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1   **Are we designing fishways for diversity? Potential selection on**  
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27

28           **Abstract**

29           Fishways are commonly employed to improve river connectivity for fishes, but the extent to  
30           which they cater for natural phenotypic diversity has been insufficiently addressed. We  
31           measured differential upstream passage success of three wild brown trout (*Salmo trutta*)  
32           phenotypes (anadromous, freshwater-resident adult and parr-marked), encompassing a range  
33           of sizes and both sexes, at a Larinier superactive baffle fishway adjacent to a flow-gauging  
34           weir, using PIT telemetry ( $n=160$ ) and radio telemetry ( $n=53$ , double tagged with PIT tags).  
35           Fish were captured and tagged downstream of the weir in the autumn pre-spawning period,  
36           2017, in a tributary of the River Wear, England, where over 95% of tributary spawning habitat  
37           was available upstream of the weir. Of 57 trout that approached the weir-fishway complex,  
38           freshwater-resident adult and parr-marked phenotypes were less successful in passing than  
39           anadromous trout (25%, 36%, and 63% passage efficiency, respectively). Seventy-one percent  
40           of anadromous trout that passed upstream traversed the weir directly. Although the fishway  
41           facilitated upstream passage, it was poor in attracting fish of all phenotypes (overall attraction  
42           efficiency, 22.8%). A higher proportion (68.2%) of parr-marked trout that approached the weir  
43           were male and included sexually mature individuals, compared with that of freshwater-resident  
44           (37.8%) and anadromous trout (37.0%). The greater passage success of anadromous trout was  
45           likely due to their greater size and locomotory performance compared to the other phenotypes.  
46           Barriers and fishways can act as selection filters, likely the case in this study, and greater  
47           consideration needs to be given to supporting natural diversity in populations when proposing  
48           fishway designs to mitigate river connectivity problems.

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

51           **1. Introduction**

52       The anthropogenic modification of rivers through the building of structures such as dams and  
53       weirs negatively impacts many aquatic species (Lucas and Baras, 2001; Reidy Liermann et al.,  
54       2012). Due to the linear nature of rivers they become easily fragmented, partitioning habitats  
55       which differ in availability and quality (Peter, 1998; Rosenberg et al., 2000; Birnie-Gauvin et  
56       al., 2017a). Furthermore, these structures often restrict the movement of aquatic fauna,  
57       especially fishes (Silva et al., 2018). For many fish species, natural movement within a river  
58       is a vital element of their life-history allowing them to make use of the spatially-separated  
59       resources required at different life stages (Lennox et al., 2019). Thus for most temperate  
60       riverine fishes, summer feeding habitat is likely different in nature and location from spawning  
61       habitat, which in turn is likely different from overwintering habitat, all of which are essential  
62       for survival, growth and successful reproduction (Lucas and Baras, 2001). Impeded passage  
63       between these habitat types is highly likely to impact on ultimate fitness for affected individuals  
64       (Thorstad et al., 2008; Lennox et al., 2019; Tamario et al., 2019).

65           Where anthropogenic barriers exist, a key river rehabilitation tool is the improvement  
66       of longitudinal connectivity between habitat patches (Wohl et al., 2015) to facilitate restoration  
67       of hydromorphic and ecological processes, including animal dispersal and migration (Radinger  
68       and Wolter, 2015; Tummers et al., 2016). Ideally this is done by barrier removal, but a range  
69       of societal constraints mean that this is often not feasible (Birnie-Gauvin et al., 2017b). For  
70       fish, the most common mitigation to support passage past obstacles, especially in an upstream  
71       direction, is the provision of fishways (Dodd et al., 2017; Silva et al., 2018). While several  
72       fishway designs may work well for target species, it is increasingly apparent that they work  
73       poorly for others (Bunt et al., 2012; Foulds and Lucas, 2013), or fail to provide adequate  
74       community-level migration and dispersal solutions (Hall et al., 2012). Human actions such as

75 fisheries can act as natural selection filters, resulting in anthropogenic induced evolutionary  
76 change (Edeline et al., 2007; Tillotson and Quinn, 2018); dams and fishways can also operate  
77 in this way (Haugen et al., 2008; Volpato et al., 2009). There is evidence that shows genetic  
78 changes within, and divergence between, populations that are partially or wholly split by  
79 barriers (Stamford and Talyor, 2005; Gouskov et al., 2016; Wilkes et al., 2018; Van Leeuwen  
80 et al., 2018). The extent to which small anthropogenic obstacles and fishways may exert a  
81 selection pressure on naturally existing phenotypic diversity within fish populations has,  
82 however, been insufficiently addressed (Haugen et al., 2008; Tamario et al., 2019).

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

97 Salmonid fishes often exhibit a variety of discrete phenotypes and life histories within  
98 a single population (Campbell, 1977; Leider et al., 1986; Bekkevold et al., 2004; Seamons et  
99 al., 2004). In any brown trout (*Salmo trutta*) population, for example, multiple phenotypic

100 groups associated with alternative life histories strategies are frequently expressed (Jonsson  
101 and Jonsson, 2011). Three of the most common life history patterns exhibited in brown trout  
102 populations are: anadromy, freshwater residence, and precocious maturation.

103 The anadromous (*An*) phenotype ('sea trout') is characterised by migration between  
104 freshwater and the sea, with individuals carrying out most body growth at sea (McDowall,  
105 1992). This migration provides access to nutrient-rich habitats in order to grow in size, and  
106 thereby increasing potential fitness, before returning to freshwater to reproduce (Klemetsen et  
107 al., 2003; Jonsson and Jonsson, 2011; Aarestrup et al., 2017). As a result, *An* individuals tend  
108 to be larger in size than those that remain in freshwater. *An* trout may travel entire river lengths  
109 during their movement between river and sea, and therefore require a high degree of river  
110 connectivity. Although larger body sizes generally result in greater burst and sustained  
111 swimming speeds that might confer advantages in passing small anthropogenic barriers over  
112 other phenotypic groups, the added energy expenditure in attempting passage is an additional  
113 cost that could have fitness consequences later on in the migration (Thorstad et al., 2008).

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

122 Some brown trout individuals become sexually mature at a relatively small size whilst  
123 retaining their markings typical of the juvenile parr-marked (*PM*) stage, exhibiting a cryptic

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

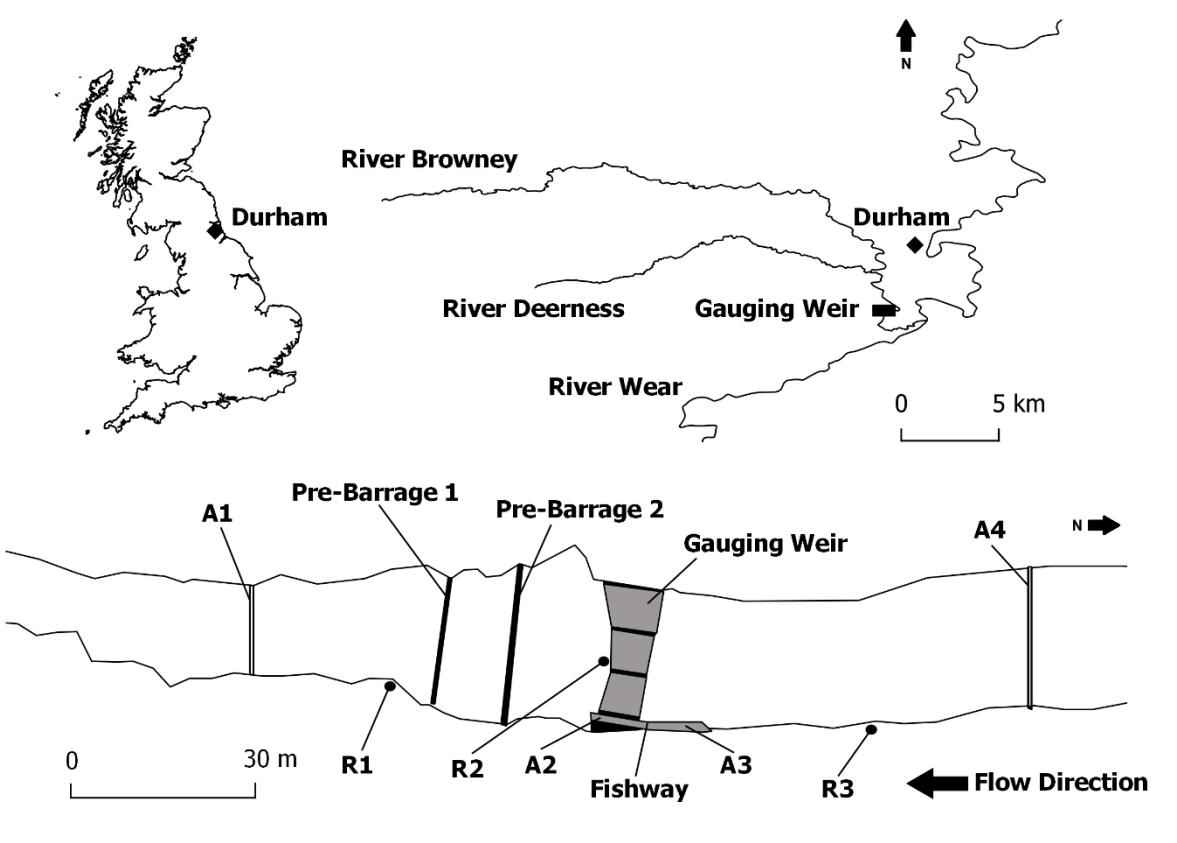
134 These different phenotypes are frequently expressed in trout from the same catchment,  
135 and as such are drawn from a common gene pool (Archer et al., 2019). Thus phenotypes are  
136 not determined solely by genetics (Ferguson et al., 2019). The initiation of the processes  
137 leading to anadromy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

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

160 **2. Materials and Methods**

161 *2.1 Study Site*

162 The River Browney, a tributary of the middle reaches of the River Wear, northeast England, is  
163 45 km long and has a mean daily discharge of  $\sim 1.6 \text{ m}^3\text{s}^{-1}$ . The tributary has plentiful spawning  
164 habitat for salmonids and is an important nursery stream for trout (Winter et al., 2016). Its  
165 spawning population comprises of *An*, *FRA* and *PM* adult phenotypes. An Environment  
166 Agency flow-gauging weir, Burnhall weir (Latitude: 54.742552; Longitude: -1.599043), 2.7  
167 km upstream of the Browney-Wear confluence, is the first obstacle encountered during  
168 upstream migration in the Browney (Figure 1). This has been demonstrated by radio tracking  
169 to be an obstacle to upstream passage of *An* phenotype trout at low to moderate flows (Tummers  
170 et al., 2016). More than 95% of salmonid spawning and nursery habitat in the Browney occurs  
171 upstream of Burnhall weir.



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

177 Burnhall weir was built in 1954 on an existing bedrock cascade. It is an 18-m wide  
 178 compound, broad-crested weir, with a 3-m gently sloping (~3%) apron and a vertical truncation  
 179 at the downstream end, with current overall head difference of 0.7 m at Q59 ( $0.50 \text{ m}^3 \text{ s}^{-1}$ ; Q  
 180 value derived from gauged data over the period 2000-2017). Two full-channel-width pre-  
 181 barrages (29-m and 16-m downstream of the weir) with step heights of ~0.25 m were built in  
 182 their current form in 1996 to facilitate passage of jumping fish. The first pre-barrage has four  
 183 equidistant notches, and the second five notches, each 2.2-m wide and 0.1-m deep, formed  
 184 from stacked timbers in slots, with a greater notch depth (0.2 m) on the left-most notch, creating  
 185 attraction flow (especially on the left side) and jumping points at low to moderate river flows  
 186 (Figure S1). Velocity (measured with a Valeport 801 EM flow meter) and depth profiles (18-  
 187 19 February 2019 at Q59) of the immediate area surrounding the weir are given in Figure S2.

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

198           2.2 *Fish Capture and Tagging*

199   Fish were captured in the Browney, 440-2240 m downstream of the weir, on eight days between  
200   22 September and 31 October 2017 (Table 1), prior to spawning (normally mid-November to  
201   late- December in this stream), using pulsed DC electrofishing. We assume that adult trout  
202   captured were either resident to, or had originated from, the tributary and expected that this  
203   would maximise the likelihood that tagged fish would migrate upstream and encounter the  
204   study weir, as reproductive homing in brown trout is well-known (Lucas and Baras, 2001).  
205   During later sampling dates, we avoided localities in the fishing zone where radio-tagged fish  
206   were, to minimise disturbance; any Passive Integrated Transponder (PIT) tagged fish  
207   recaptured were returned to the capture site immediately after fishing.

208           All trout captured in a sampling session in a given zone (Table 1) and exceeding 120  
209   mm in length were tagged and released in the same capture zone on the same day. We assumed  
210   that sexually mature individuals from all phenotypes tagged downstream of the obstacle would  
211   exhibit upstream migratory behaviour. Numbers of each phenotype tagged were dictated by

212 their availability. *An* and *FRA* phenotypes had no parr-marks, and were distinguished from  
 213 each other by colouration and size (Jonsson and Jonsson, 2011; Figure S4). These fish were  
 214 assumed to be reproductively mature. Secondary sexual characteristics were used to determine  
 215 sex (possible for all *An* and some *FRA* phenotypes). *PM* fish were identified by parr marks  
 216 (Figure S4) on the flanks but this group could be juvenile (reproductively immature parr) or  
 217 adult (reproductively mature ‘precocious parr’). The abdomens of all *PM* fish (lightly sedated,  
 218 tricaine methanesulphonate, 100 mg l<sup>-1</sup>) were gently stripped to release gametes to determine  
 219 sex and maturation status; this was only possible for those fish of advanced sexual maturity.  
 220 Following sedation, each fish was measured (fork length; mm) and weighed (g). A small  
 221 incision (~4 mm) was made anterior to the pelvic girdle on the ventral surface before a PIT tag  
 222 (for fish with fork length <160mm: half-duplex [HDX], 23x3.4 mm, 0.6 g in air, Oregon RFID,  
 223 Oregon; for fish with fork length >160mm: HDX, 32x3.7 mm, 0.8 g in air, Oregon RFID) was  
 224 inserted into the body cavity.

225 **TABLE 1.** The number of fish PIT tagged and Radio+PIT tagged, the range of fish lengths (mm),  
 226 distance of release site downstream of the weir (m) and sex (Male/Female/Unknown) based on  
 227 molecular sexing for each day of tagging split by phenotype (*PM*: Parr-marked; *FRA*: Freshwater  
 228 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	<i>PM</i>	18	143-201	-	-	1115	1/1/16
22/09/2017	<i>FRA</i>	12	147-295	-	-	1115	2/1/9
29/09/2017	<i>PM</i>	10	162-198	-	-	440	0/1/9
29/09/2017	<i>FRA</i>	1	264	1	322	440	2/0/0
29/09/2017	<i>An</i>	-	-	8	428-700	440	1/7/0
10/10/2017	<i>PM</i>	19	143-198	-	-	1315	4/1/14
10/10/2017	<i>FRA</i>	1	206	-	-	1315	0/0/1
11/10/2017	<i>PM</i>	8	145-210	1	229	2000	1/2/6

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

229

230 Samples of *An*, *FRA* and spermating male *PM* trout (and one female *PM*), greater than  
 231 170 mm in length, were double-tagged with a radio tag and a PIT tag. An incision, slightly  
 232 longer than the radio tag width, was made on the ventral surface of the fish anterior to the pelvic  
 233 girdle. Either an F1740 coded radio transmitter with a whip antenna (3.4 g in air, 11.54 pulses  
 234 per minute, ATS, Minnesota) or an F1210 coded transmitter with an internal coil antenna (11  
 235 g in air, 35 pulses per minute, ATS, Minnesota) was inserted into the body cavity of *An* trout.

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

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

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

### 253 2.3 PIT Logging Station Network

254 Four PIT antennas were installed around the weir and fishway to monitor trout upstream  
255 migration between 22 September and 14 December 2017 (Figure 1). To avoid damage by large  
256 woody debris during high flows, antennas in the main channel were flatbed designs attached to  
257 anchors drilled into the bedrock. A flatbed antenna (A1), with a vertical detection range of  
258 ~0.2 m and Q59 depth of ~0.1 m was placed 64 m downstream of the fishway entrance, to  
259 record fish approaching the weir. Two PIT antennas were placed in the fishway: one at the

260 downstream entrance (A2) and one at the upstream exit (A3). Both A2 and A3 were of loop  
261 form, set within recesses in the fishway walls, encompassing the width and height of the  
262 fishway and had horizontal detection ranges of ~0.5 m either side of the antenna. Another  
263 flatbed antenna (A4) was positioned 65 m upstream of the fishway exit. The vertical detection  
264 range of A4 was ~0.2 m and water depth over the antenna was 0.2-0.3 m at Q59. Detection  
265 ranges were tested with a 23 mm PIT tag to provide the smallest possible detection range.

266 A1 and A4 were operated as described by Bolland et al. (2009). A2 and A3 were  
267 operated as described by Lothian et al. (2019). Data (date, time, antenna number, PIT tag ID)  
268 were downloaded on each site visit. Antenna functionality and range were checked manually  
269 on each visit (every 3-4 days); all readers and antennas were operational for >94% of the study  
270 period. Field detection efficiencies of PIT antennas over the study period were estimated from  
271 the proportions of tagged fish known to have moved upstream of a given antenna based on  
272 records from passive PIT and radio stations upstream. Efficiency measurement of A4 was  
273 based on detections of double-tagged fish on radio antenna R3 and manual radio tracking  
274 upstream of A4 (Figure 1). Detection efficiency of PIT stations over the study period were: A1,  
275 87.3%; A2, 100%; A3, 100%; A4, 96.3%.

#### 276 *2.4 Automated Radio Receiver Network and Manual Tracking*

277 An automated radio receiver system was used to determine fish movement around the weir  
278 complex (Figure 1). A dipole antenna (R1, range radius ~30 m) was positioned 38 m  
279 downstream of the fishway entrance to record fish approaching the pre-barrages from  
280 downstream. A monopole (R2, range radius ~15 m) was positioned immediately downstream  
281 of the weir. R2 recorded radio tags in the weir pool but due to the weir structure itself, tags  
282 upstream of the weir were not detected. A dipole antenna (R3, range radius ~40 m) was placed  
283 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,

309 as well as the habitat characteristics in the immediate vicinity of the tagged fish. Detailed  
310 statistical approach and results of manual tracking can be found in Supplementary Material  
311 S1.1.

312 *2.5 Statistical Approach*

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

331 Approach duration was also investigated. For successful fish, approach duration was  
332 defined as the time difference between the first detection on A1 until the first detection on A4,

333 and defined as the time taken between first detection on A1 until the last detection on A1 for  
334 failed attempts. Passage duration was calculated for successful fish only, and defined as  
335 difference in time between the last detection on A1 and the first detection on A4. Passage  
336 duration was compared between fish that took the weir route or the fishway route.

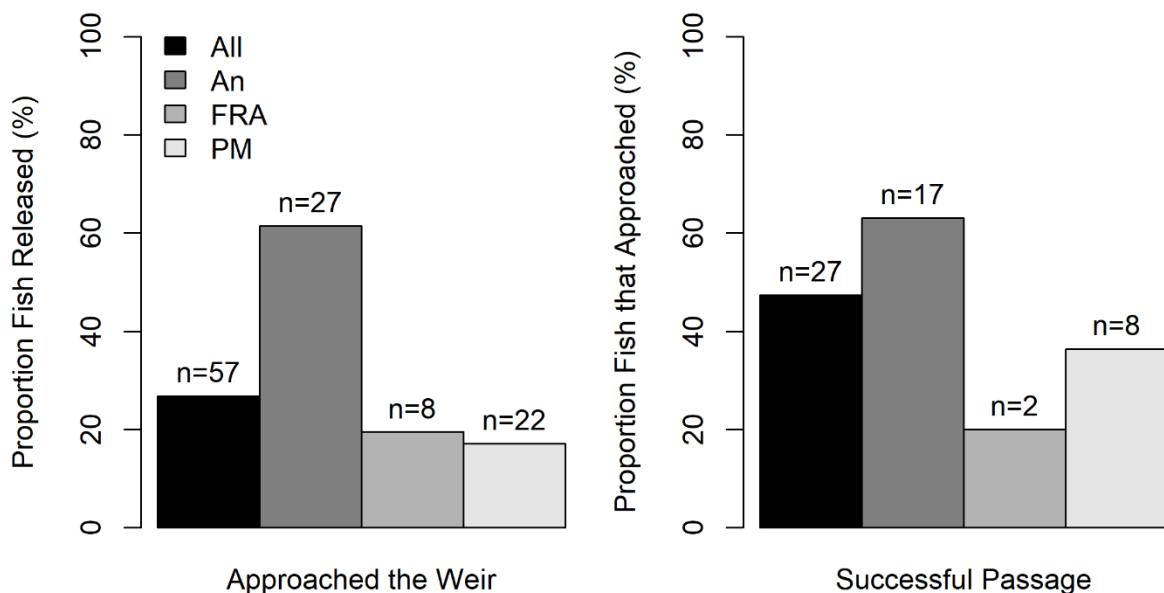
337 **3. Results**

338 *3.1 Passage Performance*

339 A total of 213 trout (*An*, 44; *FRA*, 41; *PM*, 128) were tagged and released (Table 1). These  
340 comprised 39 double-tagged and five PIT-tagged *An* phenotype; seven double-tagged and 34  
341 PIT-tagged *FRA*; seven double-tagged and 121 PIT-tagged *PM*. Fifty seven of the 213 trout  
342 approached the weir, comprising 22 *PM* (17.2% of *PM* released), 8 *FRA* (19.5% of *FRA*  
343 released) and 27 *An* (61.4% of *An* released; Table 2; Figure 2). Of the 57 fish that approached,  
344 27 were subsequently detected upstream of the weir, equating to an overall passage success of  
345 47.7% (Figure 2). Phenotype was a significant variable in the overall passage success model  
346 (LRT:  $\chi^2_2 = 6.76$ ,  $p = 0.03$ ; Table S3; S4), where *An* trout were the most successful at passing  
347 the weir with 63.0% ( $n = 17$ ) of those approaching successfully passing, followed by *PM* trout  
348 (36.4% of those that approached;  $n = 8$ ), and then *FRA* trout (25.0% of those that approached;  
349  $n = 2$ ).

350 Thirteen fish were detected entering the fishway, equating to 22.8% ( $n = 13/57$ )  
351 attraction efficiency of all those approaching the weir (attraction efficiencies per phenotype:  
352 *PM* [5/22] = 22.7%; *FRA* [2/8] = 25.0%; *An* [6/27] = 22.2%). Significantly fewer fish than  
353 expected were attracted to the fishway entrance (Chi squared test with Yates correction:  $\chi^2_2$   
354 = 6.94,  $p < 0.05$ ), but there was no difference between the phenotypes (Chi squared test with  
355 Yates correction:  $\chi^2_2 = 1.01$ ,  $p > 0.50$ ). Of those that entered the fishway, 10 were successfully  
356 detected at the upstream exit, a combined passage efficiency for the fishway route of 76.9% ( $n$

357 =10/13; passage efficiencies per phenotype: *PM*=80.0% [5/6]; *FRA*=50.0% [1/2]; *An*=83.3%  
 358 [4/5]). There was no difference in fishway passage success between each phenotype (Chi  
 359 squared test with Yates correction:  $\chi^2_2 = 1.43, p > 0.25$ ). One of the three fish that was  
 360 unsuccessful in passing via the fishway (*An* phenotype) subsequently traversed the obstacle by  
 361 the weir route, whereas the other two unsuccessful fishway fish (*PM* and *FRA*) failed to pass  
 362 the weir-fishway complex entirely.



363  
 364 **Figure 2.** The proportion of each brown trout phenotype (*An*: Anadromous; *FRA*: Freshwater  
 365 Resident Adult; *PM*: Parr-Marked) released that approached the weir (left) and the proportion of  
 366 each phenotype that approached the weir that ultimately succeeded in passing the weir-fishway  
 367 complex.

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

376 =0.72,  $p$  =0.40). Twelve male and 15 female trout succeeded in passage of the weir (Table 3).  
377 Environmental variables (temperature and river height) were not found to be significant in the  
378 overall passage success model (more information on environmental variables can be found in  
379 Supplementary S1.2).

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

386

387 *3.2 Passage Duration*

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

395

396   **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  
 397   Resident Adult).

<b>Phenotype</b>	<b>Tag type</b>	<b>No. tagged</b>	<b>No. approached (proportion of tagged fish)</b>	<b>No. successful (proportion of fish that approached)</b>	<b>No. traversed weir (proportion of successful fish)</b>	<b>No. used fishway (proportion of successful fish)</b>
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%)
<i>FRA</i>	PIT	34	7 (20.0%)	2 (28.6%)	1 (50.0%)	1 (50.0%)
<i>FRA</i>	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%)
<b>Total</b>		<b>213</b>	<b>57 (26.8%)</b>	<b>27 (47.4%)</b>	<b>17 (63.0%)</b>	<b>10 (37.0%)</b>

398

399

400 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  
 401 in passage of the weir (i.e. traversing the weir or using the fishway; *FRA*: Freshwater Resident Adult). <sup>a</sup>One FRA individual (that attempted but subsequently  
 402 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	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
<i>FRA</i>	3	4 (5 <sup>a</sup> )	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

403

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

Phenotype	Overall Passage Duration (hrs; 25 <sup>th</sup> ,75 <sup>th</sup> )	Weir Route Passage Duration (hrs; 25 <sup>th</sup> ,75 <sup>th</sup> )	Fishway Route Passage Duration (hrs; 25 <sup>th</sup> ,75 <sup>th</sup> )
Parr-marked	4.2 (3.4, 4.3)	3.4 (3.4, 3.4)	4.3 (3.6, 5.3)
<i>FRA</i>	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)
<b>Total</b>	<b>1.8 (1.1, 4.2)</b>	<b>1.3 (1.0, 0.6)</b>	<b>5.2 (3.5, 8.5)</b>

407

#### 408 **4. Discussion**

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

422

423

424        4.1 Passage Performance

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

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

446        Although few fish were attracted to and entered the fishway in this study, similar  
447        proportions of each phenotype were attracted to the fishway and succeeded in passing it,

448 indicating that the fishway did not select for a phenotype, but was simply inefficient for all  
449 phenotypes. Although *An* trout passage success was not very different between the weir route  
450 and fishway route (once they had found and entered the fishway), the passage success for *PM*  
451 and *FRA* trout for the fishway route (once they had entered the fishway) was greater than for  
452 the weir route. Furthermore, there was no significant difference in fishway passage between  
453 *An*, *FRA* and *PM* trout. This suggests that the fishway does have the potential to remove the  
454 selective pressure imposed on the trout population by the weir.

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

#### 466 4.2 Potential Evolutionary Consequences

467 Differential passage between phenotypes, and within phenotypes, can lead to changes in  
468 the population structure. Haugen et al., (2008) showed that the construction of a fishway  
469 altered the upstream assemblage of brown trout in a Norwegian river above a dam from larger  
470 to smaller fish as the fishway worked most efficiently for medium-sized fish. The weir in our  
471 study has been present since 1954, and was built on a series of natural cascades which may

472 have acted as a natural selection agent for larger (i.e. *An*) trout, although the complex hydraulics  
473 of sloping cascades can facilitate passage of small as well as larger trout (Forty et al., 2016).  
474 If the fishway in the current study on the Browney functioned effectively for sexually mature  
475 trout of all three phenotypes, a shift in population structure, and possibly genetic structure,  
476 might be seen in the future as more *FRA* and *PM* trout gain access to the mid- and upper-  
477 Browney. Given that an abundant trout population exists upstream of the weir, there may only  
478 be a limited impact on the trout population upstream as a result of the redistribution of  
479 phenotypes across the weir. However, it is important to ensure sufficient bidirectional gene  
480 mixing across partial barriers to ensure adequate diversity is maintained in a population (Wilkes  
481 et al., 2018). Population isolation as a result of barriers can cause changes in genetic structure,  
482 resulting in genetically distinct populations either side of the barriers (Stamford and Taylor,  
483 2005; Gouskov et al., 2016; Van Leeuwen et al., 2018).

484 Anadromy in salmonids is often female biased (brown trout: Campbell, 1977; Bekkevold  
485 et al., 2004, steelhead [*Oncorhynchus mykiss*]: Leider et al., 1986; Seamons et al., 2004),  
486 presumably due to the greater energy requirement for producing eggs (cf. sperm), along with  
487 the greater number of larger eggs that a larger female can produce. In this study, the sex ratio  
488 of *An* trout captured and tagged was 26F:17M and the sex ratio of *An* trout approaching the  
489 weir was near equality, as was the case for *FRA* trout, unlike for *PM* trout where over twice the  
490 number of males attempted upstream migration as females, putatively “precocious parr”.  
491 Although only 6.3% of all *PM* trout were recorded as spermating at tagging in September and  
492 October, this is a conservative estimate of the proportion becoming sexually mature as many  
493 do not begin to spermate until November in this stream (A. Lothian, unpublished data). It is  
494 unknown whether the female *PM* fish approaching the weir in this study were juvenile or  
495 reproductively mature (female brown trout can mature at 11 cm in small Norwegian streams  
496 [Jonsson and Jonsson, 2011]). Nevertheless, the overall proportion of PM tagged fish that

497 approached the weir and were migrating upstream was low (17.2%) and may reflect either a  
498 relatively low rate of precocious maturation within the parr form and/or that a large proportion  
499 of sexually mature parr morphotypes spawned locally, downstream of the weir.

500 Genetic, and phenotypic, diversity within a population is important for resilience to  
501 changing environments (i.e. climate change, anthropogenic structure construction, pollution  
502 events, etc.; King et al., 2007). For example, this study experienced what might be considered  
503 to be unusual environmental conditions (an extended low-flow period, see Supplementary  
504 S1.2), but which are also becoming more frequent. Unlike in many other studies (Jensen and  
505 Aass, 1995; Lucas and Frear, 1997; Newton et al., 2018; Tummers et al., 2018), environmental  
506 variables had almost no influence on the probability of passage success in this study  
507 (Supplementary S1.2; Figure S5). An extended dry summer in 2017 led to flows being lower  
508 than in most years and resulted in the tagging period coinciding with very low flows (Q90 or  
509 lower flow for 45.5% of the period 22 September to 15 November). Although upstream  
510 movements did correlate with elevated flows, these happened much later in the study period,  
511 after spawning had already commenced (A. Lothian, pers. obs.). Most *An* fish moved out of  
512 the Browney and into the Wear initially post-release, although over 60% of these returned back  
513 upstream later and approached the weir. This ‘drop-back’ is a documented response behaviour  
514 of captured, tagged and released salmonids (Thorstad et al., 2003; Havn et al., 2015), but, due  
515 to the low flows, may also have been a response to perceived predation/disturbance risk in what  
516 is a small stream channel. At least four tagged *An* trout are known to have been predated by  
517 otter (*Lutra lutra*) within a week of release. Similarly, radio tracked *FRA* and *PM* trout largely  
518 remained within a localised area for the majority of the study. This may be a result of tracking  
519 only during the day, as brown trout can be most active at dawn and dusk (Bunnell Jr. and Isely,  
520 1998). Indeed, *FRA* trout approaching the weir did so more regularly at night. However,  
521 overall relatively few *FRA* and *PM* trout successfully migrated upstream where the majority of

522 spawning and rearing habitat was. Therefore, genetic and phenotypic diversity is a necessity  
523 in a population to accommodate yearly environmental fluctuations.

524 **4.3 Conclusion**

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

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546 **References**

- 547 Aarestrup, K., Jepsen, N., Thorstad, E.B., 2017. Brown trout on the move – Migration ecology  
548 and methodology, in Lobon-Cervia, J., Sanz, N. (Eds.), Brown Trout: Biology, Ecology and  
549 Management. John Wiley and Sons, Chichester, UK, pp 401-444.
- 550 Alberti, M., 2015. Eco-evolutionary dynamics in an urbanizing planet. Trends Ecol. Evol. 30,  
551 114-126.
- 552 Archer, L.C., Hutton, S.A., Harman, L., O'Grady, M.N., Kerry, J.P., Poole, W.R., Gargan, P.,  
553 McGinnity, P., Reed, T.E., 2019. The interplay between extrinsic and intrinsic factors in  
554 determining migration decisions in brown trout (*Salmo trutta*): an experimental study.  
555 Front. Ecol. and Evol. 7, 1- 18. DoI: 10.3389/fevo.2019.00222
- 556 Armstrong, G.S., Aprahamian, M.W., Fewings, G.A., Gough, P.J., Reader, N.A., Varallo, P.V.,  
557 2010. Environment Agency fish pass manual: Guidance notes on the legislation, selection  
558 and approval of fish passes in England and Wales. Version 2.2. (Report No. GEHO 0910  
559 BTBP-E-E). Environment Agency, Bristol, UK.
- 560 Ayllon, F., Kjaerner-Semb, E., Furmanek, T., Wennevik, V., Solberg, M.F., Dahle, G.,  
561 Taranger, G.L., Glover, K.A., Almen, M.S., Rubin, C.J., Edvardsen, R.B., Wargelius, A.,  
562 2015. The vgl13 locus controls age at maturity in wild and domesticated Atlantic salmon  
563 (*Salmo salar* L.) males. PLOS Genet. 11, 1-15.
- 564 Bekkevold, D., Hansen, M.M., Mensberg, K.D., 2004. Genetic detection of sex-specific  
565 dispersal in historical and contemporary populations of anadromous brown trout *Salmo*  
566 *trutta*. Mol. Ecol. 13, 1707-1712.
- 567 Birnie-Gauvin, K., Aarestrup, K., Rils, T.M.O., Jepsen, N., Koed, A., 2017a. Shining a light  
568 on the loss of rheophilic fish habitat in lowland rivers as a forgotten consequence of  
569 barriers, and its implication for management. Aquat. Conserv. Mar. Freshw. Ecosyst. 27,  
570 1345-1349.
- 571 Birnie-Gauvin, K., Tummers, J.S., Lucas, M.C., Aarestrup, K., 2017b. Adaptive management  
572 in the context of barriers in European freshwater ecosystems. J. Environ. Manage. 204, 436-  
573 441.
- 574 Bolland, J.D., Cowx, I.G., Lucas, M.C., 2009. Dispersal and survival of stocked cyprinids in a  
575 small English river: comparison with wild fishes using a multi-method approach. J. Fish  
576 Biol. 74, 2313-2328.
- 577 Buck, R.J.G., Youngson, A.F., 1982. The downstream migration of precociously mature  
578 Atlantic salmon *Salmo salar* L. parr in autumn; its relationship to the spawning migration  
579 of mature adult fish. J. Fish Biol. 20, 279-288.

- 580 Bunnel Jr., D.B., Isley, J.J., 1998. Diel movement of brown trout in a Southern Appalachian  
581 River. Trans. Am. Fish. Soc. 127, 630-636.
- 582 Bunt, C.M., Castro-Santos, T., Haro, A., 2012. Performance of fish passage structures at  
583 upstream barriers to migration. River Res. Appl. 28, 475-478.
- 584 Campbell, J.S., 1977. Spawning characteristics of brown trout and sea trout *Salmo trutta* L. in  
585 Kirk Burn, River Tweed, Scotland. J. Fish Biol. 11, 217-299.
- 586 Dodd, J.R., Bolland, J.D., Hateley, J., Cowx, I.G., Walton, S.E., Cattaneo, M.E.G.V., Noble,  
587 R.A.A., 2018. Upstream passage of adult sea trout (*Salmo trutta*) at a low-head weir with  
588 an Archimedean screw hydropower turbine and co-located fish pass. Mar. Freshw. Res. 69,  
589 1822-1833.
- 590 Dodd, J.R., Cowx, I.G. Bolland, J.D., 2017. Efficiency of a nature-like bypass channel for  
591 restoring longitudinal connectivity for a river-resident population of brown trout. J. Environ.  
592 Manage. 204, 318-326.
- 593 Edeline, E., Carlson, S.M., Stige, L.C., Winfield, I.J., Fletcher, J.M., James, J.B., Haugen, T.O.,  
594 Vollestad, L.A., Stenseth, N. C., 2007. Trait changes in a harvested population are driven  
595 by a dynamic tug-of-war between natural and harvest selection. Proc. Natl. Acad. Sci. U. S.  
596 A. 104, 15799–15804. <https://doi.org/10.1073/pnas.0705908104>
- 597 Eisbrenner, W.D., Botwright, N., Davidson, E.A., Dominik, S., Elliott, N.G., Henshall, J.,  
598 Jones, S.L., Kube, P.D., Lubieniecki, K.P., Peng, S., Davidson, W.S., 2014. Evidence for  
599 multiple sex-determining loci in Tasmanian Atlantic salmon (*Salmo salar*). Heredity, 113,  
600 86-92.
- 601 Ferguson, A., Reed, T.E., Cross, T.F., McGinnity, P., Prodohl, P.A., 2019. Anadromy,  
602 potamodromy and residence in brown trout *Salmo trutta*: the role of genes and the  
603 environment. J. Fish Biol. 1-27. DoI: 10.1111/jfb.14005
- 604 Forty, M., Spees, J., Lucas, M.C., 2016. Not just for adults! Evaluating the performance of  
605 multiple fish passage designs at low-head barriers for the upstream movement of juvenile  
606 and adult trout *Salmo trutta*. Ecol. Eng. 94, 214-224.
- 607 Foulds, W.L., Lucas, M.C., 2013. Extreme inefficiency of two conventional, technical  
608 fishways used by European river lamprey (*Lampetra fluviatilis*). Ecol. Eng. 58, 423-433.
- 609 Franssen, N., 2011. Anthropogenic habitat alteration induces rapid morphological divergence  
610 in a native stream fish. Evol. Appl. 4, 791-804.
- 611 Gouskov, Q., Reyes, M., Wirthner-Bitterlin, L., Vorburger, C., 2016. Fish population genetic  
612 structure shaped by hydroelectric power plants in upper Rhine catchment. Evol. Appl. 9,  
613 394-408.
- 614 Hall, C.J., Jordaan, A., Frisk, M.G., 2012. Centuries of anadromous forage fish loss:  
615 Consequences for ecosystem connectivity and productivity. BioScience. 62, 723-731.

- 616 Haugen, T.O., Aass, P., Stenseth, N.C., Vøllestad, L.A., 2008. Changes in responses and  
617 evolutionary selection in migratory brown trout following the construction of a fish ladder.  
618 *Evol. Appl.* 1, 319-335.
- 619 Havn, T.B., Uglem, I., Solem, O., Cooke, S.J., Whoriskey, F.G., Thorstad, E.B., 2015. The  
620 effect of catch-and-release angling at high water temperatures on the behaviour and survival  
621 of Atlantic salmon *Salmo salar* during spawning migration. *J. Fish Biol.* 87, 342-359.
- 622 Heino, M., Pauli, B.D., Dieckman, U., 2015. Fisheries Induced Evolution. *Annu. Rev. Ecol.*  
623 *Evol. S.*, 46, 461-480.
- 624 Jensen, A., and Aass, P., 1995. Migration of a fast-growing population of brown trout (*Salmo*  
625 *trutta* L.) through a fish ladder in relation to water flow and water temperature. *River Res.*  
626 *Appl.* 10, 217-228.
- 627 Jones, J., Borger, L., Tummers, J., Lucas, M., Kerr, J., Kemp, P., Bazzi, B., Consuegra, S.,  
628 Marcello, L., Vowles, A., Belletti, B., Verspoor, E., Van de Bund, W., Gough, P., Garcia de  
629 Leaniz, C., 2019. A comprehensive assessment of stream fragmentation in Great Britain.  
630 *Sci. Total Environ.* 672, 756-762.
- 631 Jonsson, B., Jonsson, N., 2011. *Ecology of Atlantic Salmon and Trout: Habitat as a Template*  
632 *for Life Histories*. Springer, Dordrecht.
- 633 King, T.L., Verspoor, E., Spidle, A.P., Gross, R., Phillips, R.B., Koljonen, M.-L., Sanchez,  
634 J.A., Morrison, C.L., 2007. Biodiversity and population structure, in: Verspoor, E.,  
635 Stradmeyer, L., Nielsen, J.L. (Eds.), *The Atlantic Salmon: Genetics, Conservation and*  
636 *Management*. Oxford, Blackwell, p. 117-166
- 637 Klemetsen, A., Amundsen, P.A., Dempson, J.B., Jonsson, B., Jonsson, N., O'Connell, M.F.,  
638 Mortensen, E., 2003. Atlantic salmon *Salmo salar* L., brown trout *Salmo trutta* L. and Arctic  
639 charr *Salvelinus alpinus* (L.): a review of aspects of their life histories. *Ecol. Freshw. Fish*  
640 12, 1-59.
- 641 Larinier, M., 2001. Environment issues, dams and fish migration, in: Marmulla, G. (Eds.), *Food*  
642 *and Agricultural Organisation Fisheries Technical Paper 419. Dams, Fish and Fisheries,*  
643 *Opportunities, Challenges and Conflict Resolution*. Food and Agricultural Organisation,  
644 Rome, pp 45-89.
- 645 Larinier, M., 2008. Fish passage experience at small-scale hydro-electric power plants in  
646 France. *Hydrobiologia*, 609, 97-108.
- 647 Law, R., 2007. Fisheries-induced evolution: present status and future direction. *Mar. Ecol.*  
648 *Prog. Ser.* 335, 271-277.
- 649 Leider, S.A., Chilcote, M.W., Loch, J.J., 1986. Comparative life history characteristics of  
650 hatchery and wild steelhead trout (*Salmo gairdneri*) of summer and winter races in the  
651 Kalama River, Washington. *Can. J. Fish. Aquat. Sci.* 43, 1398-1409.

- 652 Lennox, R.J., Paukert, C.P., Aarestrup, K., Auger-Méthé, M., Baumgartner, L., Birnie-Gauvin,  
653 K., Bøe, K., Brink, K., Brownscombe, J.W., Chen, Y., Davidsen, J.G., Eliason, E.J., Filous,  
654 A., Gillanders, B.M., Helland, I.P., Horodysky, A.Z., Januchowski-Hartley, S.R., Lowerre-  
655 Barbieri, S.K., Lucas, M.C., Martins, E.G., Murchie, K.J., Pompeu, P.S., Power, M.,  
656 Raghavan, R., Rahel, F.J., Secor, D., Thiem, J.D., Thorstad, E.B., Ueda, H., Whoriskey,  
657 F.G., Cooke, S.J., 2019 One hundred pressing questions on the future of global fish  
658 migration science, conservation, and policy. *Front. Ecol. Ecol.* 7, 286. doi:  
659 10.3389/fevo.2019.00286
- 660 Lothian, A.J., Gardner, C.J., Hull, T., Griffiths, D., Dickinson, E.R., Lucas, M.C., 2019.  
661 Passage performance and behaviour of stocked and wild cyprinid fish at a sloping weir with  
662 a Low Cost Baffle fishway. *Ecol. Eng.* 130, 67-79.
- 663 Lucas, M.C., Baras, E., 2001. *Migration of Freshwater Fish*. Blackwell Science, Oxford,  
664 England.
- 665 Lucas, M.C., Frear, P.A., 1997. Effects of a flow-gauging weir on the migratory behaviour of  
666 adult barbel, a riverine cyprinid. *J. Fish. Biol.* 50, 382-396.
- 667 McDowall, R.M., 1992. Diadromy: origins and definitions of terminology. *Copeia* 1992, 248-  
668 251.
- 669 Newton, M., Dodd, J.A., Barry, J., Boylan, P., Adams, C.E., 2018. The impact of a small-scale  
670 riverine obstacle on the upstream migration of Atlantic salmon. *Hydrobiologia* 806, 251-  
671 264.
- 672 Nikora, V.I., Aberle, J., Biggs, B.J.F., Jowett, I.G. Sykes, J.R.E., 2003. Effects of fish size,  
673 time-to-fatigue and turbulence on swimming performance: a case study of *Galaxias*  
674 *maculatus*. *J. Fish Biol.* 63, 1365-1382.
- 675 Peter, A., 1998. Interruption of the river continuum by barriers and the consequences for  
676 migratory fish, in: Jungwirth, M., Schmutz, S., Weiss, S. (Eds.), *Fish Migration and Fish*  
677 *Bypasses*. Fishing News Books, Blackwell Science, Oxford, UK, pp. 99-112.
- 678 Pulido, F., 2011. Evolutionary genetics of partial migration – The threshold model of migration  
679 revisited. *Oikos* 120, 1776-1783.
- 680 R Core Team, 2014. R: A language and environment for statistical computing. R Foundation  
681 for Statistical Computing, Vienna, Austria, 0, {ISBN} 3-900051-07-0.
- 682 Radinger, J., Wolter, C., 2015. Disentangling the effects of habitat suitability, dispersal and  
683 fragmentation on the distribution of river fishes. *Ecol. Appl.* 25, 914-927.
- 684 Reidy Liermann, C., Nilsson, C., Robertson, J., Ng, R.Y., 2012. Implications of dam  
685 obstruction for global freshwater fish diversity. *BioScience*, 62, 539-548.
- 686 Rosenberg, D.M., McCully, P., Pringle, C.M., 2000. Global-scale environmental effects of  
687 hydrological alterations: introduction. *Bioscience*, 50, 746-751.
- 688 Saura, M., Caballero, A., Caballero, P., Moran, P., 2008. Impact of precocious male parr on  
689 the effective size of a wild population of Atlantic salmon. *Freshw. Biol.* 53, 2357-2384.

- 690 Seamons, T.R., Bentzen, P., Quinn, T.P., 2004. The mating system of steelhead, *Oncorhynchus*  
691 *mykiss*, inferred by molecular analysis of parents and progeny. Environ. Biol. Fish. 69, 333-  
692 344.
- 693 Silva, A.T., Lucas, M.C., Castro-Santos, T., Katopodis, C., Baumgartner, L.J., Theim, J.D.,  
694 Aarestrup, K., Pompeu, P.S., O'Brien, G.C., Braun, D.C., Burnett, N.J., Zhu, D.Z.,  
695 Fjeldstad, H.P., Forseth, T., Rajaratnam, N., Williams, J.G., Cooke, S.J., 2018. The future  
696 of fish passage science, engineering and practice. Fish Fish. 19, 340-363.
- 697 Sinclair, A.F., Swain, D.P., Hanson, J.M., 2002a. Measuring changes in direction and  
698 magnitude of size-selective mortality in a commercial fish population. Can. J. Fish. Aquat.  
699 Sci. 59, 361-371.
- 700 Sinclair, A.F., Swain, D.P., Hanson, J.M., 2002b. Disentangling the effects of size-selective  
701 mortality, density, and temperature on length-at-age. Can. J. Fish. Aquat. Sci. 59, 372-382.
- 702 Stamford, M.D., and Taylor, E.B., 2005. Population subdivisions and genetic signatures of  
703 demographic changes in Arctic grayling (*Thymallus arcticus*) from an impounded  
704 watershed. Can. J. Fish. Aquat. Sci. 62, 2548-2559.
- 705 Stuart, T.A., 1962. The leaping behaviour of salmon and trout at falls and obstacles. HMSO,  
706 Edinburgh.
- 707 Tamario, C., Sunde, J., Petersson, E., Tibblin, P., Forsman, A., 2019. Ecological and  
708 evolutionary consequences of environmental change and management actions for migrating  
709 fish. Front. Ecol. Evol. 7, 1-24. DoI: 10.3389/fevo.2019.00271
- 710 Thorstad, E.B., Naesje, T.F., Fiske, P., Findstad, B., 2003. Effects of hook and release on  
711 Atlantic salmon in the River Alta, northern Norway. Fish. Res. 60, 293-307.
- 712 Thorstad, E.B., Økland, F., Aarestrup, K., Heggerberget, T.G., 2008. Factors affecting the  
713 within-river spawning migration of Atlantic salmon, with emphasis on human impacts. Rev.  
714 Fish Biol. Fish. 18, 345-371.
- 715 Tillotson, M.D., Quinn, T.P., 2018. Selection on the timing of migration and breeding: A  
716 neglected aspect of fishing-induced evolution and trait change. Fish Fish. 19, 170-181.
- 717 Tummers, J.S., Hudson, S., Lucas, M.C., 2016. Evaluating the effectiveness of restoring  
718 longitudinal connectivity for stream fish communities: towards a more holistic approach.  
719 Sci. Total Environ. 569-570, 850-860.
- 720 Tummers, J.S., Kerr, J.R., O'Brien, P., Kemp, P., Lucas, M.C., 2018. Enhancing the upstream  
721 passage of river lamprey at a microhydropower installation using horizontally-mounted  
722 studded tiles. Ecol. Eng. 125, 87-97.
- 723 Van Leeuwen, C.H.A., Dalen, K., Museth, J., Junge, C., Vollestad, L. A., 2018. Habitat  
724 fragmentation has interactive effects on the population genetic diversity and individual  
725 behaviour of a freshwater salmonid fish. River Res. Appl. 34, 60-68

- 726 Volpato, G.L., Barreto, R.E., Marcondes, A.L., Moreira, P.S.A., de Barros Ferreira, M.F.,  
727 2009. Fish ladders select fish traits on migration – still a growing problem for natural fish  
728 populations. Mar. Freshw. Behav. Phy. 42, 307-313.
- 729 Wang, H., Chanson, H., 2018. On upstream fish passage in standard box culverts: interactions  
730 between fish and turbulence. J. Ecohydraulics 3, 18-29.
- 731 Wilkes, M.A., Webb, J.A., Pompeu, P.S., Silva, L.G.M., Vowles, A.S., Baker, C.F., Franklin,  
732 P., Link, O., Habit, E., Kemp, P.S., 2018. Not just a migration problem: Metapopulations,  
733 habitat shifts, and gene flow are also important for fishway science and management. River  
734 Res. Appl. 2018, 1-9. DOI: 10.1002/rra.3320.
- 735 Winter, E.R., Tummers, J.S., Aarestrup, K., Baktoft, H., Lucas, M.C., 2016. Investigating the  
736 phenology of seaward migration of juvenile brown trout (*Salmo trutta*) in two European  
737 populations. Hydrobiologia 775, 139-151.
- 738 Wohl, E., Lane, S.N., Wilcox, A.C., 2015. The science and practice of river restoration. Water  
739 Resour. Res., 51, 5974-5997.

740

741      **Supplementary Material**

742            *S1.1 Manual Tracking*

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

747            Of 53 radio-tagged trout, 51 were relocated at least once, comprising 7 *FRA* (2 female,  
748        5 male), 6 *PM* (1 female, 5 male), and 38 *An* (21 female, 17 male) trout. Post-release, 34 trout  
749        (33 *An* and 1 *FRA*) dropped downstream into the River Wear. Many anadromous trout ( $n = 21$ )  
750        re-entered the Browney, principally during the periods of flow elevation, especially the major  
751        flow peak in the third week of November (Figure S5) and approached the weir. Overall, fish  
752        tended to move upstream after periods of higher flows (upstream:  $0.77 \pm 1.4 \text{ m}^3\text{s}^{-1}$  [mean  
753         $\pm \text{S.D.}]$ ; downstream:  $0.49 \pm 0.6 \text{ m}^3\text{s}^{-1}$ ; Welch two sample *t*-test:  $t_{283} = -2.7, p = 0.008$ ). Of those  
754        radio tagged fish that successfully passed the weir ( $n = 14$ ; all of which were anadromous trout),  
755        13 were fish that had initially dropped back into the Wear. Tagged trout were observed  
756        spawning in suitable habitat patches downstream as well as upstream of the weir, as well as in  
757        the River Wear itself, including around the Browney confluence. Over the study duration,  
758        radio-tagged *An* trout travelled a significantly greater mean distance (mean = 8.2 km) than *FRA*  
759        (mean = 1.9 km; *t*-test:  $t_{19.1} = -4.9, p < 0.001$ ) and *PM* trout (mean = 0.6 km; *t*-test:  $t_{40.7} = -8.3, p$   
760         $< 0.001$ ; Table S2). Amongst all phenotypes, males tended to travel greater mean distances  
761        (Table S2), but this was not significant among phenotypes.

762            *S1.2 Abiotic Variables Influencing Passage Performance*

763            River temperatures ranged from 0.1°C to 14.0°C (Figure S5). River temperature at time  
764        of first detection on A1 did not have an influence on passage success (median [25<sup>th</sup> percentile,

765 75<sup>th</sup> percentile), successful attempts =9.4 °C [7.0°C, 11.9°C], unsuccessful attempts =8.1°C  
 766 [6.1°C, 11.5°C], LRT:  $\chi^2_2 = 2.27, p = 0.13$ ). A large range of flows (Q3.4-Q98.1) occurred over  
 767 the study period, but flow distribution was dominated by long periods of low flow during the  
 768 pre-spawning period. Nevertheless, fish were detected throughout this range in approaching  
 769 (Q3.4-Q96.9) and passing the weir (Q3.4-Q96.4; Figure S5). Mean daily flow at the time of  
 770 first attempt was not significant in the passage success model (LRT:  $\chi^2_2 = 0.69, p = 0.41$ ).  
 771 Anadromous trout were observed passing the weir on the greatest range of flows (Q3.4-Q94.4),  
 772 followed by *PM* (Q40.3-Q96.4), and then *FRA* (Q54.5-Q94.4). Although the fishway route  
 773 was used under a narrower range of flow conditions (Q29.1-Q96.4) than when fish traversed  
 774 the weir (Q3.4-Q94.4), there was no difference in mean daily river discharge between passage  
 775 routes (Welch two sample *t*-test:  $t_{9.5} = -1.2, p = 0.28$ ). Passage was not influenced by whether a  
 776 fish attempted during the daytime or night-time (LRT:  $\chi^2_2 = 1.53, p = 0.22$ ).  
 777

778 **TABLE S1.** The mean and range of distances travelled by male and females of each phenotype (*FRA*:  
 779 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)
<i>FRA</i>	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)

780

781 **TABLE S2.** Length (mm; mean ( $\pm$ S.D.)) of fish that approached the weir by phenotype that  
 782 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 ( $\pm 12$ )	14	174 ( $\pm 13$ )
<i>FRA</i>	2	221 ( $\pm 5$ )	6	238 ( $\pm 56$ )
Anadromous	17	559 ( $\pm 58$ )	10	562 ( $\pm 105$ )
<b>Total</b>	27	447 ( $\pm 182$ )	30	316 ( $\pm 190$ )

783

784 TABLE S3. Output of Likelihood Ratio Test (LRT) carried out on the final overall passage success  
785 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

786

787 TABLE S4. Output of final Generalised Linear Model (GLM) with binomial distribution (based on  
788 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

789

790 TABLE S5. Output of Generalised Linear Model (GLM) with binomial distribution comparing  
791 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

792

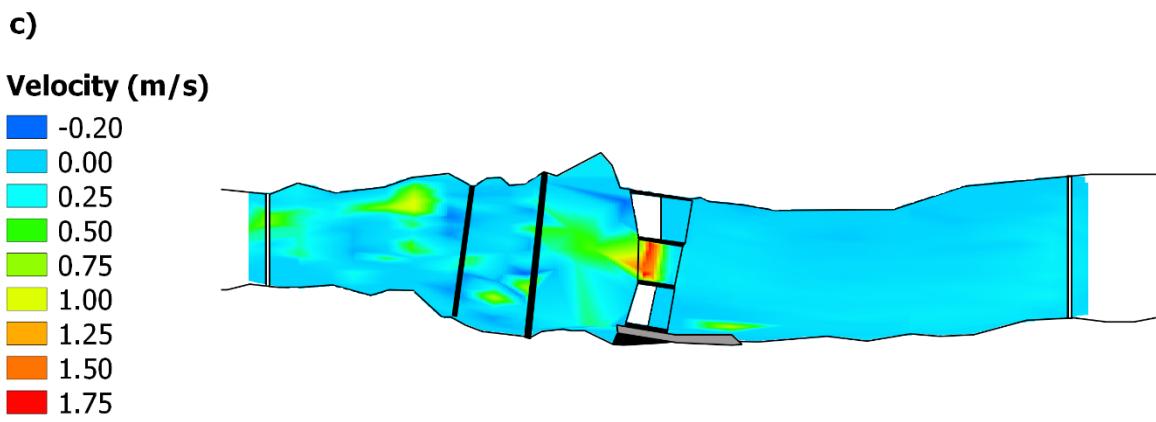
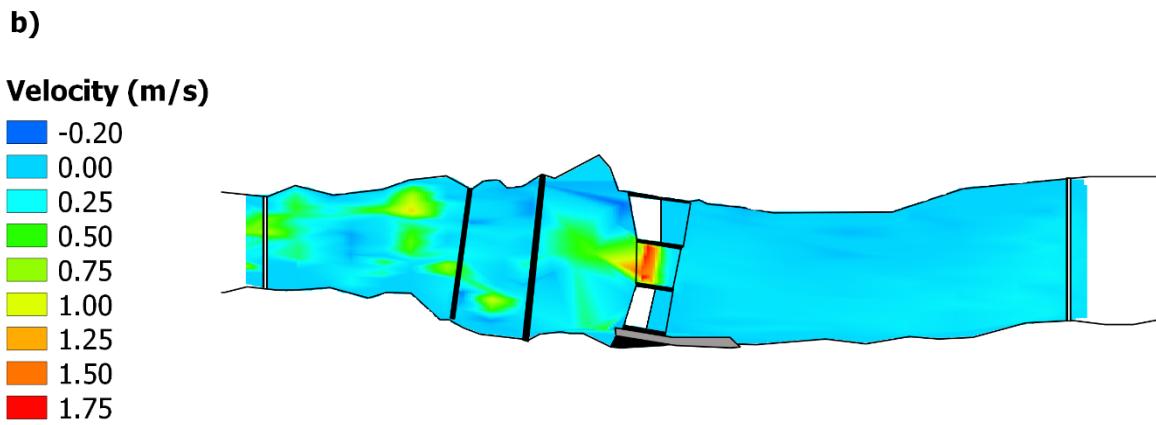
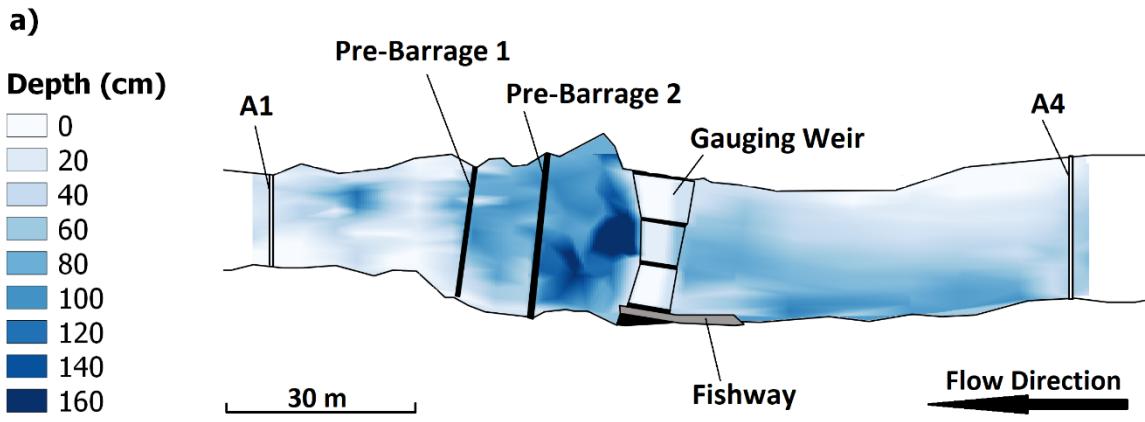


793

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

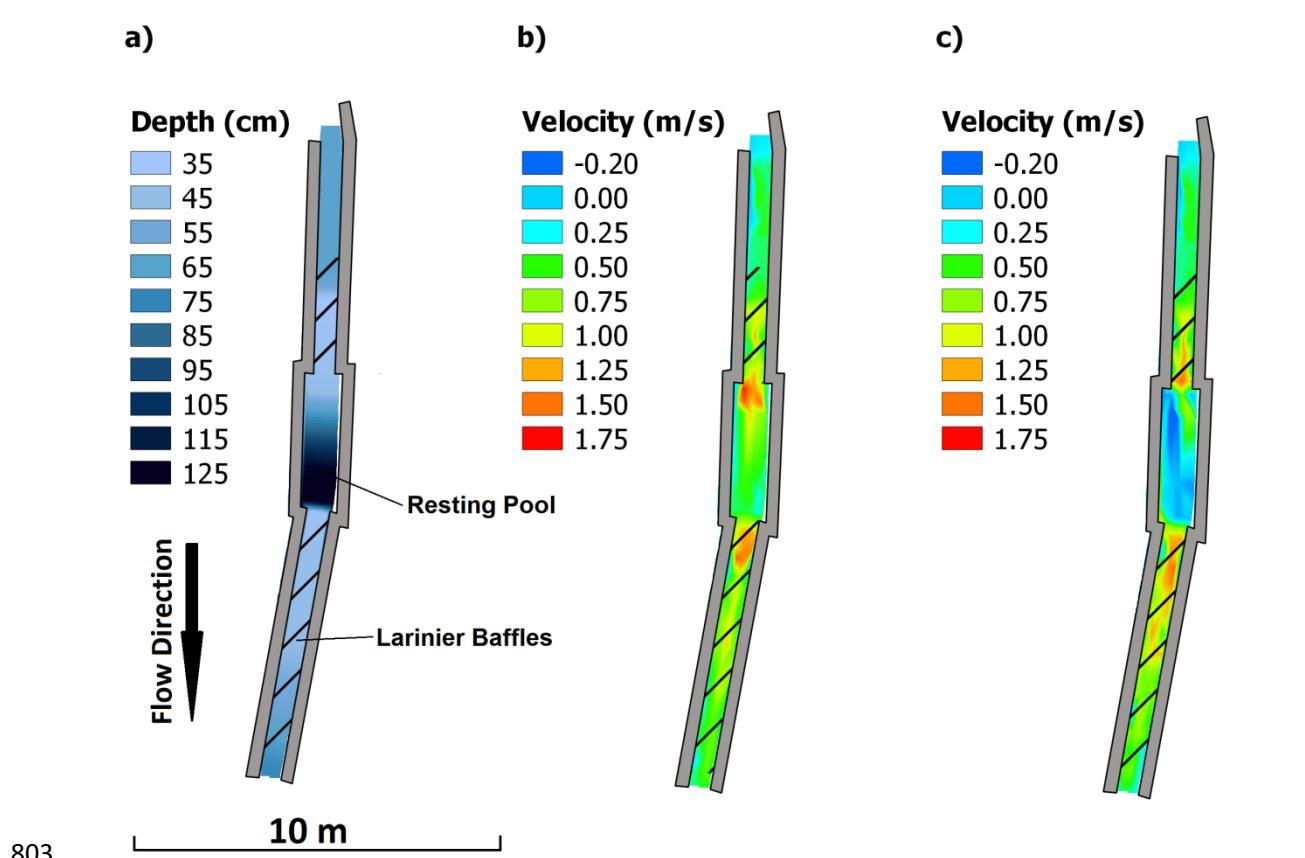
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799

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



803 **Figure S3.** a) the depth (cm) of water flowing through the fishway, b) the flow velocity ( $\text{m s}^{-1}$ ) of water  
 804 at 10% depth through the fishway, and c) the flow velocity ( $\text{m s}^{-1}$ ) at 50% depth through the fishway.  
 805 Measurements taken on 18<sup>th</sup> and 19<sup>th</sup> February 2019 at Q59.

806

807

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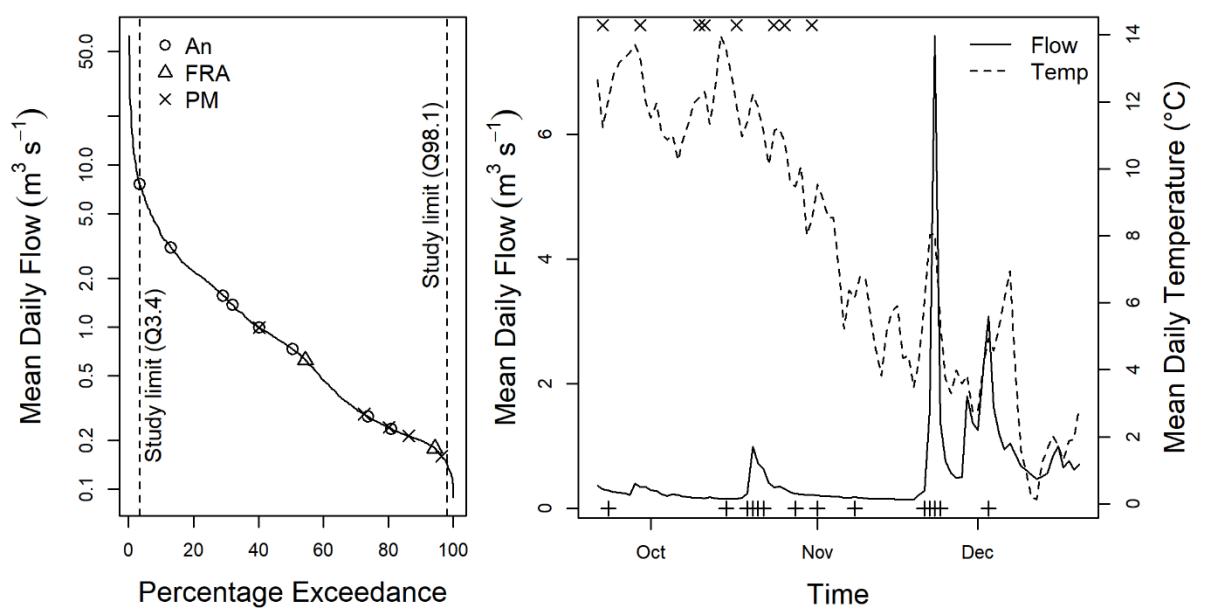


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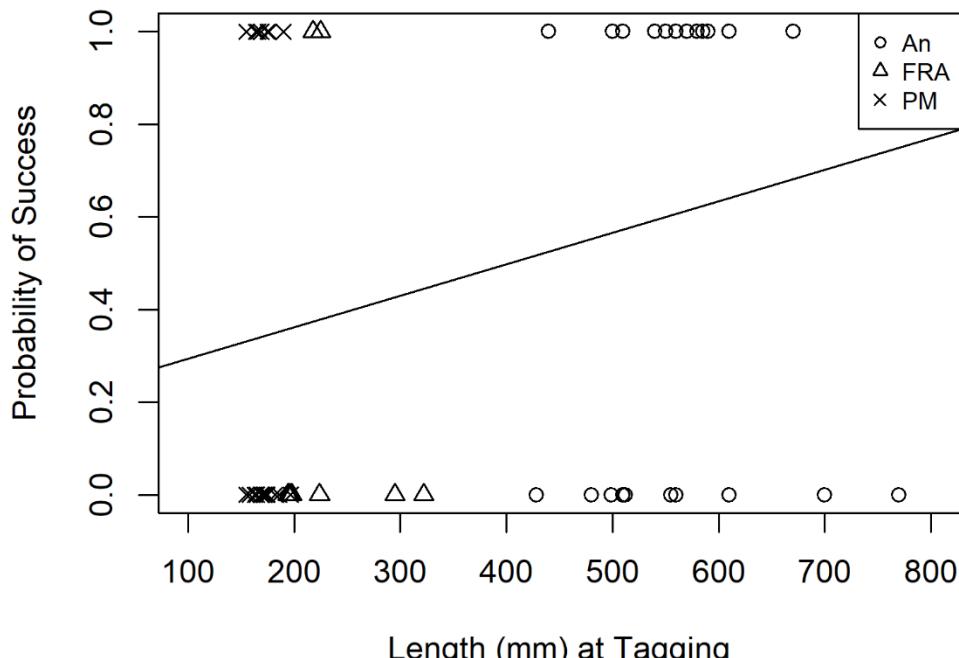


811

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



814  
815 **Figure S5.** Left: The flow exceedance curve (based on long term (2000-2017) gauged data) with  
816 minimum and maximum exceedance during the study. Flow conditions during successful passes for  
817 each phenotype (*An*: Anadromous; *FRA*: Freshwater Resident Adult; *PM*: Parr-Marked) are overlaid  
818 onto curve. Right: Mean daily flow (solid line) and mean daily water temperature (dashed line) for  
819 the study period. Releases (crosses) and successful ascents of the weir (pluses) are provided along the  
820 x-axis.



822  
823 **Figure S6.** Probability of successful passage of fish that approached the weir. Solid line represents  
824 linear regression for all fish (*An*: Anadromous; *FRA*: Freshwater Resident Adult; *PM*: Parr-Marked  
825 phenotypes).

826