Passage performance and behaviour of wild and stocked cyprinid fish at a sloping weir with a Low Cost Baffle fishway

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Abstract

Weir construction has fragmented many rivers, resulting in the exclusion of some fish populations from suitable habitat. A cheap retrofit fishway for small, sloping weirs is the Low Cost Baffle (LCB) solution - a series of notched baffles perpendicular to flow on the downstream weir face, generating an angled passage route across the weir face. To test the degree to which LCBs can pass upstream-moving, lowland-river fish at steep weirs, LCBs were fitted onto a 1:3.3-sloping gauging-weir face, in an urban tributary of the River Thames, England. The study also compared the passage of wild and stocked fish (the latter are employed to facilitate population recovery in restored English rivers). Passive Integrated Transponder (PIT) antennas were positioned on the weir to record the upstream movement of PIT-tagged barbel (*Barbus barbus*; n_{stock} =120), chub (*Squalius cephalus*; n_{stock} =119; n_{wild} =194), dace (*Leuciscus leuciscus*; n_{wild} =50), and roach (*Rutilus rutilus*; n_{wild} =30). Over six months, more stocked fish attempted passage (58.9%) than wild (14.6%; χ^2_1 =26.7, p <0.001), but there was no difference in successful passage of those that attempted (stock =34.0%; wild = 40.0%; χ^2_1 =0.5, p =0.49). Successful passage was achieved under a range of flow conditions. This study finds that LCBs have the potential to facilitate passage for cyprinid fishes at steep urban weirs that cannot readily be removed, but there is need for design improvements. This study also indicates that stocked and wild fish exhibited similar passage success, a finding with important management implications for achieving dispersal of stocked fish as a rehabilitation measure.

Keywords: barrier; fish passage; cyprinids; dispersal; longitudinal connectivity; PIT telemetry

1. Introduction

Anthropogenic river fragmentation is one of the leading causes of the decline of freshwater fish species diversity and abundance (Richter et al., 1997; Lucas and Baras, 2001). Fragmentation is often a result of the construction of river-spanning infrastructure, such as dams and weirs (Rosenberg et al., 2000), which prevent many aquatic species from migrating and / or dispersing between areas of potentially suitable habitat (Reidy Liermann et al., 2012; Radinger and Wolter, 2015). To reconnect river segments, it is desirable to remove these barriers to movement of biota and to reinstitute natural processes such as sediment transport (Birnie-Gauvin et al., 2017). However, globally, but including in the United Kingdom (UK), many of these barriers serve the purpose of gauging river height (WMO, 2010), and so the removal of them is particularly difficult to facilitate. In recent years there has been a surge in the development and implementation of fish passage options to mitigate the effects of these barriers to fish movement, thereby attempting to open-up fragmented stretches of river habitat (Castro-Santos and Haro, 2010; Cooke and Hinch, 2013; Silva et al., 2018).

In the north temperate zone, the drivers of the development of these fish passage structures has centred around the needs of economically important species, such as salmonids, often characterised by diadromous migrations between freshwater and marine environments (Bunt et al., 2012; Noonan et al., 2012). However, many fish populations undergo potamodromous migrations, wholly within freshwater, utilising different habitats for different functions such as reproduction or taking refuge (Lucas and Baras, 2001). Dispersal between habitat patches is an equally crucial ecological process enabling recolonization, gene flow and population persistence (Radinger and Wolter, 2015). Many species of several temperate-climate lowland river fish taxa, including cyprinids, catostomids and percids, exhibit seasonal patterns of upstream migration and/or dispersal, usually with a peak in spring-summer (Lucas et al., 1999; Steffensen et al., 2013; Thiem et al., 2013; Benitez et al., 2015; Kim et al., 2016). Historically, these taxa have been considered to have weaker burst and prolonged swimming performance than salmonids (Beamish, 1978; Videler, 1993; Clough and Turnpenny, 2001), although recent evidence from measuring volitional swimming in long flumes, rather than forced swimming in constrained test sections, may suggest otherwise (Sanz-Ronda et al., 2015). Moreover, the swimming ability and motivation for movement of cyprinids and other lowland river fishes through conventional fishways may not be optimized by conventional designs (Silva et al., 2018). It is therefore important that fish passage structures designed to mitigate habitat fragmentation support the behavioural characteristics and swimming abilities of all native fish that could potentially use the fishway. The importance of a fishway to be effective is further amplified by the high monetary costs involved in their construction and installation.

A potentially attractive fishway solution for low-head, sloping weirs is the relatively cheaper Low Cost Baffle (LCB) design, which consists of bolting wooden or plastic beams perpendicular to the flow directly onto the weir apron, with a fish passage route (notch) within the LCB design that runs diagonally up the weir (Servais, 2006). This arrangement slows the flow of water, and deepens the column of water flowing over the weir, with the aim of enabling weaker swimming fish species to pass upstream (Servais, 2006; Armstrong et al., 2010). The use of LCBs has been shown to be effective at enabling both juvenile and adult brown trout (*Salmo trutta*) to pass upstream (Forty et al., 2016; Dodd et al., 2018). Forty et al. (2016) measured passage efficiency as 63-82% in several experiments at an LCB-modified sloping weir with a height of 1.6 m and gradient of 1:4.2. The grey literature also suggests that LCBs can be effective for cyprinids, with one study at a typical 1:5 gradient gauging weir stating greater than 55% passage efficiency for chub, dace and roach (55.6%, 57.1% and 66.1%, respectively; Coe and Rana, 2014). However, there are no studies on cyprinid species use of LCBs in the peer review literature, nor are there any studies on the use of LCBs on steeply sloping weirs.

A current management strategy for rehabilitating areas of rivers affected by catastrophic events (e.g. pollution events, severe flooding) resulting in a large decline of the population, is to stock rivers with hatchery reared fish (Cowx, 1994; Bolland et al., 2009a). From a river rehabilitation perspective this relies on stocked fish dispersing successfully and surviving to reproduce. Stocked fish often have different physiology and behaviour to wild fish as a result of the rearing process (Pedersen et al., 2008; Urke et al., 2013). Stocked cyprinids may show greater daily activity than wild fish (Bolland et al., 2008), and can fair worse, with cyprinid stocking programs often failing (Aprahamian et al., 2004). However, Bolland et al. (2009a) found good overwinter survival and substantial dispersal of stocked cyprinids in a small lowland river, but limited in an upstream direction by impassable obstacles. It is therefore important that any fish passage structure can also facilitate the dispersal of fish stocked for rehabilitation purposes.

The primary aim of this study was to measure the passage performance and behaviour of four cyprinid species (barbel [*Barbus barbus*], chub [*Squalius cephalus*], dace [*Leuciscus leuciscus*] and roach [*Rutilus rutilus*]) at a steeply sloping gauging weir with a gradient of 1:3.3 fitted with LCBs. A secondary aim was to determine any differences in the ability of wild (chub, dace and roach) and stocked (barbel and chub) fish as they attempted passage of the weir.

2. Materials and Methods

2.1. Study Site

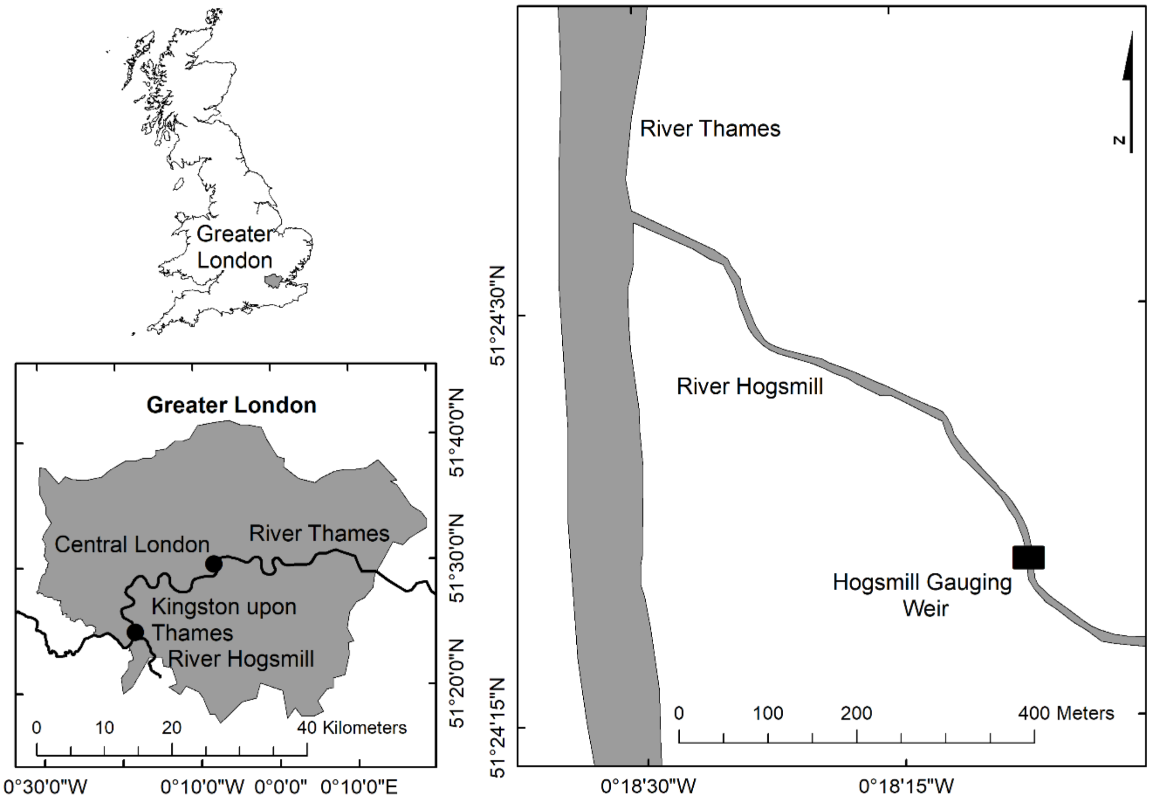

Fig. 1. Map of the Rivers Hogsmill and Thames, with the Hogsmill gauging weir labelled.

The River Hogsmill, a low-gradient tributary of the River Thames, is approximately 11 km in length and has a catchment area of approximately 73 km², meeting the Thames at Kingston-upon-Thames, Greater London (Fig. 1). The Hogsmill is situated in a highly urbanised area and as such has been classified under the European Union Water Framework Directive (EC; 2000/60/EEC) as being heavily modified and having poor ecological quality. Nevertheless, several reaches have gravel and sand habitat, macrophyte cover and sufficient habitat complexity to support a recovering fish community that includes barbel, chub, dace, roach, gudgeon (*Gobio gobio*), minnow (*Phoxinus phoxinus*), pike (*Esox lucius*), perch (*Perca fluviatilis*), 3-spined stickleback (*Gasterosteus aculeatus*), stone loach (*Barbatula barbatula*) and eel (*Anguilla anguilla*). A survey of the river identified the Environment Agency (EA) Hogsmill flow-gauging weir at Kingston-upon-Thames (51°24'20.77''N, 0°18'7.72''W; Fig.1) as the most downstream of 18 obstructions, including weirs, culverts and bridge footings on the Hogsmill. As the first obstacle for fish entering the Hogsmill from the Thames, the gauging weir posed a major obstacle to fish movement of management importance, especially larger cyprinids.

The gauging weir is approximately 600 m upstream of the Hogsmill-Thames confluence, and is a sloping weir, with a flat, 2.4 m long crest and approximately 9 m wide. The gauging weir has a height (from the crest to the bottom of the apron) of 1.44 m and a downstream apron length of 4.7 m, resulting in an apron slope of ~1:3.3. The typical operating head difference is ~1 m. Gauged river height (measured upstream of the weir) is typically between 0.11 m and 0.29 m, with a mean daily discharge of 0.98 $m^3 s^{-1}$. In non-drowned conditions water velocity on the downstream face approached 2 $m s^{-1}$ and with the thin water flow (typically < 0.05 m) made fish passage extremely difficult (T. Hull, pers. obs.). To reduce the impact of the gauging weir on fish movement, LCBs were attached to the weir apron in early February, 2017. The LCB arrangement allowed for a fish-passage route (notch width = 250 mm) offset diagonally on the weir apron (Fig. 2).

National (EA) guidelines requiring the non-obstruction of the weir crest, so as to maintain valid hydrometric calibration and operation as a flow-gauging weir, required that baffle placement on the downstream weir apron avoided the immediate zone downstream of the weir crest. As the slope of this gauging weir is greater than that previously investigated by Servais (2006; gradient = 1:5), the baffle placements had to be altered from those suggested by Servais (2006), with the first upstream baffle being placed 740 mm downstream from the weir crest (Fig. 2), and each subsequent baffle spaced at 400 mm intervals. Baffle height increased down the weir face, with the top baffle having a height of 120 mm, and the bottom baffle having a height of 288 mm (the heights [from the weir face] of each baffle from upstream to downstream are: 120 mm, 200 mm, 242 mm, 263 mm, 275 mm, 281 mm, 284 mm, 286 mm, and 288 mm, respectively). This was done in order to maintain a drowned-out coefficient of 0.6, as a result of the greater slope. A summary of water velocities and depths across the modified weir is given in Table 1.

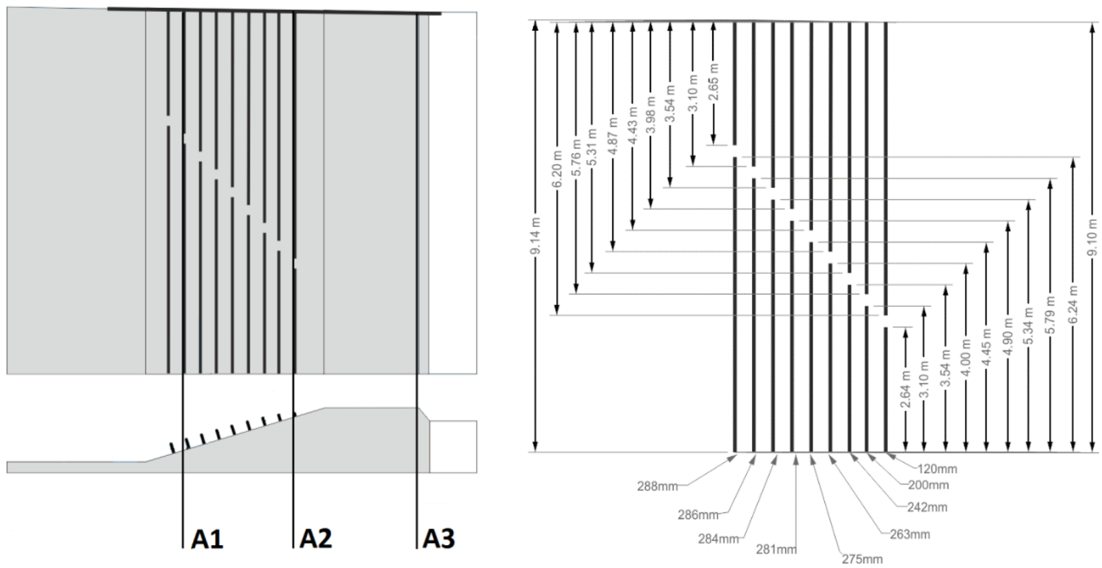

Fig. 2. Left: Plan view of the LCB arrangement on the Hogsmill weir apron with positions of antenna placement. Right: Schematic of the height and length of each baffle placed on the Hogsmill weir apron. The width of the notch in each baffle is 250 mm. The space between each baffle is 400 mm. River flow for both left and right panels is from right to left.

Table 1. Summary of the average water velocities and depths across the modified weir at different flow conditions (presented left to right, as downstream locations to upstream locations). Percentage stage exceedance is reported from the Worcester Road gauging weir.

Date	% Stage exceedance	Weir pool		Notch 7 – 9		Notch 4 – 6		Notch 1 – 3		Pre-Baffles		Crest		Upstream of Weir	
	(River stage (m))	$m\ s^{-1}$ (SD)	cm (SD)	$m\ s^{-1}$ (SD)	cm (SD)	$m\ s^{-1}$ (SD)	cm (SD)	$m\ s^{-1}$ (SD)	cm (SD)	$m\ s^{-1}$ (SD)	cm (SD)	$m\ s^{-1}$ (SD)	cm (SD)	$m\ s^{-1}$ (SD)	cm (SD)
21/02/2017	S 81.8 (1.06)	0.21 (0.13)	48.3 (11.9)	0.12 (0.07)	33.3 (4.9)	0.3 (0.25)	35.7 (6.1)	0.13 (0.93)	33.3 (4.0)	1.74 (0.16)	8.0 (0.5)	0.68 (0.13)	14.3 (3.2)	0.28 (0.03)	47.3 (10.7)
25/07/2017	S 93.9 (1.01)	0.24 (0.22)	28.1 (3.1)	0.24 (1.43)	18.0 (0)	0.71 (0.26)	16.7 (1.5)	0.46 (0.73)	13.0 (3.5)	1.30 (0.15)	2.0 (0)	0.44 (0.18)	3.6 (1.1)	0.09 (0.03)	23.2 (3.6)

2.2. Stocked Fish Tagging and Release

Hatchery reared, immature, barbel and chub that were aged 1+ and greater than 160 mm in length were selected for tagging at the EA Coarse Fish Rearing Unit at Calverton Fish Farm, UK, on the 7th February 2017. The stock fish were produced from wild broodstock and reared in tanks and ponds, always exposed to flow. Fish were anaesthetised (stage 4 on 6-stage scale) in an aerated solution of rearing-tank water and buffered tricaine methanesulphonate (MS-222; 100 mg l^{-1}) before being measured in length (fork length; mm) and mass (g). A small incision, approximately 4 mm in length, was made posterior to the pelvic girdle in a ventro-lateral position (Skov et al., 2005; Bolland et al., 2009b) and a Passive Integrated Transponder (PIT) tag (HDX, 23 x 3.4 mm, 0.6 g in air, Oregon RFID) inserted anteriorly into the body cavity. Fish were left to recover in a well-aerated tank before being transferred to a ~2 m^3 holding tank (see Bolland et al., 2009b for information on water treatment and circulation on site). Fish remained in their species-specific holding tanks at a water temperature of approximately 9.5 °C, and were fed several times per week at a maintenance ration on commercial pellet diet and gamma radiated natural diet, before being transported and stocked in the Hogsmill on the 2nd March, 2017.

Fish were transported from Calverton Fish Farm by custom-built fish transporting vehicles fitted with two tanks (300 l). To reduce fish stress induced by transport, a solution of Protex (0.003 ml l^{-1}; to enhance the fish ability to respond to temperature and ammonia fluctuations), Verkon (0.003 g l^{-1}; a water disinfectant) and Vida Life (0.067 ml l^{-1}; to aid in mucous replacement in areas of damage) were added to the water in the transport tanks. Transit time for fish to reach the stocking site (~250 m downstream of the gauging weir; 51°24’26.86’’N, 0°18’15.59’’W; Fig. 1) was approximately 4.5 hours. Once the fish had reached the stocking site they were left in the transport tanks for 15 min to settle before river water was added to the tanks to create a 50:50 river water to transport water solution. Fish were left in this solution for 15 min to allow for acclimation to river water temperature and quality. Fish were released into the river at 1500 hrs. No mortalities occurred during tagging, recovery or stocking. Stocked fish handling mimicked the current management practices of the UK, enabling for the data to be interpreted in a way that would best inform management practices and decisions. All procedures were conducted in compliance with the UK Animals (Scientific Procedures) Act 1986 under a Home Office issued licence.

2.3. Wild Fish Capture and Tagging

Fish were captured from the Hogsmill using depletion electrofishing on 21st February 2017. The Hogsmill downstream of the weir was separated into three sections by stop-nets (15 mm mesh) starting ~500 m downstream of the gauging weir, and ending ~110 m downstream of the gauging weir. Section 1 was 90 m (three fishing runs) in length, Section 2 was 147 m in length and Section 3 was 130 m in length (two fishing runs in each section). Fishing was not conducted within 110 m of the gauging weir to avoid tagging fish that could be more likely to reside at the base of the weir, and would therefore be repeatedly detected (increasing blocking of detection of other PIT tags; Cooke et al., 2012) despite potentially not attempting to pass the gauging weir.

A team of six individuals performed the electrofishing, using three anodes and three hand nets. A generator (Honda EU inverter 20i; replaced with a Honda EB 1900x after the first fishing run of Section 2) and electrofishing control unit (Electracatch WFC4-96, at 220 V and 1 Amp) were placed on a small boat that was pulled behind the electrofishing team. Fish that were captured from the river were placed into a large holding tank filled with oxygenated river water that was pulled behind the electrofishing team on a separate small boat. After each run, fish were moved to land-based holding tanks (also filled with oxygenated river water) at the processing site (Fig. 1) and split by species (i.e. chub, dace, roach and other). Fish from successive runs in a section were combined, but fish from different sections were kept separately. By keeping fish separated by river sections, we could ensure that fish released in the centre of their respective sections would have been displaced no further than 75 m, thereby reducing the disturbance effect within the system.

Based on Bolland et al (2009b), chub, dace and roach greater than 140 mm were chosen for tagging with 23-mm HDX tags. Fish were processed using the same methodology as described for stocked fish tagging. After tagging, fish were left to recover in well-aerated tanks until they were swimming strongly and appeared fully recovered from the anaesthetic. Post-processing, all fish from one section were placed in a single, large holding tank and released as one group at the midpoint of each respective section to facilitate shoaling behaviour. Fish were released between 1400 and 1730 hours.

2.4. PIT Logging Station Network

Three HDX PIT, vertical swim-through antennas were constructed across the gauging weir between 8th and 10th February 2017, and monitored the movements of PIT tagged fish from 21st February until 31st July 2017. This monitoring period encompassed the known reproductive periods and main upstream migration periods, for each of the wild species tagged (reproductive periods for chub, dace and roach are May-June [Guerreiro, 2007], March-April [Mann, 1974], and April-May [Kestemont et al., 1999], respectively). Stocked barbel and chub were immature, while typical median sizes at first maturity for chub, dace and roach are ~20, 18 and 14 cm respectively (www.Fishbase.org). Two antennas were built on the gauging weir apron and one on the upstream edge of the gauging weir crest. The first (A1) was built onto the second most downstream baffle, where the top of the weir pool meets the weir apron. This was considered the ideal position to reduce the chance of reoccurring false detections from fish residing in the weir pool but not attempting to pass the weir. The second antenna (A2) was constructed on the upstream most baffle, ~2.8 m upstream of A1, with the third antenna (A3) being located on the most upstream edge of the flat weir crest as it begins to slope towards the upstream river bed, and at a distance of ~3.1 m from A2.

PIT antennas were built to the dimensions of 9 x 0.7 m in order to accommodate the width of the weir and the flood height of the water above the weir apron without compromising the detection range. All antennas were constructed with 6 mm, copper braided wire to ensure sufficient detection range (~0.3 m perpendicular) for fish swimming rapidly, particularly across the flat crest. Read rates were ~15 times per second. Antennas were checked and adjusted for optimal tuning approximately every 30 sec after the initial system start-up by individual Dynamic Tuning Units (DTUs; Wyre Microdesign) to allow for changes to antenna shape during the study. The three antennas were interrogated by one Master (A1) and two Slave (A2 and A3) reading units (Wyre Microdesign, Mk4) which were connected in series and synchronised through the Master reading unit. The system was powered by trickle-charging a 110 Ah 12 V leisure battery from mains power (240V AC) through a linear supply leisure battery charger. This ensured a constant supply of power to the PIT system while suppressing electrical noise from the mains power supply which can otherwise interfere with the PIT system. The time, date, antenna number and code of each tag detected was stored on a stand-alone data-logger which was downloaded at least once a week.

PIT systems were checked both prior to the release of tagged fish and throughout the study at each visit to the study site to ensure that there were no detection gaps within the antennas. This was performed by manually passing a PIT tag through the antenna at various places along the plane of the antenna, as well as testing that the detection range (approximately 0.2 m either side of the antenna perpendicular to its plane) and performance of the antennas were constantly high by passing the tag through the antennas at speeds of approximately 1 ms^{-1}, multiple times at various locations within the antenna's plane. Further testing of the antennas was continuously carried out throughout the study by fixed marker tags (Oregon RFID) attached perpendicularly to the plane of each antenna in the upper, inside corner. These marker tags were active for 1 sec every 15 min.

Antenna 1 was operational for 93% of the study period, and A2 and A3 for 91%. All antennas were damaged during a high flow event and subsequently not operational between 7th and 8th of June 2017, followed by fuses in reader boxes blowing on 8th June (for an unknown reason) and not being fixed until 19th June. Readers for antennas 2 and 3 also blew fuses and were not operational between 27th April and 1st May 2017, believed to be a result of the signal cable being damaged.

2.5. Environmental Data Collection

River stage was recorded every 15 min from the Worcester Road gauging weir, approximately 5.2 km upstream of the Hogsmill gauging weir. Data from the Worcester Road gauging weir was used rather than the Hogsmill gauging weir due to malfunction of the

Hogsmill gauging weir recorder between 21st February and 28th April 2017, precluding use of the Hogsmill gauging data for that portion of the study. A sewage treatment plant was positioned between the two gauging weirs (~1.1 km upstream of the Hogsmill gauging weir) which expelled water continuously throughout the day, and typically had two flow peaks (at approximately 1200 and 2200 hrs; A. Lothian, pers. obs.), which were therefore not recorded on the Worcester Road gauging weir. However, an analysis of variance indicated that the mean daily stage from Worcester Road gauging weir, for the period after the Hogsmill gauging weir was calibrated correctly, was positively correlated with the mean daily stage recorded at the Hogsmill gauging weir (r^2=0.64; residuals normally distributed), and therefore the stage data obtained from Worcester Road was used as a substitute. Water temperature was recorded at 15 min intervals, 20 m downstream of the weir (HOBO, Pendant Temperature Data Logger [UA-001-XX]).

Fine scale river flow velocities (m s^{-1}) and depth (cm) across a grid from downstream to upstream of the weir were recorded on 21st February and 25th July 2017 (Table 1). Flow velocities were recorded at 0.2 m lateral and longitudinal intervals, beginning 2 m downstream of the weir and finishing 2 m above the weir. Flow measurements were taken using a Valeport Model 801 EM Flow Meter at 10% and 50% water column depths

2.6. Statistical Analyses

Proportions of fish attempting passage were calculated as those fish detected on A1 against all fish released. Proportions of fish succeeding in passage of the LCBs were calculated as those that were detected on A2 against those that were detected attempting passage on A1. Proportions of fish that succeeded passage of the weir were calculated as those that were detected on A3 against those that were detected attempting on A1. Comparisons of proportions were conducted using Chi-squared tests for given proportions to compare species proportions within stocked and wild groups, and to compare proportions between stocked and wild groups as wholes for attempted passage and LCB passage. As it was recognised that some fish were missed by either A1 or A2 (one wild chub and one stocked chub were successful, but not detected on A1; it is not possible to know if any fish were missed by A3 due to the absence of a further upstream antenna), estimations of detection efficiencies for A1 and A2 were calculated from the proportion of fish known to have passed each, relative to those recorded. Antenna A3 detection efficiency was estimated as the average of those for A1 and A2. The estimated numbers of tagged fish at A1, A2 and A3 were calculated using the detection efficiencies to correct the observed numbers.

Two binary Generalised Linear Mixed Effect Models (GLMMs) with a logit function were generated to examine variables that might influence the probability of a passage attempt being successful (using the *lme4* package R [Bates et al., 2014]). Separate models were made for stocked fish and wild fish, as it could not be assumed that the motivations for upstream passage were the same between the two groups (stocked fish, known to be immature, were thought to be dispersing upstream, exploring the environment and /or in search for available feeding habitat, whereas at least a proportion of wild fish may have been migrating upstream for reproductive purposes).. The length of time a unique passage attempt occurred over was determined on a per species (grouped by source) basis by calculating the time interval between successive detections on A1, and identifying the time taken until the first interval that was greater than 20 sec (Castro-Santos and Perry, 2012). Passage attempts were therefore deemed to have lasted: 2180 sec for stocked barbel, 240 sec for stocked chub, 120 sec for wild chub, 60 sec for wild dace, and 100 sec for wild roach. A lapse between two detections on A1 that was greater than the respective passage attempt times were deemed to be the threshold of a new attempt. The success of a passage attempt (i.e. “0” for failed passage attempt, and “1” for successful passage attempt) was modelled against river temperature, mean daily river stage (obtained from Worcester Road gauging weir), Julian date of the year, day or night (temperature, river stage, Julian date and day or night were recorded at time of attempt), species and fish length (at time of tagging). Both models included fish ID as a random effect to account for pseudo-replication as a result of repeated attempts by each fish. Only the attempts until first passage of the weir were included (i.e. for those fish that passed the weir on several occasions, only those attempts prior to and including the first passage was used). Fish that were successful but not detected on A1 (one stocked chub and one wild chub were not included in these models describing passage success, as no attempts were discernible. Model selection was performed using a step-down approach and was based on minimising Akaike’s An Information Criterion (AIC), with the Likelihood Ratio Test (LRT) being reported for each variable.

Success probability was then modelled for overall success rather than on a per attempt basis by generating two Generalised Linear Model (GLMs) with a logit function. Separate stocked and wild models were made for the same reasons as above for the GLMMs predicting whether a passage attempt was successful, and used the same variables at time of first detection on A1. Model selection followed the same procedure as for the GLMMs, with the LRT reported for each variable (see Table S2). To identify whether the passage success was influenced by the twice daily increases in water level at the Hogsmill gauging weir as a result of the upstream sewage treatment plant, another binomial GLM with a logit function was made for only those fish that attempted passage after the 28th April 2017 (using valid Hogsmill weir gauged Stage), with the stage at time of ascent (to the nearest 15 min) as an independent variable was made. Model selection for this was performed by LRT, by comparing the model with one the independent variable.

To determine if species successfully passed the weir under certain river conditions, an ANOVA was used to compare the percentage stage exceedance (measured at the Worcester Road gauging weir) against species. Time to pass the weir was calculated as the difference in time between a fish's first detection on A1 to its first detection on A3. Passage duration for successful attempts was calculated as the difference in time between a fish's last detection on A1 to its first detection on A3, resulting in a length of time it took the fish to move through the LCBs and over the weir crest, completing an uninterrupted passage of the weir. An ANOVA was performed to test whether species (grouped by stocked or wild) had significantly different times to pass the weir from first attempt. If a significant effect was found, then a Tukey post-hoc test was performed to identify the sources of difference. The same analysis was used to test for any difference in the passage duration of successful attempts between species, grouped by wild or stocked, and the length of time fish remained on the gauging weir apron (i.e. from last detection on A1 to last detection on A2). The passage duration, and the time spent on the gauging weir apron were log-transformed to fit the ANOVA assumptions, but time taken to pass the weir met ANOVA assumptions and so was not transformed. All statistical approaches were performed in RStudio (v1.1.423) using R (v3.4.3; R Core Team, 2014). Tukey post-hoc tests were performed using the *lsmeans* package (Lenth, 2016).

3. Results

3.1. Passage performance

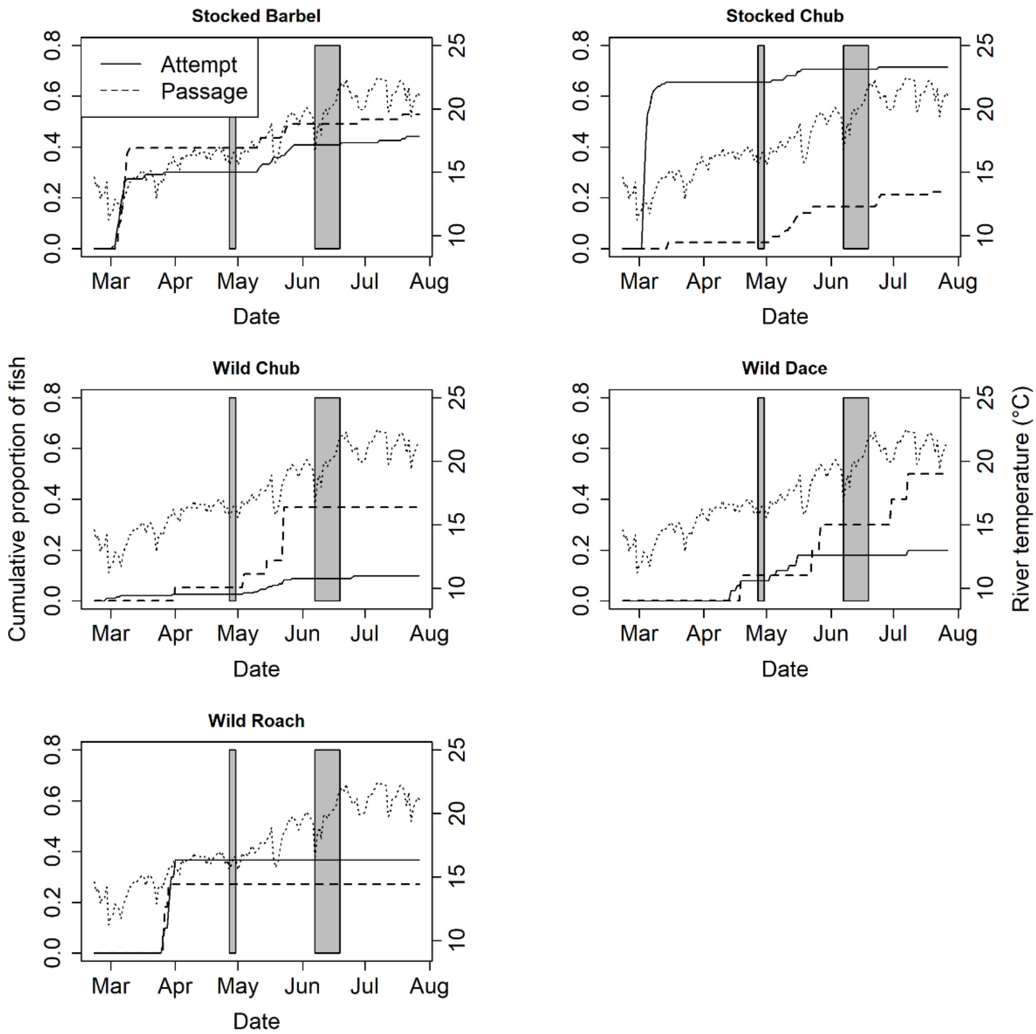

Fig. 3. The cumulative proportion of fish released that attempted passage (solid lines) and the cumulative proportion of attempting fish that were successful in ascending the weir (dashed line) over time, with mean daily river temperature (dotted line) overlaid. Grey box indicates time during which PIT antennas were not operational.

The detection efficiency for A1 was 98.9% (known to have missed two fish: one stocked chub and one wild chub) and A2 was 90.1% (known to have missed eight fish: 5 stocked chub and 3 wild chub. It was not possible to calculate a detection efficiency for A3 due to the absence of an antenna upstream of the weir, but an average of A1 and A2, applied to A3 is 94.5%. This may have been a result of the downtime experienced by the antennas due to blown fuses. There was no evidence of significant migration on either side of the downtime experienced by these antennas (Fig. 3), and so it was not believed that large numbers of fish were missed.

A total of 120 and 119 hatchery reared barbel and chub, respectively, were PIT tagged and released, along with 194 wild chub, 50 wild dace and 30 wild roach (Table 2). Of the 513 fish tagged in this study, 181 were detected attempting passage of the weir, equating to an overall proportion of fish attempting passage of 35.3%. A significantly greater proportion of stocked fish attempted passage (58.0%) than wild fish (14.6%; $\chi^2_1 = 26.7$, $p < 0.001$; Fig. 4). Among stocked fish, a significantly greater proportion of chub (72.3%) attempted passage than barbel (44.1%; $\chi^2_1 = 6.8$, $p = 0.01$). A smaller proportion of wild chub (10.3%) attempted passage than dace (20.0%) or roach (33.3%). Two stocked barbel were detected at A1 at times when A2 and A3 were not operational, and so were removed from the rest of the analyses. There were no differences in the proportions of stocked or wild fish that successfully passed the LCBs (stocked = 44.6%; wild = 47.5%; $\chi^2_1 = 0.1$, $p = 0.76$), that successfully moved from the top of the LCBs to pass the weir (stocked = 77.4%; wild = 85.0%; $\chi^2_1 = 0.4$, $p = 0.55$) or that passed the entire gauging weir (i.e. the LCB and the post-LCB complex; stocked = 34.5%; wild = 40.0%; $\chi^2_1 = 0.4$, $p = 0.52$; Table 3). There was also no significant difference in the proportions of fish that successfully passed the LCBs, and those that passed the entire gauging weir (LCBs = 45.2%; weir = 35.8%; $\chi^2_1 = 1.1$, $p = 0.29$; Table 3). However, a greater proportion of fish were successful at moving from the top of the LCBs to pass the gauging weir (i.e. from A2 to A3; post-LCBs = 81.2%) than completing the LCBs (i.e. from A1 to A2; LCBs = 45.2%; $\chi^2_1 = 10.3$, $p = 0.001$).

Table 2. Summary of the source, number, fork lengths and masses of each species tagged.

Species	Source	No.	Length (mm)		Mass (g)	
			Mean (SD)	Range	Mean (SD)	Range
Barbel	Stocked	120	190.5 (8.1)	168 – 210	78.5 (10.50)	53 – 109
Chub	Stocked	119	177.4 (8.9)	160 – 209	75.8 (13.8)	53 – 129
Chub	Wild	194	319.3 (92.9)	178 – 525	604.8 (558.7)	71 – 2494
Dace	Wild	50	186.7 (24.0)	142 – 227	99.8 (39.5)	35 – 202
Roach	Wild	30	220.8 (41.3)	142 – 300	223.6 (132.6)	46 - 501

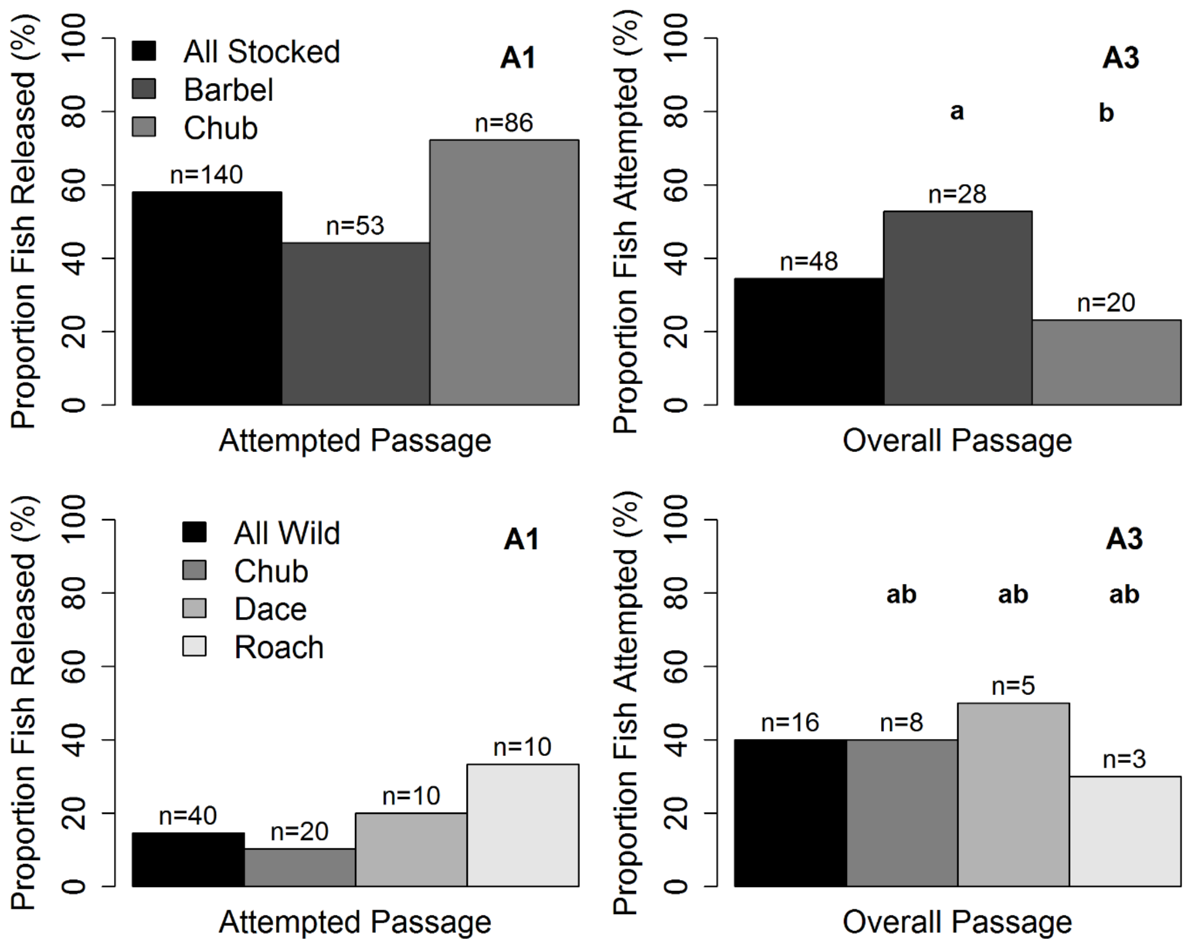

Fig. 4. The proportions of fish attempting passage and successfully ascending the weir (overall passage efficiency) for stocked barbel and chub (top), and wild chub, dace and roach (bottom), with the number of all individuals combined and also separated by species.

Species was a significant variable in the stocked fish overall passage probability model (LRT: $\chi^2_1 = 13.4$, $p < 0.001$). A Tukey post-hoc test identified that a significantly greater proportion of stocked barbel (52.8%) successfully passed the gauging weir than stocked chub (22.4% (23.2% including fish not detected on A1); Fig. 3; Fig. 4). There was no difference in the proportions of wild species (wild chub = 36.8% (40.0% including fish not detected on A1);

wild dace = 50.0%; wild roach = 30.0%; Fig. 3; Fig.4) that successfully passed the gauging weir (LRT: $\chi^2_2 = 4.22$, $p = 0.12$).

There was no difference in the proportion of successful attempts made by each species in either the wild fish model (LRT: $\chi^2_2 = 4.19$, $p = 0.26$) or the stocked fish model (LRT: $\chi^2_1 = 2.45$, $p = 0.12$). The proportion of successful attempts for stocked barbel and stocked chub were 4.1% and 4.7%, respectively, and both species had a median (25th percentile, 75th percentile) of 4 (stocked barbel: 2, 8; stocked chub: 2, 7) failed attempts per individual before either succeeding or giving up attempting passage (Table 4). The proportion of successful passage attempts for wild chub, dace and roach were 12.7%, 27.8% and 5.6%, respectively (Table 4). The median (25th percentile, 75th percentile) number of failed attempts before either the first successful attempt or giving up attempting passage for wild chub, dace and roach were 2 (1, 3), 1 (1, 2), and 3 (3, 10), respectively.

Table 3. Summary of the number of fish known to have passed each antenna (based on actual detections and known missed detections by A1 and A2), the proportions of fish detected on A2 and A3 that were also detected on A1 for each species, the proportion of fish detected on A3 that were also detected on A2, and the estimated proportion of fish that passed A3 and completed passage based on the calculated and estimated detection efficiencies. * includes two fish detected on A1 when A2 and A3 were not operational.

Species	Source	No. fish A1	No. fish A2 (proportion of A1)	No. fish A3 (proportion of A2; proportion of A1)	Estimated No. fish A3 (proportion of A1)
Barbel	Stocked	53 (55*)	36 (67.9%)	28 (77.8%; 52.8%)	30 (56.6%)
Chub	Stocked	86	26 (30.2%)	20 (76.9%; 23.2%)	21 (24.4%)
Chub	Wild	20	10 (50.0%)	8 (80.0%; 40.0%)	9 (45.0%)
Dace	Wild	10	5 (50.0%)	5 (100.0%; 50.0%)	5 (50.0%)
Roach	Wild	10	4 (40.0%)	3 (75.0%; 30.0%)	3 (30.0%)
Total		**179 (181*)**	**81 (45.3%)**	**64 (79.0%; 35.8%)**	**68 (38.2%)**

Table 4. The number of failed and successful attempts until the first successful attempt per fish, and the proportion of the total that were successful. * includes fish missed by A1 and so not included in the analyses.

Species	Source	Median No. Failed Attempts per Fish (25th and 75th percentile)	Failed Attempts	Successful Attempts	Total Attempts	Proportion successful
Barbel	Stocked	4 (2, 8)	649	28	677	4.1%
Chub	Stocked	4 (2, 7)	383	19 (20*)	402	4.7%
Chub	Wild	2 (1, 3)	48	7 (8*)	55	12.7%
Dace	Wild	1 (1, 2)	13	5	18	27.8%
Roach	Wild	3 (3, 10)	50	3	53	5.6%
Total		**3 (2, 7)**	**1143**	**62 (64*)**	**1205**	**5.1%**

Length of wild fish was a significant variable in the model predicting the proportion of successful attempts for wild fish (LRT: χ^2_1 = 5.01, p = 0.03), but not in the stocked fish model (LRT: χ^2_1 = 0.24, p = 0.62), with larger fish tending to have a reduced probability of a successful attempt. When success probability was modelled for overall success rather than on a per attempt basis, a significant length effect was still evident for wild fish (LRT: χ^2_1 = 6.09, p = 0.01), but not stocked fish (LRT: χ^2_1 = 0.01, p = 0.99). Specifically, larger wild chub (mean ± SD = 382 ± 102 mm) were more successful than smaller wild chub (mean ± SD = 261 ± 59 mm; Wilcoxon rank sum test: W = 79, p = 0.02). Further information and analysis of lengths for fish that did and did not succeed in passage is given in Table S2.

3.2. Abiotic variables effect on passage probability

Temperature was not found to have an effect in the wild passage attempt success model (LRT: χ^2_1 = 0.03, p = 0.73), but was found to be a significant variable in the stocked passage attempt success model (LRT: χ^2_1 = 28.60, p < 0.001). Stocked fish attempts were found to be more than 1.5% more successful with each 1°C increase. The median temperature (5th percentile, 95th percentile) that stocked attempts were successful and unsuccessful were 16.7°C (12.3°C, 21.2°C) and 14.0°C (11.7°C, 22.0°C), respectively.

Day or night (LRT: χ^2_1 =0.11, p = 0.73; LRT: χ^2_1 = 0.01, p = 0.98) and Julian date (LRT: χ^2_1 = 0.73, p = 0.39; LRT: χ^2_1 = 0.05, p = 0.82) failed to show an effect on the wild and stocked passage attempt success models, respectively. All roach had attempted and either succeeded or failed to ascend the weir within 6 days between Julian dates 84 (25 March 2017) and 90 (31 March 2017), with all other species attempting passage across a wider range of days (stocked barbel = 141 days; stocked chub = 113 days; wild chub = 119 days; dace = 85 days).

The median Julian dates for stocked barbel and stocked chub attempts were 66 (7 March 2017) and 63 (4 March 2017), respectively. The median Julian dates for wild chub, dace and roach were 135 (15 May 2017), 124 (4 May 2017) and 88 (29 March 2018), respectively (Fig. 3).

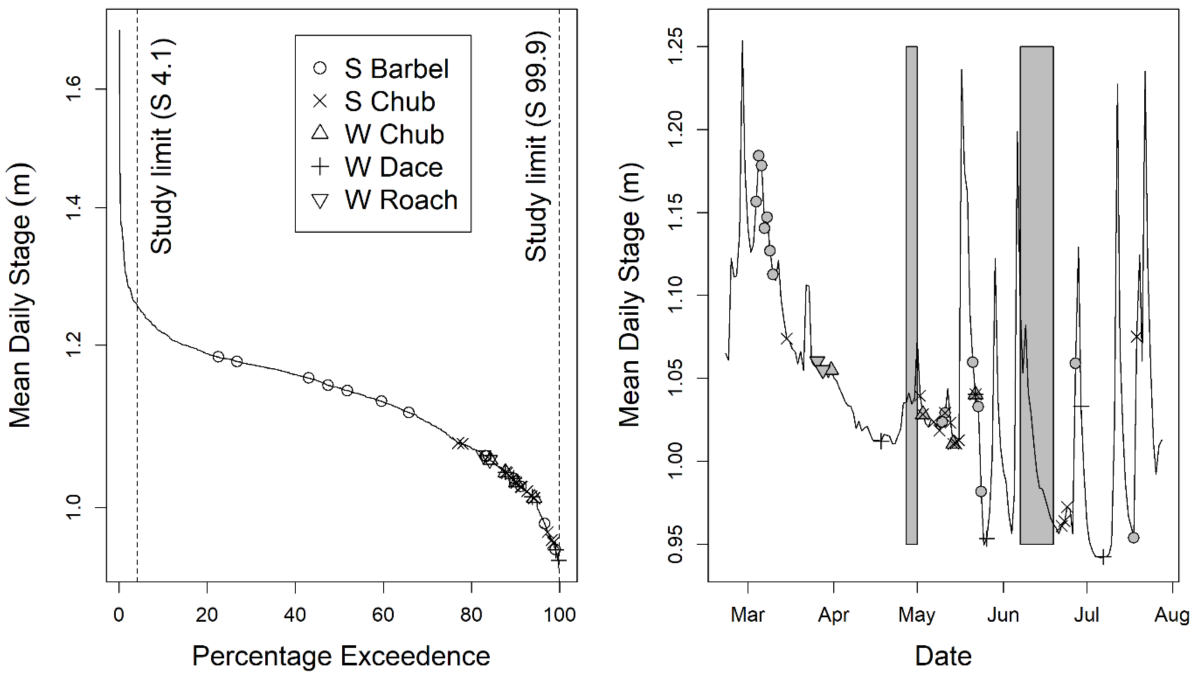

Fig. 5. Left: Stage exceedance curve with successful fish ascents (points split by species grouped by source; S, stocked; W, wild) overlaid. Right: Mean daily stage for the study period with successful fish ascents (points split by species, grouped by source). Grey boxes indicate times during which PIT antennas were not operational.

River stage was found not to be significant in the models predicting the proportion of successful attempts for either wild fish (LRT: χ^2_1 =1.29, p = 0.26) or stocked fish (LRT: χ^2_1 = 0.13, p = 0.71). The river stages (Worcester Road gauging station) experienced during this study ranged from 0.94-1.25 m. Fish were observed to pass the weir across a range of these river stages (0.94-1.23 m), but this varied significantly between species (ANOVA: $F_{4,\,57}$ =

11.3, $p < 0.001$; Fig. 5). Stocked barbel tended to pass the weir during periods of greater river height (range = 0.95-1.18 m; mean ± SD = 1.11 ± 0.06) in comparison to stocked chub (range = 0.96-1.24 m; mean ± SD = 1.0 ± 0.06), wild chub (range = 1.01-1.05 m; mean ± SD = 1.03 ± 0.01), and dace (range = 0.94-1.03 m; mean ± SD = 0.99 ± 0.04). Roach were not found to be statistically different from any other species (range = 1.05-1.06; mean ± SD = 1.06 ± 0.00).

For fish that attempted passage of the weir after 28th April 2017 (n = 52), when the Hogsmill gauging weir was calibrated and working again, there was no effect of locally recorded river stage (at 15 min intervals) on the passage probability of fish at the time of attempted passage (LRT: $\chi^2_1 = 0.08$, $p = 0.77$). No abiotic variables were found to be significant in the overall passage success probability models (Table S1).

3.3. Time to pass from first detection, and passage duration of successful passage attempts

Time taken to pass the gauging weir (from first detection on A1 to first detection on A3, i.e. including intervals between repeat attempts for those individuals that attempted on multiple occasions) differed significantly between species grouped by source (ANOVA: $F_{4, 57} = 15.1$, $p < 0.001$). Tukey post-hoc comparison indicated that stocked chub (median = 99353.0 min, range = 0.2 – 197821.6 min) were significantly slower than stocked barbel (median = 1182.2 min, range = 2.1 – 11584.7 min; $t_{57} = -7.3$, $p < 0.001$), wild chub (median = 1389.1 min, range = 1.0 – 10368.4 min; $t_{57} = 4.8$, $p < 0.001$) and roach (median = 0.5 min, range = 0.1 – 909.4 min; $t_{57} = 3.6$, $p < 0.01$). There was no significant difference between dace and any other groups (median = 56406.7 min, range = 2.0 – 83970.9 min).

The passage duration for successful attempts (i.e. last detection on A1 to first detection on A3) was also found to significantly differ between species grouped by source (ANOVA: $F_{4, 57}$ = 3.4, p < 0.01). Tukey post-hoc comparison indicated that stocked barbel (median = 30.7 min, range = 2.1 – 174.9 min) were significantly slower than roach (median = 0.5 min, range = 0.1 – 7.7 min; t_{57} = 3.2, p = 0.02). Neither stocked barbel nor roach significantly differed from stocked chub (median = 13.0 min, range = 0.2 – 185.6 min), wild chub (median = 13.3 min, range = 0.3 – 15.3 min) or dace (median = 2.0 min, range = 0.2 – 58417.6 min)

The length of time fish were on the gauging weir apron and therefore within the LCB complex (i.e. from last detection on A1 until last detection on A2) was found to be significantly different between species grouped by source (ANOVA: $F_{4, 66}$ = 4.8, p = 0.02). Stocked barbel were found to spend a greater amount of time on the weir apron within the LCBs (median = 23.1 min, range = 0.5 – 921.6 min) than both stocked chub (median = 6.2 min, range = 0.1 – 185.6 min; t_{66} = 2.9, p = 0.04) and roach (median = 0.3 min, range = 0.1 – 7.7 min; t_{66} = 3.6, p = 0.05). Wild chub and dace did not spent significantly more or less time on the weir face than each other (wild chub: median = 11.0 min, range = 0.9 – 15.3 min; dace: median = 1.9 min, range = 0.1 – 58417.6 min), or in comparison to the other groups.

4. Discussion

This is the first study to quantify the passage performance of lowland-river fishes at a steep (gradient = 1:3.3) low-head gauging weir fitted with LCBs. Passage efficiencies of between 23.2% and 52.8% were measured for four common cyprinid species, but estimated passage efficiency when taking into account the detection efficiency were between 24.4% and 56.6%. Caution is needed for the passage efficiency measures of wild dace and roach, which were based on small sample sizes attempting (n = 10 for both species; see below). Lucas & Baras (2001) have suggested a passage efficiency exceedance of 90% as a target for diadromous and strongly potamodromous fishes for population recovery. Although the passage efficiency measured in this study is well below that target, all of the species are facultative migrators (Lucas & Baras, 2001), while the naïve, immature, stocked fish were dispersing as they explored the environment into which they were stocked (sensu Bolland et al., 2009a). Under these circumstances, much lower passage efficiency targets might still achieve population persistence or restoration, and enable bidirectional gene flow (Wilkes et al., 2018). The use of LCBs has potential in achieving upstream passage for these species at steeply sloping (up to 1:3.3), low head urban weirs that cannot readily be removed. Unlike in other studies that have monitored brown trout passage at LCBs at non-gauging weirs where the baffles were positioned up to the weir crest (Forty et al., 2016), the hydrometric gauging standards to prevent interference with gauged river level at the crest on the weir in this study precluded placing baffles for a short distance (0.74 m) below weir crest, resulting in an area of high velocity and low water depth. Improved design standards for hydrometric gauging in the future may allow baffle placement all the way to the crest.

Although the study was conducted to include the spawning migration period for each wild species, relatively low proportions of wild fish attempted passage. Of those fish that were detected on the PIT array around the weir, they were within the known timeframes of the respective spawning season (see Section 2.4; Mann, 1974; Kestemont et al., 1999; Guerreiro, 2007), and so were likely to be migrating for spawning purposes. Many temperate lowland-river fishes including rheophilic (e.g. dace, chub) and eurytopic (e.g. roach) cyprinids are, however, facultative, not obligate migrators (Lucas and Baras, 2001) and in most telemetry studies on these species only a proportion of mature fish tagged are demonstrated to exhibit upstream migration in spring (Lucas and Batley, 1996; Clough and Beaumont, 1998; Geeraerts et al., 2007). For a potamodromous Iberian barbel (*Luciobarbus bocagei*) only 7.1% of PIT tagged fish caught downstream of a dam and fishway were detected in the fishway entrances during the spring migration season, whereas 62.5% of fish translocated from upstream to below the weir were detected (Bravo-Córdoba et al., 2018). It is likely that the motivation to move upstream past a point is present in only a fraction of such facultative migratory populations, whether in a rather fixed behaviour pattern among individuals (partial migrants) or exhibited more plastically.

It is possible that many wild fish tagged could have moved back into the Thames prior to the spawning season, potentially due to the effects of capture and tagging, which has been observed in dace and roach, both of which are particularly susceptible to handling effects and the negative impacts of electrofishing (Jepsen and Berg, 2002). As an alternative to a low fraction of upstream-directed potamodromous behaviour, such a post-tagging stress response could potentially explain the low number of wild fish attempting passage of the weir. However, radio tracked roach have been shown to move between rivers and tributaries during the spawning period (Geeraerts et al., 2007), and so it is also plausible that many of the tagged fish travelled back into the River Thames and potentially into another tributary of their own volition for spawning, rather than through any handling effect. The greater number of passage attempts exhibited by stocked fish in comparison to wild fish is likely to have resulted from initial habitat exploration post-release (Thorfve, 2002; Bolland et al., 2009a). Bolland et al. (2009a) noted that PIT detections of juvenile chub dispersing away (upstream and downstream) from stocking sites were particularly high in the first 6 weeks after release.

The same tendency for strong dispersal activity of chub upstream, and presumably also downstream, in this study was very evident.

Table 5. Summary of passage efficiency for sloping weirs and fishways for barbel, chub, dace and roach, with the mean length of fish studied, as reported in the literature.

Authors	Weir / Passage Structure (Slope gradient)	Barbel (length range ; mm)	Chub (length range ; mm)	Dace (length range ; mm)	Roach (length range ; mm)
This study	Low Cost Baffle (1: 3.3)	52.8% (168-210)	23.2%-40.0% (160-525)	50.0% (142-227)	30.0% (142-300)
Lucas and Frear, 1997	No fishway / Flat–V weir (1:5)	40% (mean = 529)	-	-	-
Lucas et al., 2000	Denil baffle (1:5)	-	25.8% (100 – 580)	10.0% (100 – 190)	16.7% (100 – 300)
Calles and Greenberg, 2007	Nature-like bypass (1:40)	-	81.8% (280 – 435)	-	50% (116 – 284)
	Nature-like bypass (1:55.6)	-	100.0% (128 – 480)	-	-
Coe and Rana 2014	Low Cost Baffle (1:5)	-	55.6% (225 – 400)	57.1% (145 – 280)	66.1% (145 – 290)
Ovidio et al., 2017	Pool and Weir (1:22.9)	7.1% (180 – 596)	-	-	-
Piper et al., 2018	Larinier baffle (1:6.6)	-	45% (79 – 472)	81% (93 – 238)	10% (84 – 296)
Benitez et al., 2018	Vertical slot (unknown)	66.7% (245 - 742)	94.3% (231 – 524)	-	-

The passage efficiency per species reported in this study is within the range reported for a variety of fishways at low-head barriers for the same species (Table 5). However, the fish in this study had lower passage efficiency than those reported in Coe and Rana (2014) for an LCB fishway, potentially as a result of the steeper weir apron slope on the Hogsmill gauging weir, though more data is required on a range weir apron slopes and species to draw appropriate conclusions. The passage efficiency for trout at LCBs was also reported to be higher (63% for non-displaced trout [Forty et al., 2016]; 91% for displaced and non-displaced trout combined [Dodd et al., 2018]) than recorded at the Hogsmill gauging weir in this study. But this may also be a result of differences in weir apron gradient (1: 3.3 in this study compared to 1:4.2 [Forty et al., 2016] and 1:9.3 [Dodd et al., 2018]). There were also similar or higher passage efficiencies recorded for taxa with fusiform or ventrally flattened, elongate morphology at Vertical Slot fishways (Hatry et al., 2016: 88% for silver redhorse (*Moxostoma anisurum*), 50% for river redhorse (*Moxostoma carinatrum*), and 69% for shorthead redhorse (*Moxostoma macrolepidotum*); Sanz-Ronda et al., 2016: 71% for Iberian barbel, and 70% for straightmouth nase (*Pseudochondrostoma duriense*). The passage efficiencies presented in this study could be a conservative estimate of the real passage efficiency, due to two periods of antenna downtime. Fish that attempted and failed at passage may have returned and succeeded during either period of antenna downtime, which overlaps with the main migratory period for chub and dace. However, there was no sign of large-scale fish movements around these periods, and so it was unlikely that many fish were failed to be detected.

The probability of fish to succeed in passing the gauging weir tended to favour smaller fish and intermediate-sized fish over the very largest fish, particularly for wild fish where a greater range of fish sizes was available. We provide two hypotheses for this outcome: Firstly, that the depth and velocity of water flowing over the weir crest was not conducive to larger fish moving between A2 and A3. Historically, we might have assumed that the high velocity above the top baffle approaches the Critical Burst Swimming Speed, 7.4-8.4 body lengths s^{-1} range for cyprinids (Clough and Turnpenny, 2001), and so it might not have been surprising if some fish could not complete passage for this reason. However, recent studies on the sprinting performance of Iberian barbel suggest that the sprinting performance of fusiform, rheophilic cyprinids could have been underestimated, and that 18 cm long Iberian barbel, under similar conditions of this study (where water velocity was equal to approximately 1.5 m s^{-1} at its most extreme) have a median sprint speed of 11 body lengths s^{-1} (1.88 m s^{-1}; Sanz-Ronda et al., 2015). Such a performance would comfortably enable traversal of the fastest water at the LCB-modified Hogsmill gauging weir. Alternatively, large roach and chub have deep bodies relative to their length, and so these fish will have difficulty remaining vertical when proceeding through fast, shallow water, thereby increasing the likelihood that the fish will give up its passage attempt. As a fish's body depth approaches or exceeds the water depth its swimming efficiency decreases (Videler, 1993), and chub exceeding 40 cm usually have a maximum body depth exceeding 10cm, the water depth on the portion of weir upstream of the baffles. Further research is required on the relationship between swimming performance and flow depth to better understand the relationship and inform fish passage designs at obstacles with a shallow depth.

In this study, however, the drop in the number of fish (observed in all species) detected between A2 and A3 was not significant, and there was no noticeable failure of larger fish at this point of passage. This drop in passage between A2 and A3 could be a result of missed detections on A3, but this seems unlikely based on detection efficiency estimates for A1 and A2. Therefore, although there is a known effect of the transition from deep to shallow water, relative to body depth, on the ability for fish to complete passage of a weir, our data does not suggest this to be the primary cause in this particular scenario.

Our second hypothesis of the reduced passage of larger fish is that the necessity for large fish to position themselves diagonally on the weir apron to use the passage route hindered their ability to move from A1 to A2. This is a more plausible hypothesis because many of the large fish that attempted passage failed to reach A2 altogether. Smaller fish, and indeed benthic fish such as barbel, could potentially make use of reduced velocities in the boundary region at the gauging weir face (Watson et al., 2018), and by virtue of their small size, their ability to utilise (and rest) in the spaces between the baffles (as seen in small trout by Forty et al., [2016]), where there is negligible water velocity. On the other hand, large fish would need to maintain an oblique direction of movement through successive notches against a flow of water acting against the fish's flank. A previous LCB study with brown trout found no passage improvement with size, but tested only a modest number of trout over a limited size range (148-269 mm, Dodd et al., 2018). While Forty et al. (2016) did find a clear positive body size effect, with all large trout passing the LCB-modified weir, all of these did so during spates when water was streaming over the baffles.

Irrespective of either hypothesis, the potential consequences of larger fish not succeeding in passage may include low population reproductive fitness, particularly for barbel, chub and roach (the larger and, in the case of roach, deeper-bodied species). Female fecundity in fish species usually increases with size so failure of large individuals to pass could impact egg deposition levels. Although the data might suggest that barbel would not be as impacted by this effect as chub and dace, due to the ability of barbel to use the boundary layer more effectively, the length of barbel at age of first maturity is approximately 30 cm (Britton and Pegg, 201l; Vilizzi et al., 2013). This is somewhat larger than the barbel of this study, and so the effect cannot be ruled out entirely. As this size effect was not seen at shallower gradient weirs (Coe & Rana, 2014), further research is needed on the utility of LCBs at sloping weirs to facilitate upstream passage of various sizes of mature members of potentially impacted populations to identify if this persists as an effect of the steep slope of the weir, or in the study of Coe & Rana (2014) was a result of the lack of larger fish individuals in their studies of LCBs at lower-gradient weirs.

Passage success was not determined by any environmental variable, although sample sizes for wild fish especially were low, and limited statistical power. Fish were able to pass on a large range of flows, an important factor in evaluating a weir's impact on connectivity (Larinier, 2001; Armstrong et al., 2010). The flows associated with occurrence of passage tended to be lower rather than higher, but these reflected the prevailing flow conditions during passage attempts. Despite a water treatment works upstream of the weir that released water twice daily, there were no specific times of day that fish were observed to pass the weir in response to the altered flows.

The elevated overall time from first attempt taken to pass the gauging weir by stocked fish is likely a result of the initial habitat exploration post-release, with fish visiting and leaving the gauging weir, before returning at a later date to complete passage. However, many wild chub and dace also exhibited an extended time to pass from first detection, suggesting that despite the LCB structure, substantial barrier effects of the modified gauging weir remain. This is further supported by the low passage success rate per attempt exhibited by all species, which is exemplified by barbel, showing that only 28 attempts (until first successful ascent per fish) out of a total 677 were successful. This could have some ramifications, by increasing potential risks like predation and disease spread (Thorstad et al., 2008). However, for passage duration of successful attempts, both stocked and wild chub had similar passage times, suggesting little performance difference between both groups. Stocked barbel passage, from first attempt, was significantly slower than all other fish groups, but this is most likely due to their body shape, small size and benthic behaviour that enabled them to reside between the baffles, resulting in them remaining on the gauging weir for a longer period of time than the other species. This behaviour of using the baffles as refuge is further demonstrated by the residency time of stocked barbel at A1 (2180 sec) in comparison to the other species.

We conclude that the use of LCBs has substantial potential as a cost-effective retrofit method to improve upstream passage for fluvial cyprinids within lowland rivers that are fragmented by sloping weirs. However, to ensure fish can complete ascent of gauging weirs, which are difficult to remove for societal reasons and that must have unobstructed crests, design improvements for LCBs and their placement on the weir apron are required. Not only are design improvements necessary, but further research is required on the effectiveness of LCBs at enabling upstream passage of a range of fish species and sizes at a range of retrofitted sloping weirs with different gradients. This would provide a clearer picture of the effectiveness and utility of this cheap and novel design. This is particularly important due to the caution required in interpreting this study's results for dace and roach as a result of the low sample sizes attempting passage. Importantly in this study, a substantial proportion of stocked fish were able to ascend the weir and disperse upstream, a finding with important management implications for stock restoration.

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Supplementary Material

Table S1. Mean and standard deviations of successful and unsuccessful fish in each species grouped by source, with the associated Wilcoxon Rank Sum Test result comparing successful and unsuccessful fish.

Species	Source	Length of Successful Fish (mm)		Length of Unsuccessful Fish (mm)		Wilcoxon Rank Sum Test
		Mean	SD	Mean	SD	
Barbel	Stocked	189	9	192	7	$W = 424$, $p > 0.05$
Chub	Stocked	179	10	176	9	$W = 552.5$, $p > 0.05$
Chub	Wild	261	55	382	102	$W = 79$, $p = 0.02$
Dace	Wild	168	13	186	26	$W = 18$, $p > 0.05$
Roach	Wild	210	6	204	35	$W = 6$, $p > 0.05$

Table S2. The results of the Likelihood Ratio Tests for each variable in the wild and stocked Overall Passage Success model.

Variable	Wild Model	Stocked Model
Length	LRT: $\chi^2_1 = 6.09$, $p = 0.01$ *	LRT: $\chi^2_1 = 0.01$, $p = 0.99$
Species	LRT: $\chi^2_2 = 4.22$, $p = 0.12$	LRT: $\chi^2_1 = 13.4$, $p < 0.001$ *
Temperature	LRT: $\chi^2_1 = 0.01$, $p = 0.92$	LRT: $\chi^2_1 = 0.51$, $p = 0.47$
River Stage	LRT: $\chi^2_1 = 0.22$, $p = 0.63$	LRT: $\chi^2_1 = 0.03$, $p = 0.63$
Julian Date	LRT: $\chi^2_1 = 0.03$, $p = 0.84$	LRT: $\chi^2_1 = 0.24$, $p = 0.63$
Day or Night	LRT: $\chi^2_1 =0.22$, $p = 0.64$	LRT: $\chi^2_1 = 0.74$, $p = 0.38$