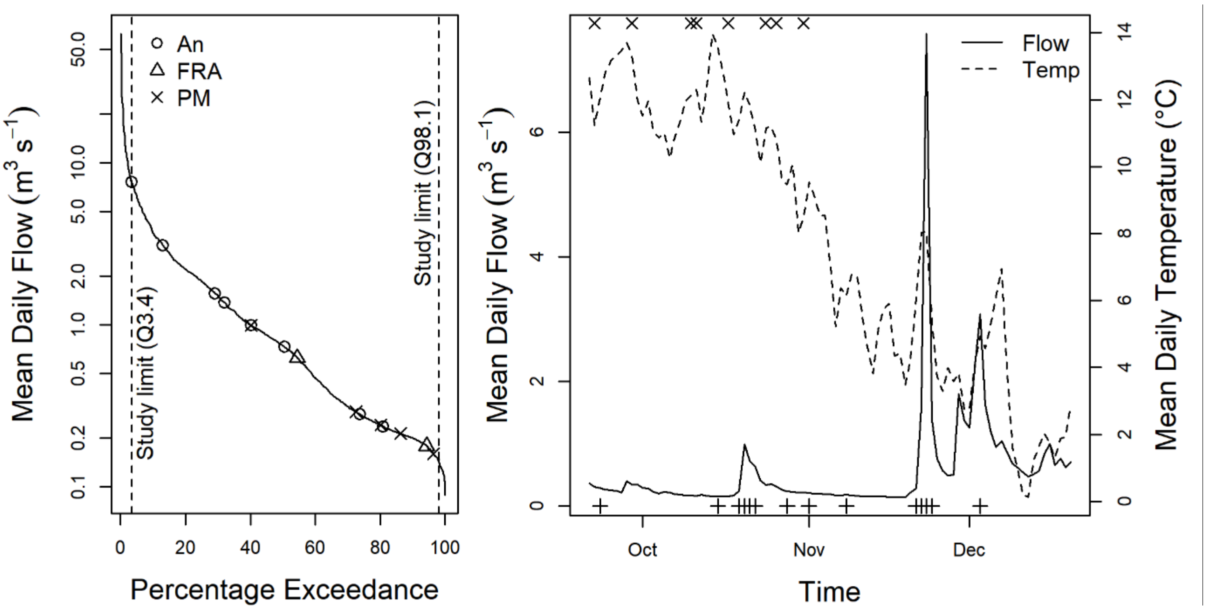

Figure S5. Left: The flow exceedance curve (based on long term (2000-2017) gauged data) with minimum and maximum exceedance during the study. Flow conditions during successful passes for each phenotype (*An*: Anadromous; *FRA*: Freshwater Resident Adult; *PM*: Parr-Marked) are overlaid onto curve. Right: Mean daily flow (solid line) and mean daily water temperature (dashed line) for the study period. Releases (crosses) and successful ascents of the weir (pluses) are provided along the *x*-axis.

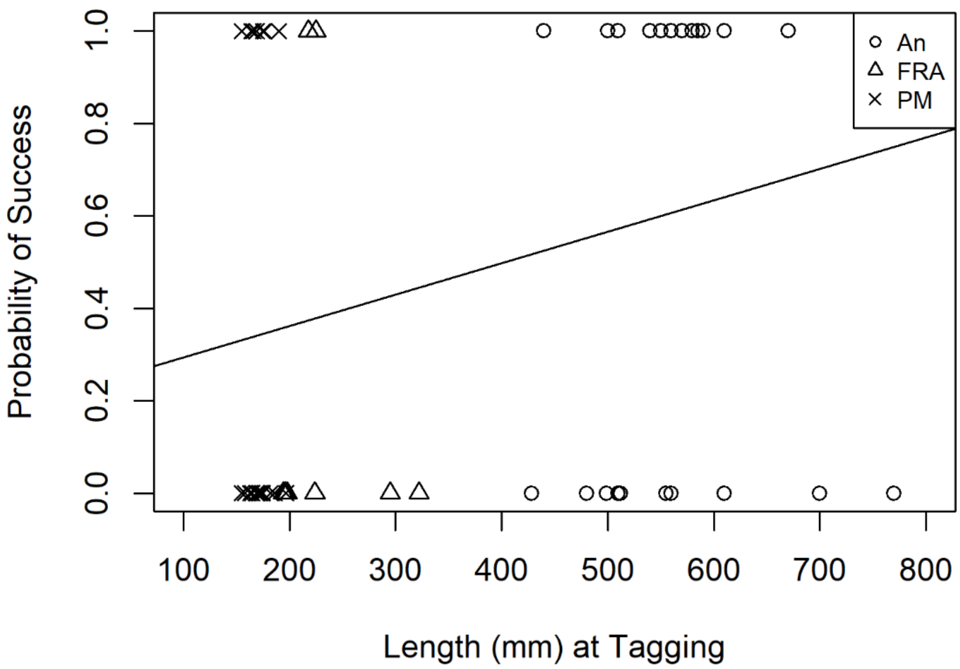

Figure S6. Probability of successful passage of fish that approached the weir. Solid line represents linear regression for all fish (*An*: Anadromous; *FRA*: Freshwater Resident Adult; *PM*: Parr-Marked phenotypes).