1   **Not just for adults! Evaluating the performance of multiple fish passage designs at**

2   **low-head barriers for the upstream movement of juvenile and adult trout** *Salmo*

3   *trutta*

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16   **Abstract**

17   Longitudinal connectivity in salmonid streams is vital for juvenile as well as adult fish,

18   yet most upstream passage studies consider only larger adults. Upstream passage of

19   juvenile and adult brown trout *Salmo trutta* at low-head (< 3 m) structures on two River

20   Ribble tributaries (NW England) was investigated using Passive Integrated Transponder

21   (PIT) telemetry during summer-autumn 2013 and 2014. The efficiency of a Servais low-

22   cost baffle (LCB) fish pass was evaluated for the first time, along with two pool-weir

23   (PW) passes, an embedded rock ramp (ERR) and an open culvert (C), the latter a man-

24   made structure within predicted swim speed, acting as an experimental control. We used

25   a combination of naturally migrating trout and displacement experiments. Resident fish

26   were displaced from above to below structures, utilising their homing instinct to

27   instigate their ascent of the structure, with up to 91% of displaced trout attempting to

28   pass. Approximately 30% of parr morphotype trout released at their capture locations

29   attempted to pass upstream of structures in both streams. Passage efficiencies of up to

30   82% for the LCB pass design were similar to the PW (up to 79%) and better than the

31   ERR (71%), but below that for C (96% - 100%). Significant differences occurred

32   between fish passes in time to passage, and number of attempts to pass, with all but

33   PW1 having significantly longer time to passage than the control culvert. Median time

34   to passage at PW2 decreased almost fifty fold between 2013 and 2014, following

35   modification to equalise step heights at the structure. Logistic regression demonstrated a

36   strong body-length effect on passage success at passes, with 50% probability of

37   successful passage (82-132 mm) varying, but not significantly, between passes. We

38   conclude that small trout, including juveniles, can and do exhibit functionally

39 significant upstream movement and that greater consideration should be given of their

40 passage needs as well as for large, adult trout.

41

1. Introduction

Connectivity is a fundamental element of landscape structure and ecological processes and the longitudinal connectivity dimension is especially important in rivers (Fausch et al., 2002; Taylor et al., 1993). The ecological impacts of impoundment by in-stream structures such as dams, weirs and culverts on river systems can be extensive, especially upon fish populations, altering habitat and creating upstream and downstream obstacles to migration and dispersal (Aarestrup & Koed, 2003; Larinier, 2001; Lucas and Baras, 2001). Loss of free passage due to artificial barriers can lead to habitat fragmentation and limit fish distribution in water courses by reducing access to key habitats such as spawning grounds (Fausch et al., 2002; Lucas et al., 2009). River systems are particularly susceptible to fragmentation (Nilsson et al. 2005; Calles & Greenberg, 2009) as one barrier has the potential to isolate large sections of river from one another (Jager et al., 2001). Where a structure acts as a total barrier to upstream fish passage it can result in stark changes in community structure due to isolation (Pringle et al., 2000; Thorncraft and Harris, 2000). For fish which rely on migration to reach different habitat patches for life-cycle completion, especially diadromous fishes which may need to traverse large numbers of structures on their migration between the sea and freshwater, fragmentation can lead to extinctions upstream of structures (Lucas & Baras, 2001; McDowall, 1992). Loss of longitudinal connectivity can also decrease abundance more widely in the catchment when recruitment is reduced by lack of access to spawning/rearing grounds or due to reduced downstream migration success (Levin & Tolimieri, 2001; McDowall, 1992).

In contrast to high-head dams (> 15 m; Poff and Hart, 2002), the effects of small structures such as low-head dams, weirs and culverts are less well studied (Alexandre

68 and Almeida, 2010; Lucas & Frear, 1997; McLaughlin et al., 2006; Ovidio & Philippart,

69 2002). While small structures are often considered to be passable by strong swimmers

70 and jumpers like salmonids (McLaughlin et al., 2006) they can still bring about

71 migration delays while they are being negotiated (Svendsen et al., 2004), reducing the

72 condition of spawning fish and increasing exposure to predators. Kiffney et al. (2009)

73 showed that access to small streams was particularly important in the rearing of juvenile

74 salmonids, providing important habitat benefits for growth and survival. The presence

75 of these structures, such as culverts, has been reported to have negative effects on the

76 dispersal (Gibson et al., 2005; Park et al., 2008; Warren and Pardew, 2008) and

77 distribution (Pépino et al., 2012) of fish populations with impacts on genetic diversity

78 similar to those of natural waterfalls (Torterotot et al., 2014).

79 In order to mitigate the negative effects of obstacles on upstream migration, fish passage

80 technologies have been developed, such that there is now a wide variety of designs,

81 categorised as either technical (e.g. vertical slot, pool and weir, baffle-type) or nature-

82 like (e.g. by-pass channels and rock ramps) (Clay, 1995; Katopodis and Williams,

83 2012). Evaluation of the performance of fish passage structures has indicated that the

84 degree of success achieved can be very variable and site specific (Kemp, 2012). Even if

85 a high proportion of fish manage to pass using a fishway, negative impacts are often

86 still incurred, including migration delay, with fish attempting to pass structures on

87 multiple occasions (Foulds and Lucas, 2013; Gowans et al., 1999; Haro and Kynard,

88 1997; Hasler et al., 2011; Laine, 1995; Keefer et al., 2004). The ability to understand the

89 effects of migration delay have been limited by our ability to quantify it (Castro-Santos

90 & Haro, 2003). With 25,000 known man-made barriers on UK rivers alone, and an

91 increased ambition to provide free fish passage, it is important to determine the

92   functionality of fish passage designs (Gough et al., 2012). This is especially true within

93   tributaries where the impacts of barriers are less well investigated than in main stems of

94   rivers where fish passage facilities have mainly been constructed (Clay, 1995; Marmulla

95   & Ingendahl, 1996; Ovidio & Philippart, 2002).

96   Although fish passes have a long history (e.g. Denil, 1909) there remains a paucity of

97   good quality empirical information about the true effectiveness of differing types of

98   pass for different species of migratory fish (Bunt et al., 2012). Many fish pass designs

99   originated to accommodate adult salmonids with strong swimming capacities and a

100   persistent desire to pass upstream (Stuart, 1962, 1964). However, there is a range in

101   swimming ability present not only across species, but different life stages also, for

102   which passage structures are not always designed to accommodate. Free passage is not

103   only important for adult fishes but can also be vital for juveniles where it is required for

104   them to recover from disturbance events such as displacement by high flows (Ottaway

105   & Clarke, 1981) or pollution incidents (Baras and Lucas, 2001), for the seeking of

106   resources and seasonal shifts in distribution (Baras and Lucas, 2001), or where juvenile

107   morphotypes mature (e.g. male precocious salmonid parr) and contribute towards

108   population survival through alternative spawning strategies (Garcia-Vazquez et al.,

109   2001).

110   In order to achieve effective fish passage solutions that allow free migration and assist

111   in lifecycle completion, better quality information is required as to the performance of

112   fish pass designs. This study used passive integrated transponder (PIT) technology

113   (Castro-Santos et al., 1996; Lucas et al., 1999; Calles & Greenberg, 2005; Bunt et al.,

114   2012; Foulds & Lucas, 2013) to evaluate the performance of three types of low-head

115   fish pass (pool-weir, rock ramp, low-cost baffle) for the upstream passage of both adult

116 and juvenile brown trout (*Salmo trutta*) utilising both natural migration and in-nature

117 displacement experiments. The current study includes the first quantitative evaluation of

118 the low-cost baffle design of Servais (2006) that is increasingly being used in the UK as

119 a cheap retrofit fish passage solution for low-head sloping weirs.

120

121 **2. Materials and methods**

122 *2.1 Study area*

123 This study was conducted on two streams in the River Ribble catchment (1133 km^2),

124 one of the main river basins in northwest England. The Ribble drains limestone bedrock

125 in its headwaters, running south and then west before flowing in to the Irish Sea. The

126 two study streams were Swanside Beck (~100 m.a.s.l.), a minor tributary (5-12 m wide

127 at study site) of the Ribble, and Chipping Brook (~150 m.a.s.l.), a minor tributary (5-10

128 m wide at study site) of the River Loud (Fig. 1). Both streams have substantial but

129 recovering salmonid populations, including anadromous elements, with typical juvenile

130 trout densities of 7.4 - 63.3 100 m^{-2} (Swanside Beck) and 33.0 – 66.8 100 m^{-2} (Chipping

131 Brook) (M. Forty unpublished data). Both streams have riparian landscapes that

132 predominantly consist of grassland which is subject to dairy and sheep farming. The

133 substratum is predominantly composed of gravel, pebbles and cobbles in both streams.

134 Swanside Beck runs for 6 km with moderate gradient (*ca.* 12.2 m km^{-1}) impeded by

135 three low-head obstacles (< 3 m) (Fig. 1) while Chipping Brook runs for 4.5 km with a

136 higher gradient of *ca.* 42.6 km m^{-1} and has six low-head obstacles (Fig. 1). A total of

137 five structures were assessed across the two years, three on Swanside Beck and the first

138 and second on Chipping Brook (Fig. 1). Of these, four were recently constructed fish

139   passage structures: two pool-weir (PW1, PW2) traverse fish passes, one embedded rock

140   ramp (ERR; large cobbles densely embedded in concrete), and one low-cost baffle

141   (LCB) pass (Table 1, Fig. S1). The other structure was an unmodified open (uncovered)

142   culvert (C) which was used as a control, contextualising observations at fish passes

143   (Cooke & Hinch, 2013), representing a man-made structure which might pose a

144   minimal barrier impact being well within expected swimming performance of brown

145   trout (Table 1, Fig. S1) (Beamish, 1978; Tudorache et al., 2008).

146   *2.2 Passive integrated transponder (PIT) logging stations*

147   PIT telemetry was used to measure passage metrics of tagged trout at instream

148   structures. Each site was monitored using a logging station comprising either two half-

149   duplex (HDX) readers (Texas Instruments S2000, USA) in a master-slave configuration

150   (Castro-Santos et al., 1996) and data logger (Flinka Fiskar, Sweden), or a Texas

151   Instruments HDX multiple antennae reader and data logger (Oregon RFID, USA).

152   These configurations interrogated each antenna 8 and 6 times per second respectively

153   via a tuning unit connected to the logger. Two antennae loops (6 mm multi-stranded

154   high quality copper speaker cable, 777 x 0.1 mm strands) were constructed across the

155   stream channel at the downstream and upstream extents of each structure, interrogating

156   the full stream width and depth, such that the direction and success of passage by

157   individuals could be identified. Each loop was tuned to maximum detection range and

158   efficiency. Tests with pole-mounted 12 mm and 23 mm tags were carried out by passing

159   the tag through the loop at speeds of 1-1.5 ms^{-1} to simulate burst-swimming fish. In

160   addition, PIT loop detection efficiencies were measured by calculating the proportion of

161   tagged fish per array which were detected at the downstream antenna that were also

162   detected upstream antenna as well as, where possible, the proportion of fish detected at

163   the upstream antenna of an array that were also detected at PIT sites further upstream.

164   Logging stations were powered using two 12 V, 110 Ah deep-cycle leisure batteries, run

165   in parallel, which were changed every 3-4 days to avoid power supply failure. Data was

166   downloaded at each battery change and the antennae loops tested as described above to

167   ensure they were functioning correctly.

168   Four structures (C, PW1, PW2, LCB) were studied during summer-autumn 2013 using a

169   two-part methodology investigating passage for naturally migrating trout in addition to

170   utilising the homing instinct of individuals through displacement experiments. At each

171   structure, fish (mostly parr and some adult freshwater-resident 'brown' trout) were first

172   captured by electric fishing (pulsed DC Electracatch WFC4, Wolverhampton, UK and 1

173   KVA Honda generator), tagged and released where they originated within sections of a

174   reach *ca.* 10-180 m downstream of the structure (Table 2). These fish were then

175   monitored for between 13 and 21 days (Table 2). Following this, fish were captured in

176   the first 100 m upstream of the structure, tagged and displaced 100 m downstream of

177   the structure invoking a homing response (Armstrong & Herbert, 1997) but not inflated

178   attraction values (Cooke & Hinch, 2013). In addition fish were tagged on the same day

179   100-200 m upstream of each structure, but released there and free to move to sites

180   further upstream during migration. During autumn, opportunistic electronic fishing was

181   carried out in pools in reaches up to 2 km downstream of the structures, in order to

182   capture upstream-migrating adult freshwater-resident ('brown') and anadromous ('sea')

183   trout. Logging stations ran until mid-December (Table 2) by which time naturally

184   upstream-migrating individuals were expected to have completed spawning.

185   PW2 (Chipping Brook) was modified in early summer 2014 to correct an erroneous

186   0.37 m difference between the head drop at the first notch and that at the most upstream

187   notch of the pass to 0.25 m between each pool (Table 1). A new embedded rock ramp

188   (ERR) was also constructed on a flat-faced weir 20 m upstream of PW2 at the same

189   time. Both of these structures were investigated in summer 2014 along with repeat

190   studies of the LCB and C on Swanside Beck. All sites monitored in 2014 were subject

191   only to short term displacement experiments conducted using the same format as in

192   2013 but with monitoring of the logging stations for the first 15 days following

193   displacement as 73% of displaced fish in 2013 at LCB were detected attempting passage

194   within this period (71-88% for fish passes in 2014). As PW2 and ERR were in close

195   proximity, fish were captured above ERR and then displaced 100 m below PW2 using

196   the same displacement group to test both structures.

197   PIT stations ran continuously during experiments with the exception of PW1 (13:00 12

198   Sept 2013 – 18:00 16 Sept 2013) and PW2 (12:00 12 Sept 2013 – 18:30 16 Sept 2013)

199   which both experienced equipment failure at the beginning of displacement

200   experiments. PIT antennae were washed out of the control culvert on 21 Oct 2013 and

201   water levels then remained too elevated to re-install loops within reasonable time so

202   monitoring was ceased at that point.

203   *2.3 Experimental fish*

204   Captured fish were placed in to covered reservoirs providing aeration and circulation by

205   means of a 12 V submersible aerator pump (1732 L hr^{-1}). Trout were PIT tagged with

206   one of two tag sizes depending on whether their fork length was between 80 and 130

207   mm (12 x 2.12 mm, 0.1 g) or greater than 130 mm (23 x 3.65 mm, 0.6 g) based upon

208   Larsen et al. (2013). Prior to tagging fish were immersed individually in an anaesthetic

209   bath of 2-phenoxyethanol (250 μL L^{-1}) until they reached stage III anaesthesia

210   (McFarland, 1959). Fish were then measured (fork length), classed by phenotype and

211 life stage (juveniles with parr marks, not expressing gametes; freshwater-resident

212 'brown' trout without parr marks; anadromous 'sea' trout without parr marks but

213 silvered body) and a PIT tag inserted in to the peritoneal cavity via a 3-5 mm incision

214 on the ventral surface anterior to the pelvic girdle. The incision was left un-sutured as

215 studies have indicated this not to be necessary for small incisions (Bolland et al., 2009;

216 Larsen et al., 2013). Tagged fish were placed in a recovery reservoir of aerated fresh

217 water for observation ensuring they were able to maintain equilibrium and were

218 responsive to external stimuli before release.

219 ### 2.4 Environmental data

220 Water stage (level) and temperature were recorded on Swanside Beck and Chipping

221 Brook in pool habitat 5 m upstream of the LCB and PW2 structures respectively. These

222 were measured at 15 minute intervals using an automatic logger (HOBO U20-001-01-

223 Ti; accuracy: 0.05 cm, $0.044^{o}C$ from 0°-$50^{o}C$) placed in a stilling well affixed securely

224 upright at the bank. Water level was then calibrated using a single point reading of

225 depth at the data logger and hourly mean barometric pressure readings from a weather

226 station at Bingley (53.81 N 01.87 W). The engineered structures were surveyed by

227 measuring water depth and velocity in and immediately below each structure at base

228 flow. Water velocity was measured using an electromagnetic velocity meter (Valeport,

229 model 801) over 10 seconds, calculating the mean and standard deviation at 0.6 of the

230 depth. At pool-weir type structures measurements were taken across the channel from 1

231 m downstream of each notch and at three equally spaced points in three cross sections

232 within each notch. Measures were taken at LCB from 1 m downstream of the structure

233 and then in the middle of the break in each set of baffles. In C, measurements were

234   taken at 0.25 m increments across transects beginning 1 m downstream of the entrance,

235   at the entrance and then at 2 m intervals.

2.5 Data analysis

237   In order to assess performance for fish passage at each structure several metrics were

238   calculated. *Passage efficiency* was defined as the percentage of fish which successfully

239   ascended a structure compared to those which were detected at the downstream antenna

240   loop, attempting to ascend. *Proportion of Displaced fish Attempting Passage* (PDAP)

241   was defined as the proportion of fish which attempted to ascend a structure compared of

242   those which were displaced below it (note that this is not the same as attraction

243   efficiency in many studies [Cooke & Hinch, 2013], but it is a useful metric of

244   motivation of fish seeking to pass an obstacle to return to their home area). *Time to*

245   *passage* was measured as the time between first detection at the downstream loop and

246   the first detection at the upstream loop of a structure. An additional measure of passage

247   delay impact was calculated, the *number of attempts* made by a fish before successful

248   passage, where an attempt is defined as detection at the downstream antenna, not within

249   5 minutes of a previous detection. Data presented are the first recorded ascents of

250   individuals and do not consider repeat ascents from fish which have fallen back

251   downstream. Five fish (2% at PW1 and 1% at PW2 of those detected) included fish pass

252   vicinities within their home range and persistently moved between the lower and upper

253   antenna over multiple days. These fish were excluded from analysis. Non-parametric

254   testing was used to compare these passage metrics between structures.

255   The effect of body length on the passage success of trout at structures was tested using

256   binary logistic regression. This provides a useful method for modelling a binary

257 response variable (successfully or unsuccessfully ascending a structure) based on a

258 predictor variable (length) (Bewick et al., 2005; Starrs et al, 2011). Models were

259 constructed using 2013 data and tested for significance against the Null model. A model

260 for 2014 PW2 after modification was constructed for comparison to 2013 PW2. Logistic

261 regression was not fitted where complete separation arose due to 100% passage

262 efficiency (Field, 2005). All analyses were conducted using R version 2.15.2 (R Core

263 Team, 2012).

264

265 **3. Results**

266 3.1 Migration and passage efficiency

267 A total of 845 and 337 trout were PIT tagged in 2013 and 2014 respectively across the

268 two study streams, with fork lengths ranging from $80 - 450$ mm (Table 2). In situ

269 detection efficiencies of tagged fish averaged 98.5% for upstream antennas and 94.9%

270 for downstream antennas, for all five sites and both years. On Chipping Brook, the

271 proportion of non-displaced parr morphotype trout detected attempting to move

272 upstream was 29% ($n =137$) of which 38% were successful at PW2. On Swanside Beck

273 the proportion of non-displaced trout of parr morphotype exhibiting upstream

274 movement was 32% ($n = 278$) of which 100%, 56% and 65% were successful at C,

275 LCB and PW1 respectively. Of these, the proportion moving from downstream of C

276 was 15% ($n = 32$) to LCB and 13% to PW1. Of those tagged between C and LCB the

277 proportion moving upstream to PW1 was 10% ($n = 108$).

278 Of the four structures investigated in 2013, passage efficiency for trout was observed to

279 be highest at the control C (100%; Table 3) as expected. Within the three fish passes

280   highest overall passage efficiency (from displacement and non-displaced samples

281   combined) was observed at PW1 (76%) followed by the LCB (68%; Table 3). Passage

282   efficiency values for PW1 and PW2 are minimums due to short periods of PIT logger

283   down-time. In 2014 the LCB demonstrated the best passage efficiency (82%, Table 4)

284   of the three fish passes studied, with the control culvert again exhibiting near complete

285   passage efficiency (96%). Of the two cumulative structures in close proximity the most

286   downstream of them, PW2 (79%), recorded a higher passage efficiency than the ERR

287   (71%). The LCB structure was also more efficient in 2014 than 2013 (Table 4) in

288   displacement experiments by 15%.

289   In long-term experiments in 2013 the Proportion of Displaced fish Attempting Passage

290   (PDAP) was highest at the LCB (91%; Table 3), much higher than for the control

291   culvert (51%), characterised by a large, deep pool immediately downstream. Within the

292   15-day displacement experiments PDAP was higher in 2014 for C and the LCB which

293   were studied in both years (Table 2). PDAP was very similar between PW2 (87%) and

294   the LCB (88%) in 2014, with the ERR having a lower value than PW2 immediately

295   downstream of it.

296   Stage and water temperature data from 2013 (Fig. 2) and 2014 (Fig. 3) are displayed in

297   relation to cumulative passage success. During fish displacement experiments on

298   Swanside Beck water level was slightly but significantly higher in 2013 than 2014

299   (Independent t-test, $t = 6.43$, df = 2768.1, $P < 0.001$) and water temperature was *ca.*

300   3°C lower in 2013 than 2014 ($t = -77.70$, df = 4099.78, $P < 0.001$). This was also found

301   to be the case on Chipping Brook during fish displacement experiments for water level

302   ($t = -18.88$, df = 2484.62, $P < 0.001$) and temperature ($t = -30.57$, df = 2901.09, $P <$

303   0.001) between 2013 and 2014.

3.1 Delay before successful passage

In the 2013 long-term migration experiments, significant differences were found in time to passage between the four structures (Kruskal-Wallis test, $H(3) = 54.7$, $P < 0.001$) as well as in the number of attempts (Kruskal-Wallis test, $H(3) = 68.5$, $P < 0.001$). Time to passage was shortest at control C (median = 0.70 h; Fig. 4) and longest at PW2 (median = 127.22 h). Time to passage at each structure in long-term experiments was significantly different from the control C with the exception of PW1 (Mann-Whitney test, $U = 774$, $P < 0.31$; Fig. 4). Significant differences were also found in displacement experiments between structures, for time to passage (Kruskal-Wallis test, $H(4) = 42.2$, $P < 0.001$; Fig. 5) as well as number of attempts (Kruskal-Wallis test, $H(4) = 24.5$, $P < 0.001$). Though C still provided the shortest passage time in 2014 displacement experiments (median$_{2014}$ = 0.51), longest passage times were experienced at the LCB in 2013 (median = 4.01 h) but were notably, though not significantly, shorter in 2014 (median = 0.97 h). Time to passage was also significantly shorter at PW2 in 2014 (median = 2.37; $U = 2740$, $P < 0.001$) following adjustments in its construction after long delays were observed in long-term experiments in 2013 (median = 108.29 h). Of the fish passage structures the ERR provided the least impact both in terms of time to passage and number of attempts (median = 0.66 h and 1 respectively).

As with time to passage passage, the number of attempts before successful passage was lowest at C (median = 1; Fig. 4) and greatest at PW2 (median = 7). Number of attempts was significantly greater for all structures compared against control C (Fig. 4) in long term experiments, while only the LCB exhibited significantly higher numbers of attempts before successful passage in comparison with C in displacement experiments in 2013 ($U = 1075$, $P < 0.02$) and 2014 ($U = 1050$, $P < 0.01$).

328   **3.2 Fork-length and passage success**

329   Significant logistic regression models ($P < 0.05$) were created for three structures (LCB,

330   PW1, PW2) based on data from long-term experiments collected in 2013 (Fig. 6, Table

331   5) and the displacement data from 2014 for PW2 following its alteration. Although the

332   50% probability of passage (P_{50}) did not differ significantly between fish passes, the

333   models suggest that PW1 functioned best for smaller trout, with a P_{50} for a length of 91

334   mm (Fig. 6). Of the other two structures PW2$_{2013}$ (P_{50} = 132 mm) performed worse than

335   the LCB (P_{50} = 113 mm) for smaller fish. All structures had a P_{90} under 250 mm with

336   PW1 (P_{90} = 199 mm) showing evidence of better performance than LCB (P_{90} = 222

337   mm) and PW2 (P_{90} = 222 mm). After alteration, PW2$_{2014}$ showed an increase in

338   performance for all lengths of fish (Fig. 6, Table 5), outperforming the other structures

339   for smaller fish (P_{50} = 82 mm, P_{90} = 192 mm). A significant model could not be

340   constructed for the control culvert C due to complete separation arising from 100%

341   passage efficiency and the model for ERR was insignificant.

342

343   **4. Discussion**

344   This study provides field evidence of the varying performance of three fish passage

345   designs for upstream passage of both juvenile and adult *Salmo trutta* at low-head

346   barriers and the variation in delay that can be incurred even between similarly designed

347   passes. We provide the first passage efficiency measurements (67-82%) of a low-cost

348   baffle (Servais, 2006) fish pass for trout of a wide range of sizes. This performed quite

349   similarly in terms of passage efficiency to the other fish pass designs tested, even

350   though operating at nearly double the gradient (24% vs 12% in our study; Table 1).

351 Predictive models suggested that passage success was closely related to fork length of

352 individuals with probability of passage reduced for smaller fish. About 30% of tagged

353 parr released at their capture site attempted passage at one or more structures and this,

354 as well as upstream dispersal and homing demonstrates that small (including juvenile),

355 as well as large adult trout need to be considered in terms of effective upstream passage

356 provision. Additionally short-term displacement experiments of resident trout combined

357 with PIT telemetry was identified to potentially provide a rapid performance assessment

358 tool for determining trout passage at structures and to aid fine-tuning of fish pass

359 modifications.

360 Passage efficiencies observed at fishways in this study were all below the minimum

361 90% target that recommended as a minimum for sustaining and recovery of populations

362 of diadromous and markedly potamodromous species (Lucas and Baras, 2001), but well

363 above the average passage efficiency (48%) recorded in a large meta-analysis by Bunt

364 et al. (2012).Only control C, a 20 m culvert with 4% slope, exceeded the minimum 90%

365 passage efficiency target (96-100% passage efficiency) with water velocities which

366 were well within the swimming performance abilities of *S. trutta* (Beamish, 1978;

367 Tudorache, 2008; Videler, 1993). In addition to this, passage efficiencies were found to

368 be variable between and within design types with differences also observed across

369 years. Bunt et al. (2012) reported that passage efficiency varied broadly across a range

370 of fishway types when conducting a meta-analysis of 19 studies of 26 species at

371 instream barriers to migration. Where fish had to pass two structures in close proximity

372 at PW2 and then the ERR both passage efficiency and PDAP were lower at the

373 upstream structure, despite shorter passage time and lower number of attempts at the

374 ERR. Due to the close proximity of these structures it is hard to discern whether this

375   result is influenced more by the individual design of the structures or whether the

376   energy expended in passing the first structure reduces a fish's motivation to attempt the

377   second or impacts the likelihood it will pass both structures. Given this, the values for

378   passage efficiency and PDAP at ERR may be considered conservative values.

379   Cumulative barriers to migration can potentially have substantial effects on upstream

380   passage even when individual structures pose what seem to be a negligible impact

381   (McKay et al., 2013).

382   In this study 50% probability of successful upstream passage at fishways was associated

383   with lengths representative of trout in the 1+ age cohort for this catchment (80 – 132

384   mm; M. Forty, unpublished). Swimming capacity has been shown to be a factor of body

385   length (Beamish, 1978; Videler, 1993). Tudorache et al. (2008) suggested, based on

386   flume experiments, that maximum flow velocity in culverts for brown trout of fork

387   length 78 ± 2 mm at 15°C should be 0.45 ms^{-1}. High passage success was observed at

388   the control culvert despite having higher base flow velocities at the entrance than this

389   recommendation (0.80 ms^{-1}). This may be explained by trout having been able to use

390   burst swimming to enter the structure and then utilise local flow refugia while moving

391   through the culvert, where the observed mean velocity was lower (0.46 ms^{-1}). High

392   passage efficiencies have been previously observed in nature-like fishways

393   characterised by high maximum water velocities for both weak (Calles & Greenberg,

394   2007) and strong (Calles & Greenberg, 2005, 2009) swimming species. Successful

395   passage of some individuals at fishways with locally high velocities may be indicative

396   of their strong motivation to pass upstream and their abilities in the wild to outperform

397   maximum swimming speeds observed in confined flumes (Haro et al., 2004; Peake &

398   Farrell, 2004). The use of flow refugia may also partially explain the high passage

399   success observed at LCB and ERR, where sustained swimming at higher velocities

400   (mean = 1.42 and 1.13 ms^{-1}) is required as these pass types lacked well-defined resting

401   areas as provided by pool-weir type passes. The short length of these structures (< 10

402   m) will also contribute to a moderately high passage success of small fish in our studies;

403   reducing the duration of swimming at these velocities and allowing fish with a greater

404   range of swimming abilities to pass.

405

406   Creating fish passage structures in small streams so that they are passable by juvenile

407   fish as well as adults would allow for recovery of populations following disturbance

408   events such as high stream flows or pollution incidents, and would also facilitate

409   upstream dispersal. High stream flows can result in the displacement of juvenile

410   salmonids downstream of structures impacting their survival (McMahon & Hartman,

411   1989; Ottaway & Clarke, 1981) where they may end up in unsuitable habitats such as

412   deeper pools potentially increasing susceptibility to predation from larger piscivorous

413   fishes, or in juvenile habitat with increased population density due to displacement,

414   generating increased intraspecific competition causing density-dependent fitness

415   impacts. Our displacement experiments mimicked such upstream movements. Mature

416   parr morphotype salmonid males (precocious parr) have been identified to contribute

417   towards spawning success of populations (Dellefors & Faremo, 1988; Garcia-Vazquez

418   et al., 2001; Hutchings & Jones, 1998). In this study *ca.* 30% of non-displaced parr

419   morphotype trout were observed to exhibit upstream movement in both study streams in

420   2013 with a number of those tagged below the most downstream site on Swanside Beck

421   observed passing over 3 km upstream through all three structures during the autumn.

422   We hypothesise these individuals were mature male parr.

423   While the site-specific displacement experiments were comparable in terms of the

424   monitoring duration following displacement, there were limitations in resource

425   availability precluding exactly simultaneous experiments and there were also

426   differences between sites in the availability of fish of different sizes for tagging.

427   Improved passage efficiency at C and the LCB in 2014 may have been due to

428   significantly higher stream temperatures (approximately 3°C higher for Swanside Beck

429   and 1°C higher for Chipping Brook) in 2014 compared to 2013 during the displacement

430   experiments. Water temperature may influence swimming capacity of fish as it has been

431   found to affect the muscle contraction speed of fish (Beach, 1984; Wardle, 1980).

432   However, brown trout swimming performance was observed to be similar in summer

433   (15°C) and winter (5°C) as long as fish had acclimatised to those temperatures by Day

434   & Butler (2005). Also, Jain & Farrell (2003) demonstrated that rainbow trout

435   (*Oncorhynchus mykiss*) performed better acclimated at lower temperatures (ca. 5°C)

436   than higher temperatures (*ca.* 17°C) in a repeated swimming performance experiment.

437   Each of the structures studied were designed and constructed across the width of the

438   stream to maximise attraction flow, and as such did not have to compete for attraction

439   flow as would occur for a fish pass at a large dam or main river weir (e.g. Gowans et al.,

440   1999). Despite this there was much variation in PDAP between structures during

441   displacement experiments, being higher for fish passes $(71 - 88\%)$ than for the control

442   culvert (49%) in 2014 (Table 4). The habitat characteristics created in areas downstream

443   of instream structures could be a potential factor in determining the motivation for

444   displaced fish to approach and attempt to pass a structure; C had a constrained surface-

445   positioned entrance above a large, deep scour pool, which may have limited attraction,

446   even though the whole of the stream flow entered via C. While plunge pools and dam

447 tailwaters, supplied with well oxygenated water and an abundance of food can provide

448 propitious habitats for a number of fish species, they may also have the potential to

449 reduce motivation for smaller fish to pass through them due to exposure to predation

450 from larger piscivorous fishes that reside in deeper pool habitat (e.g. Schlosser, 1987).

451 The lower PDAP values observed at PW1 and PW2 in 2013 are likely an artefact of

452 data loss due to equipment failure in the period directly after displacement in that year.

453 Time to passage was found to be highly variable between structures. Passage times were

454 slightly shorter within displacement experiments than long-term experiments, likely

455 because of the shorter duration of monitoring post-displacement biasing towards fish

456 which may have a greater motivation to pass upstream than ones which wait longer

457 before attempting. As with improved passage efficiency, the LCB structure also showed

458 improved performance in terms of reduced time to passage in 2014 compared with

459 2013, perhaps due to increased temperature in 2014 experiments. The improvement

460 works on PW2 between 2013 and 2014 appear to have been successful in addressing the

461 issues with long delays, suggesting that these were due to conditions caused by the

462 unsuitable head drop at the entrance notch to the structure. In addition to providing a

463 complete barrier for some individuals, delays incurred at instream structures during

464 upstream passage can have detrimental impacts on spawning success and survival where

465 the excessive energy expenditure interferes with physiological and behavioural

466 processes (Mesa et al., 2003) and increases the risk of predation (Peake et al., 1997;

467 Rieman et al., 1991). In situations where fish have to pass multiple in-stream structures

468 these effects can be compounded, threatening survival of anadromous populations and

469 potentially driving facultatively anadromous species such as *Salmo trutta* towards

470 resident-dominated populations (Baras & Lucas, 2001).

471   While the passage efficiencies of fishways in this study did not attain the minimum 90%

472   target recommended by Lucas and Baras (2001), the study areas were dominated by

473   spawning and nursery habitat, and therefore such high passage efficiencies may be

474   unnecessary to sustain the population and key processes such as dispersal and

475   migration. Further, due to the size-selective effects of the fish passes, larger adults (> 30

476   cm), with high fecundity, did have passage efficiencies above 90% for all pass types for

477   which size effects could be modelled. Nevertheless, supporting passage for the full

478   range of life stages and sizes within populations may be important; for salmonids the

479   emphasis on upstream pass provision is normally for large adults only, because

480   (especially for females) these have high fecundity and economic value, but this ignores

481   the wider functionality of upstream movements in juveniles and small adults. Our

482   results suggest that in tributaries for salmonid spawning, greater consideration should be

483   made towards facilitating naturally occurring upstream migration and dispersal of

484   juvenile morphotype salmonids.

485   This study identifies that field studies are a vital component of evaluating and

486   optimising fish pass effectiveness, informing management decisions. This is

487   demonstrated by improvements in passage observed in 2014 following the actions that

488   could be taken after the identification of long delays incurred at Pool-Weir 2 during

489   2013 in this study. The number of fish passage structures which have been evaluated in

490   relation to the large number constructed globally is very small (Schmutz et al., 1998).

491   This is particularly true of low-head instream structures present within smaller streams

492   (Alexandre & Almeida, 2010; Ovidio & Philippart, 2002). As demonstrated in this

493   study, there is a wide variation in performance between and within fish pass designs,

494   especially in terms of passage efficiency for different life stages and in the delays which

495   can be incurred even between similarly designed structures. This indicates that as much

496   as improved understanding of factors influences the effectiveness of fish passes, detail

497   needs to be paid to the build quality of technical passes.

498

499

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Figure legends

709 Fig. 1. Map of study area with in-stream structures shown as black circles (top and

710 bottom right).

711 Fig. 2. Mean daily stage (solid-black) and mean daily water temperature (solid-grey)

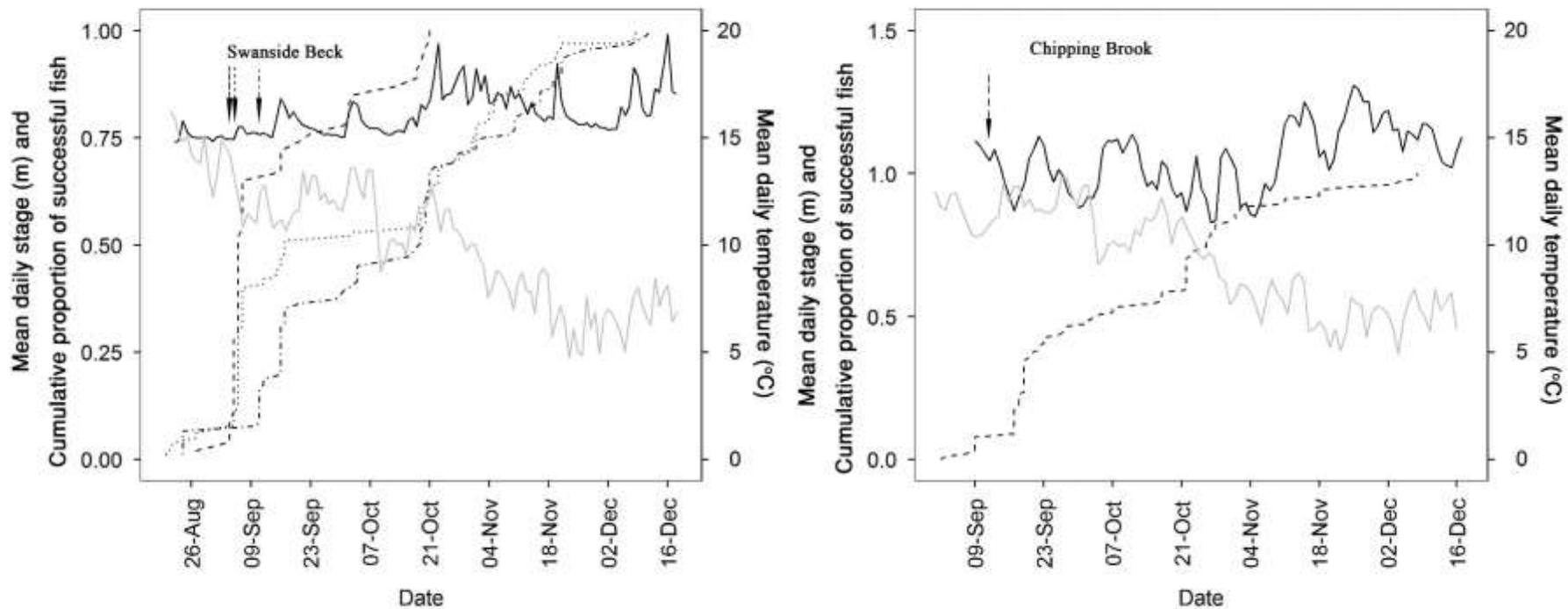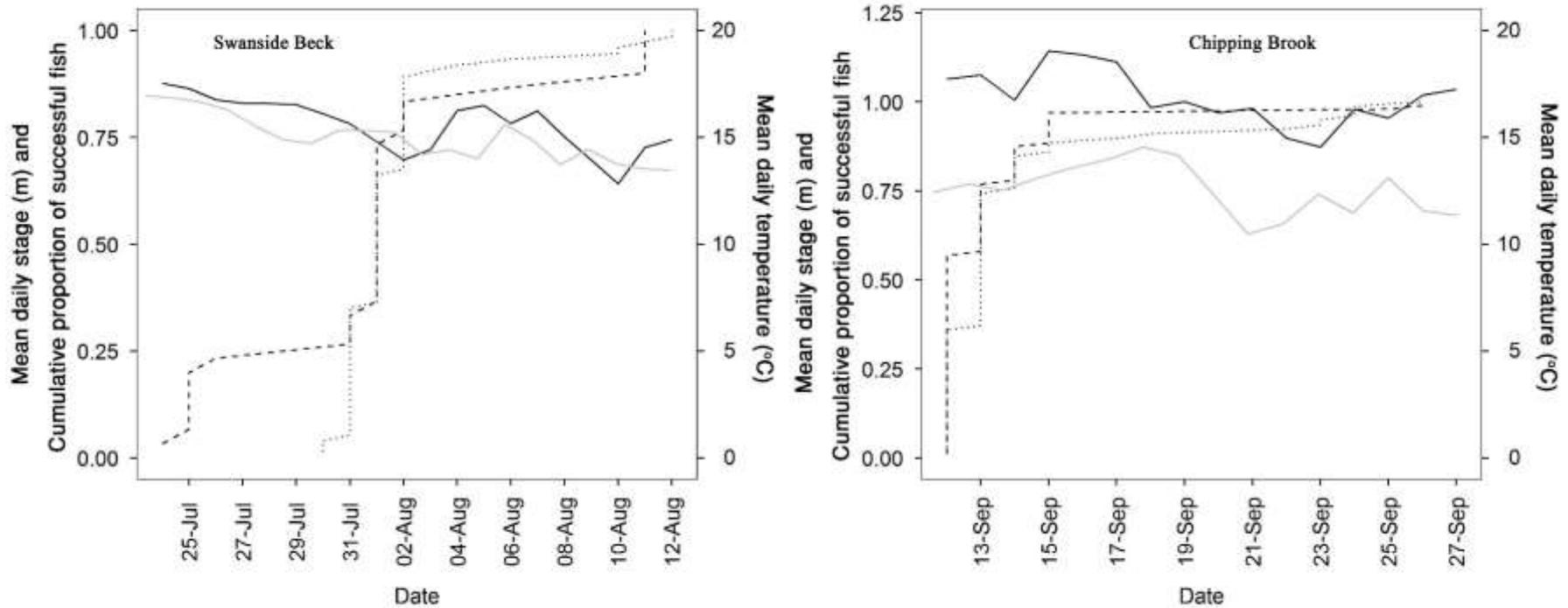712 plotted with the cumulative proportion of successful fish in 2013 on Swanside Beck

713 (left) for Culvert (dashed), Low-Cost Baffle (dotted) and Pool-Weir 1 (dot-dash), and

714 Chipping Brook (right) for Pool-Weir 2 (dashed). Arrows indicate dates of displacement

715 respectively.

716 Fig. 3. The cumulative proportion of successful fish in displacement experiments in

717 2014 on Swanside Beck (left) for Culvert (dashed) and Low-Cost Baffle (dotted)

718 structures and Chipping Brook (right) for Pool-Weir 2 (dashed) and Embedded Rock

719 Ramp (dotted) fish passes plotted with mean daily stage (solid-black) and mean daily

720 water temperature (solid-grey).

721 Fig. 4. Boxplots of the passage time (h) and number of attempts before successful

722 passage for long term experiments in 2013. Boxplots display the median, 1st and 3rd

723 quartiles and the 95% confidence interval of the median with outliers. Pairs not joined

724 by the same letter represent where there were significant differences between structures

725 (or years). Delays and attempts were analysed separately as were long term and

726 displacement experiments (Mann-Whitney U test with Bonferroni corrected significance

727 at $P < 0.035$).

728 Fig. 5. Boxplots of the passage time (h) and number of attempts before successful

729 passage for short term displacement experiments (2013 and 2014). Boxplots display the

730 median, 1st and 3rd quartiles and the 95% confidence interval of the median with

731 outliers. Pairs not joined by the same letter represent where there were significant

732 differences between structures (or years). Delays and attempts were analysed separately

733 as were long term and displacement experiments (Mann-Whitney U test with

734 Bonferroni corrected significance at $P < 0.035$).

735 Fig. 6. Logistic regression models for LCB, PW1 and PW2 in 2013 and after alteration

736 in 2014 showing predicted probability of passage of an individual based on its length

737 and ultimate passage success data collected during study with 95% confidence intervals

738 (grey area). All models significant against the Null model at $P < 0.05$.
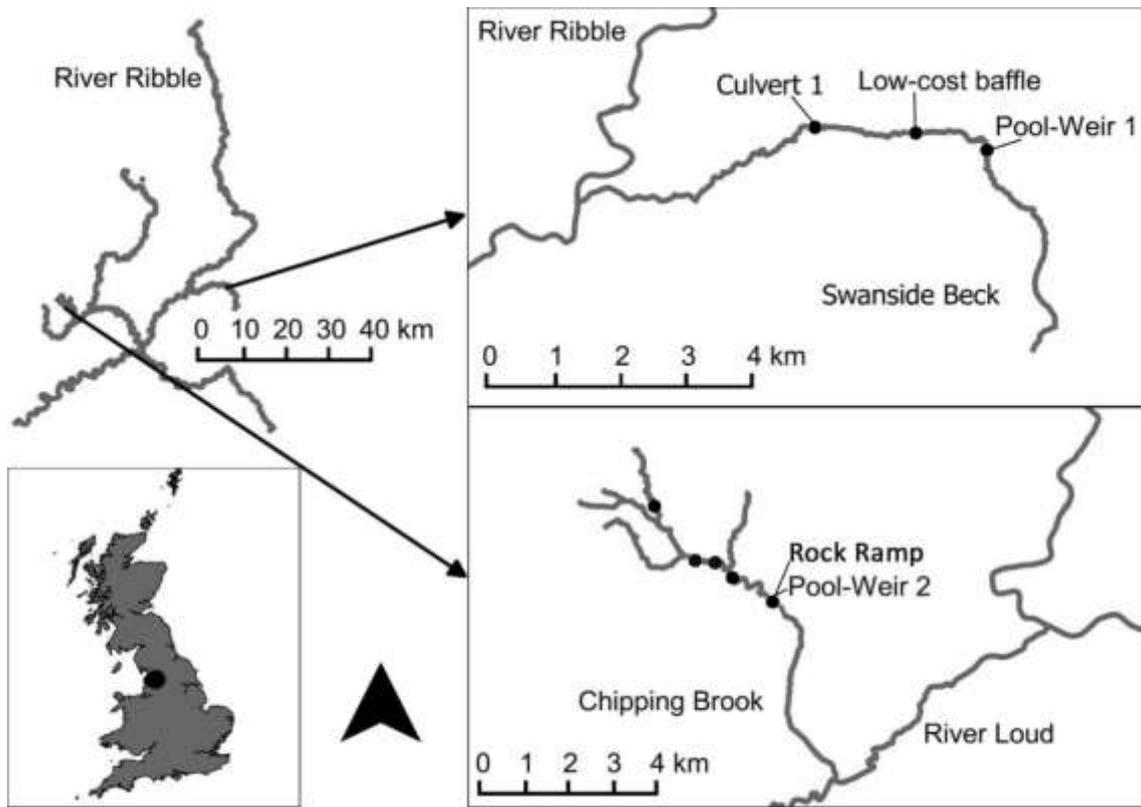
Figures

Fig. 1. Map of study area with in-stream structures shown as black circles (top and bottom right).

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750

Fig. 2. Mean daily stage (solid-black) and mean daily water temperature (solid-grey) plotted with the cumulative proportion of successful

fish in 2013 on Swanside Beck (left) for Culvert (dashed), Low-cost baffle (dotted) and Pool-Weir 1 (dot-dash), and Chipping Brook

(right) for Pool-Weir 2 (dashed). Arrows indicate dates of displacement respectively.

754
755

756   Fig. 3. The cumulative proportion of successful fish in displacement experiments in 2014 on Swanside Beck (left) for Culvert (dashed) and

757   Low-cost baffle (dotted) structures and Chipping Brook (right) for Pool-Weir 2 (dashed) and Embedded Rock Ramp (dotted) fish passes

758   plotted with mean daily stage (solid-black) and mean daily water temperature (solid-grey).
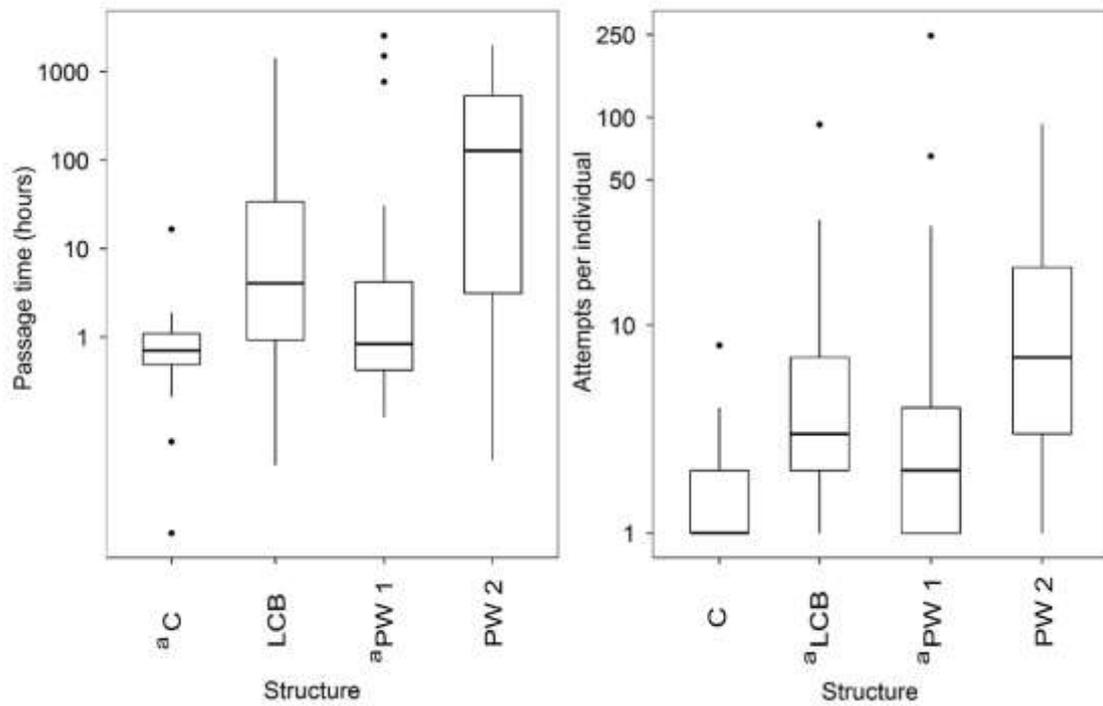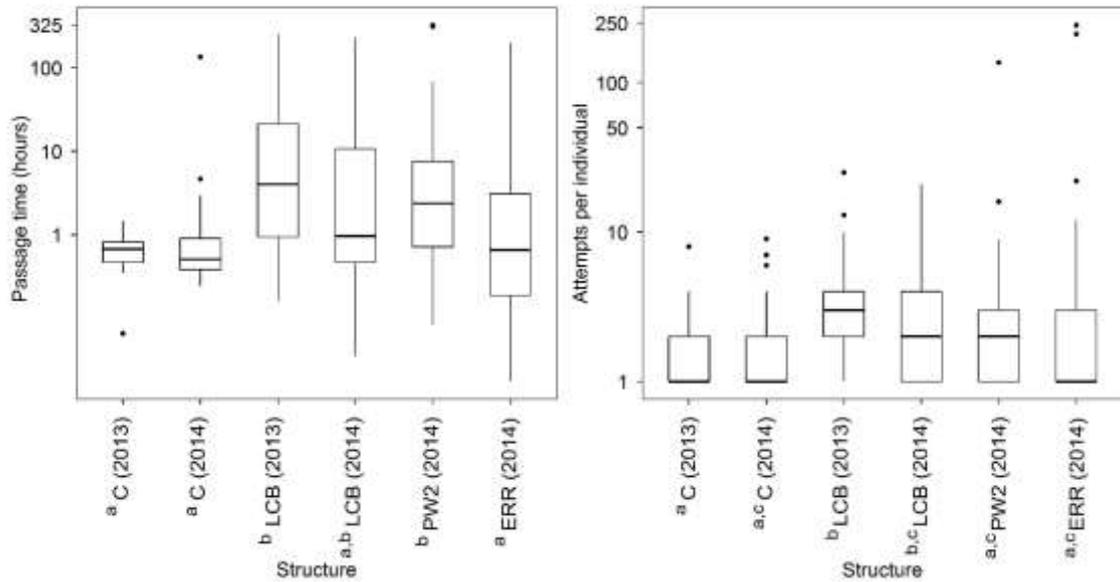
759

760 Fig. 4. Boxplots of the passage time (h) and number of attempts before successful

761 passage for long term experiments in 2013. Boxplots display the median, 1st and 3rd

762 quartiles and the 95% confidence interval of the median with outliers. Pairs not joined

763 by the same letter represent where there were significant differences between structures

764 (or years). Delays and attempts were analysed separately as were long term and

765 displacement experiments (Mann-Whitney U test with Bonferroni corrected significance

766 at $P < 0.035$).

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Fig. 5. Boxplots of the passage time (h) and number of attempts before successful

passage for short term displacement experiments (2013 and 2014). Boxplots display the

median, 1st and 3rd quartiles and the 95% confidence interval of the median with

outliers. Pairs not joined by the same letter represent where there were significant

differences between structures (or years). Delays and attempts were analysed separately

as were long term and displacement experiments (Mann-Whitney U test with

Bonferroni corrected significance at $P < 0.035$).
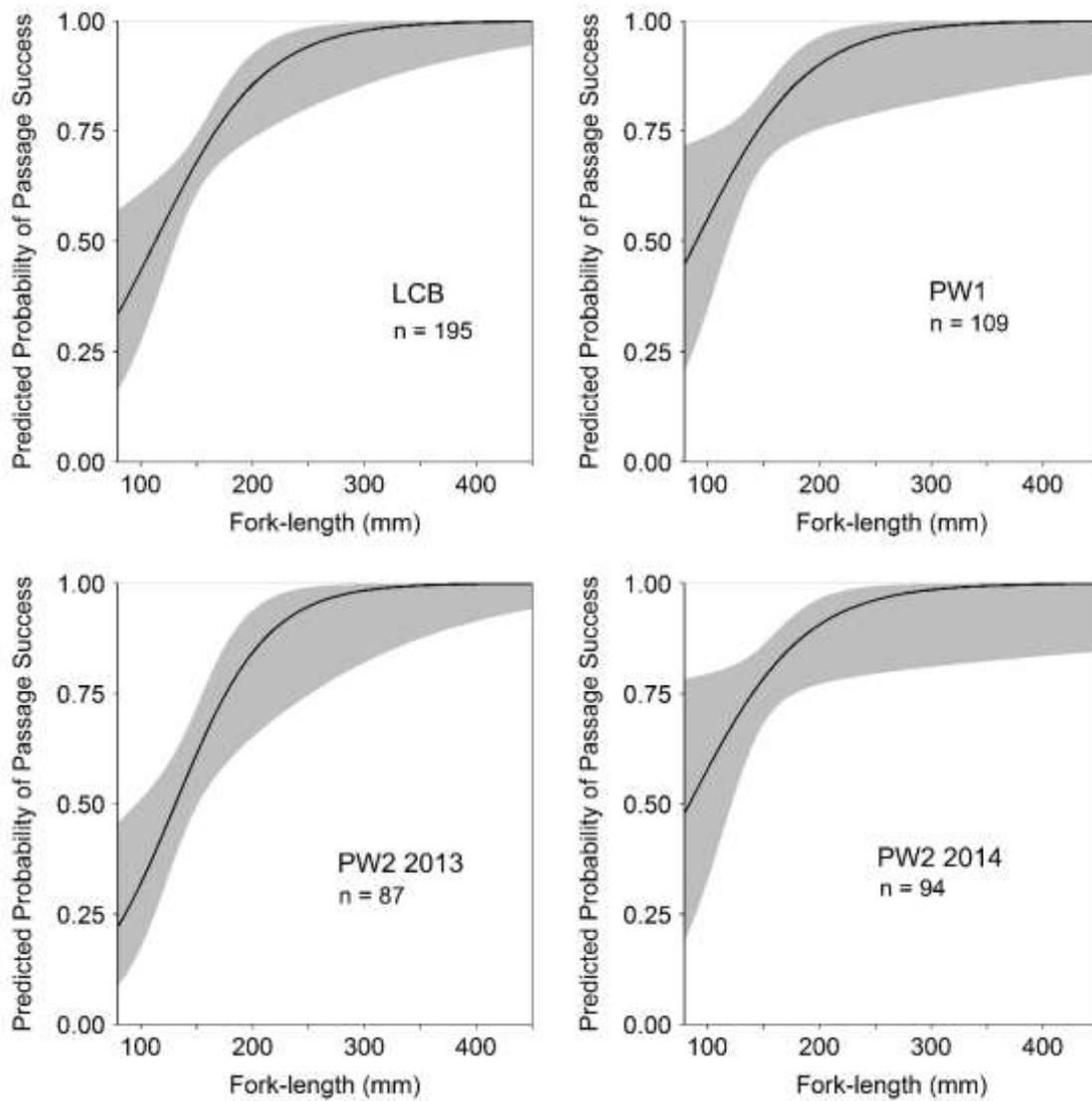
778

779 Fig. 6. Logistic regression models for LCB, PW1 and PW2 in 2013 and after alteration

780 in 2014 showing predicted probability of passage of an individual based on its length

781 and ultimate passage success data collected during study with 95% confidence intervals

782 (grey area). All models significant against the Null model at $P < 0.05$.

783 **Tables**

784 **Table 1**

785 Physical characteristics of studied structures.

	Culvert (control)	Fish passes				
		Low-cost baffle	Pool-Weir 1	Pool-Weir 2 (2013)	Pool-Weir 2 (2014)	Embedded Rock Ramp
Length (m)	20	6.70	8.43	7.20	7.20	4.57
Width (m)	0.50	7.6 - 9.7	6.20	8.65 - 10.50	8.65 - 10.50	6.80
Head (m)	0.80	1.60	1.16	0.84	0.84	0.55
Slope (%)	4%	24%	12%	12%	12%	12%
Mean base flow velocity at entrance (ms^{-1})	0.80	1.85	1.87	1.97	1.91	1.28
Mean entrance depth at base flow (m)	0.12	0.15	0.06	0.10	0.10	0.30
Mean velocity in structure (ms^{-1})	0.46	1.42	0.45*	0.84*	0.78*	1.13
Notch width (m)	-	0.35	0.60	0.60	0.60	-
Baffle height (m)	-	0.20	-	-	-	-
Pool step height (m) downstream, upstream	-	-	0.25-0.33	0.49, 0.23, 0.12	0.25	-
Number of pools	-	-	3	3	3	-
Number of notches	-	16	4	4	4	-

786 *based on measures in flow entering pools from notches at transects 0.5 and 1 m away from notch.

787 **Table 2**

788 Summary of experimental groups of *Salmo trutta* PIT tagged during 2013 and 2014.

Source	Date	Number tagged	Length [mean SD (range), mm]
Swanside Beck			
Culvert downstream	19/08/2013	33	163.9 ± 35.3 (101 - 266)
Culvert upstream	04/09/2013	12	128.1 ± 38.0 (82 - 191)
Culvert displaced	04/09/2013	68	119.7 ± 34.8 (82 - 191)
	24/07/2014	53	152.4 ± 42.4 (80 - 294)
Low-cost baffle downstream	20/08/2013	101	154.5 ± 24.1 (114 - 233)
Low-cost baffle upstream	05/09/2013	49	133.0 ± 31.6 (80 - 213)
Low-cost baffle displaced	05/09/2013	118	148.2 ± 28.9 (83 - 298)
	30/07/2014	101	154.5 ± 34.1 (112 - 293)
Pool-weir 1 downstream	21/08/2013	93	127.3 ± 21.3 (94-211)
Pool-weir 1 displaced	11/09/2013	72	130.8 ± 29.7 (80 - 208)
Swanside Beck supplementary migrants			
Culvert downstream	19/09/2013	5	222 ± 30.4 (191 - 256)
	28/10/2013	1	425
	06/11/2013	1	450
	12/11/2013	4	329.3 ± 80.7 (220 - 410)
	22/11/2013	1	413
Total Swanside Beck	**2013**	**558**	**142.4 ± 42.6 (80 - 450)**
	2014	**158**	**156 ± 39.3 (80 - 294)**
Chipping Brook			
Pool-weir 2 downstream	30/08/2013	146	135.0 ± 38.3 (80 - 254)
Pool-weir 2 displaced	12/09/2013	141	159 ± 51.6 (109 - 443)
Pool-weir 2 and Embedded Rock ramp displaced	12/09/2014	179	145 ± 40.6 (102 - 326)
Total Chipping Brook	**2013**	**287**	**153.4 ± 49.0 (80 - 443)**
	2014	**179**	**145.0 ± 40.6 (102 - 326)**

789 **Table 3**

790 Passage success of *Salmo trutta* during long-term experiments in 2013. Proportion of

791 Displaced fish Attempting Passage (PDAP) values are calculated for trout displaced from

792 upstream to below the structure only; these fish may be expected to attempt to return home.

	C	LCB	PW1*	PW2*
Number displaced	68	128	73	139
Number attempted				
Displaced	35	117	48	119
Non-displaced	7	78	61	87
Total	42	195	109	206
Passage efficiency (%)				
Displaced	100	74	79	53
Non-displaced	100	63	74	59
Total	100	68	76	55
PDAP (%)	51	91	66	86

793 *Minimum estimates of attempts, passage efficiency and PDAP due to 4-day (3.4 – 3.8% of total
794 experiment duration) periods of equipment failure shortly after fish displacement; measures of non-
795 displaced fish passage efficiency are expected to have been least affected.

796

797 **Table 4**

798 Passage success of *Salmo trutta* within 15 days following displacement below structures in

799 2013 and 2014 showing passage efficiency and Proportion of Displaced fish Attempting

800 Passage (PDAP).

	2013				2014			
	C	LCB	PW1*	PW2*	C	LCB	PW2	ERR
Number displaced	68	128	73	139	53	101	178	154
Attempted	25	94	48	52	26	89	154	109
Succeeded	25	63	38	37	25	73	121	77
Passage efficiency (%)	100	67	79	71	96	82	79	71
PDAP (%)	37	73	66	37	49	88	87	71

801 *Minimum estimates of attempts, passage efficiency and attraction efficiency due to 4-day (26% of
802 total experiment duration) periods of equipment failure shortly after fish displacement

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806 **Table 5**

807 Summary of logistic regression models of length and successful passage based on long-term
808 observations in 2013 and 15-day displacements in 2014.

Site	Coefficient	Std. Error	z statistic	$P <$	$\chi 2$	df	$P <$	Likelihood ratio test	df	$P <$
						Wald test				
LCB_{2013}	0.02	0.007	2.998	0.003	9	1	0.003	13.672	1	0.0002
P-W 1_{2013}	0.02	0.009	2.331	0.02	5.4	1	0.02	7.8	1	0.005
P-W 2_{2013}	0.02	0.008	2.977	0.003	8.9	1	0.003	13.669	1	0.0002
P-W 2_{2014}	0.02	0.009	2.121	0.03	4.5	1	0.03	6.30	1	0.01

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