Can’t pass or won’t pass: the importance of motivation when quantifying improved connectivity for riverine brown trout *Salmo trutta*

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ABSTRACT

Reversing the negative impacts anthropogenic habitat fragmentation have on animal movement is a key goal in management of landscapes and conservation of species globally. Accurate assessment of measures to remediate habitat fragmentation, such as fish passage solutions in rivers, are imperative but are particularly challenging for territorial species which are less likely to leave their existing home range or populations composed of both migratory and resident individuals (i.e., partial migration). This investigation quantified the movements of translocated (captured upstream of the impediment and released downstream) and non-translocated (captured and released downstream of the impediment) riverine brown trout (*Salmo trutta* L.), a species known to perform a homing movement, through a fish pass using Passive Integrated Transponder (PIT) telemetry. A significantly higher proportion of translocated fish approached, entered and passed (on a wider range of flows) compared to non-translocated fish, consistent with the theory that motivation is a key driver in fish pass use. Translocated fish that entered the pass were significantly larger than those that approached but did not enter, presumably due to physiological capability. Translocated fish were a more reliable indicator of the fish passage solution effectiveness than non-translocated fish. Our findings hence imply that many fish passage solutions globally, and potentially measures to remediate habitat fragmentation for other taxa, may have been mistakenly assessed for unmotivated animals. Studying both non-translocated and translocated fish is recommended to provide more accurate and cost-effective fish passage solution assessments.

Key words: Habitat fragmentation; Longitudinal Connectivity; Migration; Translocation Experiment; Telemetry; Fish passage;

1 INTRODUCTION

Reduction in global biodiversity is a concern that must be urgently addressed (Sage 2020) and anthropogenic habitat fragmentation and reduced landscape connectivity are major reasons for the decline of many taxonomic groups (Andrén 1994; Tilman et al. 1994; Young et al. 1996; Hobbs and Yates 2003; Barr et al. 2015; Crooks et al. 2017). Conservation management often involves reconnecting fragmented or disconnected habitats to facilitate movement (Keeley et al. 2019), such as highway under and overpasses (Caldwell and Clip 2020), High Conservation Value Areas (HCVAs) for forest connectivity (Scriven et al. 2019) and with engineered fish passage solutions in rivers (Bunt et al. 2012). How animals use measures to remediate anthropogenic habitat fragmentation remains poorly understood, especially for species that are less likely to leave their existing home range (Van Leeuwen *et al.,* 2018). For example, territorial animals may hold an area for greater feeding opportunity and reduced predation risk, or a population may be composed of both migratory and resident individuals, i.e., partial migration (Brodersen et al., 2008; Skov et al., 2010; Chapman et al., 2012 a, b). In these instances, an inaccurate portrayal of effectiveness may be gathered if unmotivated animals are studied as these may approach a barrier but have no intrinsic motivation to pass.

More widely, movement of animals within their environment is rarely a random process, involving complex behavioural mechanisms, physiological constraints, interactions with spatially heterogeneous and temporally variable landscapes and individual choice (Kramer et al. 1997; Schick et al. 2008), with the latter influenced by food availability, presence of predators, stage of development and size (Rasmussen and Belk 2017). Such processes affect individual fitness by changing growth and survival, but also influence their distribution and abundance, with genetic and evolutionary consequences. Consequently, knowing and understanding 'why' an animal moved, i.e., the animal's internal state, is one of the ultimate objectives for movement ecologists. However, simply knowing 'when' an animal moved does not directly correspond to understanding 'why' animals moved because the extrinsic and intrinsic factors that caused it to move, change its movement direction or stop moving cannot easily be disentangled. This is reflected in the volume of research dedicated to investigating the spatiotemporal and individual-level determinants of wild animal movements (Börger et al. 2006, 2008; Nathan et al. 2008; Baguette et al. 2013).

One option to further our understanding of extrinsic influences on animal movement is to control intrinsic factors, i.e. 'why' they move, by artificially motivating them to do so. Homing pigeon (*Columba livia*; selectively bred from the domestic pigeon) is perhaps the most well-known animal to perform a homing movement after long distance translocation, enabling the sensory and spatial (map)-representational mechanisms that guide avian navigation to be investigated (Bingman 2018). Experimental translocation of territorial wild birds and mammals have been used to study the impact of anthropogenic fragmentation and functional connectivity of terrestrial landscapes during homing (Bakker and Van Vuren 2004; Desrochers et al. 2011; Valente et al. 2019). Freshwater and marine fishes also perform homing movements after translocation (Stott et al. 1963; Huntingford et al. 1998; Lucas and Baras 2001; Girard et al. 2007; Shima et al. 2012; Gardner et al. 2015), including during fish pass studies for both up and downstream migrations (Forty et al. 2016; Tummers et al., 2016; Dodd et al., 2017*;* Ovidio et al. 2017; 2020; Bravo-Córdoba et al. 2018; Celestino et al*.*, 2019; Sanz-Ronda et al.,2021, Bravo-Córdoba et al*.*, 2023). However, we are not aware of any experiments, terrestrial, avian or aquatic, that incorporate both translocated and non-translocated animals (released freely at the same location) to specifically and explicitly quantify the importance of homing motivation during studies on landscape fragmentation or reconnection.

Freshwater ecosystems are one of the most diverse ecosystems on earth and sustain more species of fish than the sea (Bosshard 2015). Riverine (i.e., non-diadromous) species hold a key role in maintaining healthy riverine ecosystem functioning and have high economic value (Unfer and Pinter 2018; Lima et al. 2020). However, almost one third of freshwater biodiversity globally is facing extinction (IUCN 2019) with anthropogenic reductions to longitudinal connectivity in rivers routinely cited as one of the primary causes for the decline (Nicola et al. 1996; Humphries and Winemiller 2009; Liermann et al. 2012; Dias et al. 2017; Pavlova et al. 2017). Even small barriers can have drastic alterations on the behaviour of populations by potentially causing phenotypical life strategy changes, such as fish becoming more resident (Branco et al, 2017). Engineered fish passage solutions are constructed to return these delicate riverine ecosystems back to a healthy state (Clay 1995; Lucas and Baras 2001; Bunt et al. 2012), often in response to local legislation (e.g., European Union Water Framework Directive (WFD) (EC; 2000/60/EEC)) and at huge expense (Weyand et al. 2006). Studies quantifying fish pass performance are scarce in comparison to the number of fish passes constructed (Cooke and Hinch 2013). The majority of fish passage investigation are usually performed on migratory diadromous or potamodromous species, often close to or during a key life stage migratory period (e.g., spawning) to account for migration motivation (Gowans et al. 2003; Dodd et al. 2018). Assessing the performance of fish passage solutions is inherently difficult for riverine species, when all key life stage habitats are met within a home range downstream of an impediment. Indeed, such fish may not be motivated to pass the impediment because passage is not an obligatory requirement to complete their lifecycle. Crucially, the dominant longitudinal dimension of streams coupled with efficiently sampled fishes provide an excellent system for studying the proximate mechanisms that influence animal movement (Rodriguez 2002).

Previous fish passage investigations that have translocated riverine fish to initiate homing movements have not explicitly quantified the influence of motivation on fish pass performance, although its importance is often acknowledged (Weibel and Peter, 2013). Conversely, studies on translocated riverine fish do not incorporate non-translocated fish and fail to acknowledge the possibility for differences in motivation between the two groups when interpreting the results (e.g., Wright et al. 2016). Likewise, studies that incorporated both translocated and non-translocated fish have typically combined data from both groups during analysis (Lucas et al. 1999; Goerig et al. 2016; Dodd et al. 2017, 2018; Ovidio et al. 2017). While others have only considered the influence of motivation on selected passage metrics. For example, Bravo-

Córdoba et al. (2018) merely reported fish origin influenced fishway attraction and passage efficiency. Goerig and Castro-Santos (2017) reported no difference in attempt rate (index of motivation) between translocated and non-translocated fish released in a cage secured to the downstream extremity of the impediment, and thus non-translocated fish were not at liberty in their existing home range. Meanwhile, Forty et al. (2016) calculated the Proportion of Displaced fish Attempting Passage (PDAP) (equivalent to available fish in this study) but did not have an equivalent metric for non-displaced fish. Consequently, it remains unknown if translocated riverine fish, which are assumed to be more motivated to pass the impediment during a homing movement, enable a far more accurate and robust assessment of fish pass performance to be performed than if only non-translocated fish were studied.

Riverine brown trout (*Salmo trutta fairo* L.) are a territorial species (Jenkins 1969; Johnsson and Forser 2002), with good swimming capability (Ojanguren and Braña 2003; Castro-Santos et al. 2013) and spawn in autumn across Europe (Jonsson and Jonsson, 2011). There is high migratory dimorphism within the species (Jonsson and Jonsson, 1993; Ferguson et al., 2019), including partial migration, likely affected by a number of factors including opportunity, season, body size, predation risk and competition (Brodersen et al., 2008; Skov et al., 2010; Chapman et al., 2012 a, b). Brown trout are also known to perform a homing movement when translocated (Halvorsen and Stabell 1990; Armstrong and Herbert 1997; Forty *et al.*, 2016), and thus represent an ideal species to explicitly quantify intrinsic and extrinsic influences on fish pass performance. During this field investigation, the movements of translocated and non-translocated riverine brown trout through a fish pass were compared to understand the importance of motivation when studying the improved connectivity of fragmented habitats. A range of fish pass efficiency metrics, number of approaches, passage times, fish sizes (i.e. capacity of the individual) and passage flows (i.e. external factors affecting movement) were compared to quantify whether the fish *can't pass* through the remediation measure for behavioural or physiological reasons or *won't pass* due to a lack of motivation. It is hypothesised that translocated fish will provide a more accurate and robust assessment of the fish passage solution as non-translocated fish have all access to all key life stage habitats downstream of the impediment, and thus are not motivated to migrate.

2 MATERIAL AND METHODS

All fish were treated in compliance with the UK Animals (Scientific Procedures) Act 1986 Home Office licence number PPL 60/4400.

2.1 Study site

Mallorie Weir (54.133412, -001.537873) located in North Yorkshire, England, was an active crump weir gauging station on the lower reaches of the River Laver, 400 m upstream of the confluence with the River Skell (54.131309, -001.535786) (Fig. 1). The weir had been collecting data on river level for over 40 years. The impediment was 10.0-m wide and had a head difference of 2.3-m. The impediment had three sections, consisting of two pre-barrage stilling pools and a flat concrete apron. Pre-barrages, similar to that of a pool and impediment fish pass design, are an inexpensive common solution (Larinier et al. 2002) to allow fish to clear fairly low obstacles (Larinier 2008). The downstream stilling pool was 3.5-m long and 0.7-m deep, with a 1.0-m wide and 0.3-m deep notch in the centre of the downstream wall (Fig. 2). The upstream stilling pool was 2.5-m long and 0.6-m deep with a 0.6-m wide and 0.5-m deep notch just left of centre of the downstream wall. The apron of the impediment was 3.4-m long, with a 1:5 slope. In September 2015, a Low Cost Baffle (LCB) fish pass consisting of six recycled plastic baffles (0.2-m high and 0.1-m thick) was attached to the impediment apron perpendicular to the flow. Each baffle had a 0.3-m gap that was offset across the impediment apron, located on the left hand bank at the upstream end of the impediment to 2.5-m from the left hand bank at the downstream end.

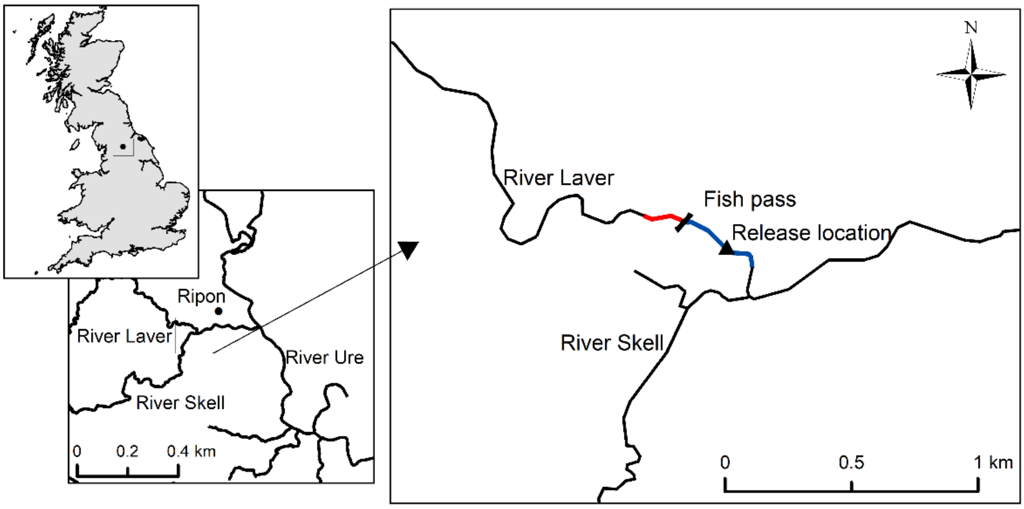

Figure 1. A map of Great Britain (top left), the location of the River Laver in the River Ure catchment (middle) and the location of Mallorie Weir fish pass (right), including the tagged fish release location and areas of fish capture downstream (blue) and upstream (red) highlighted.

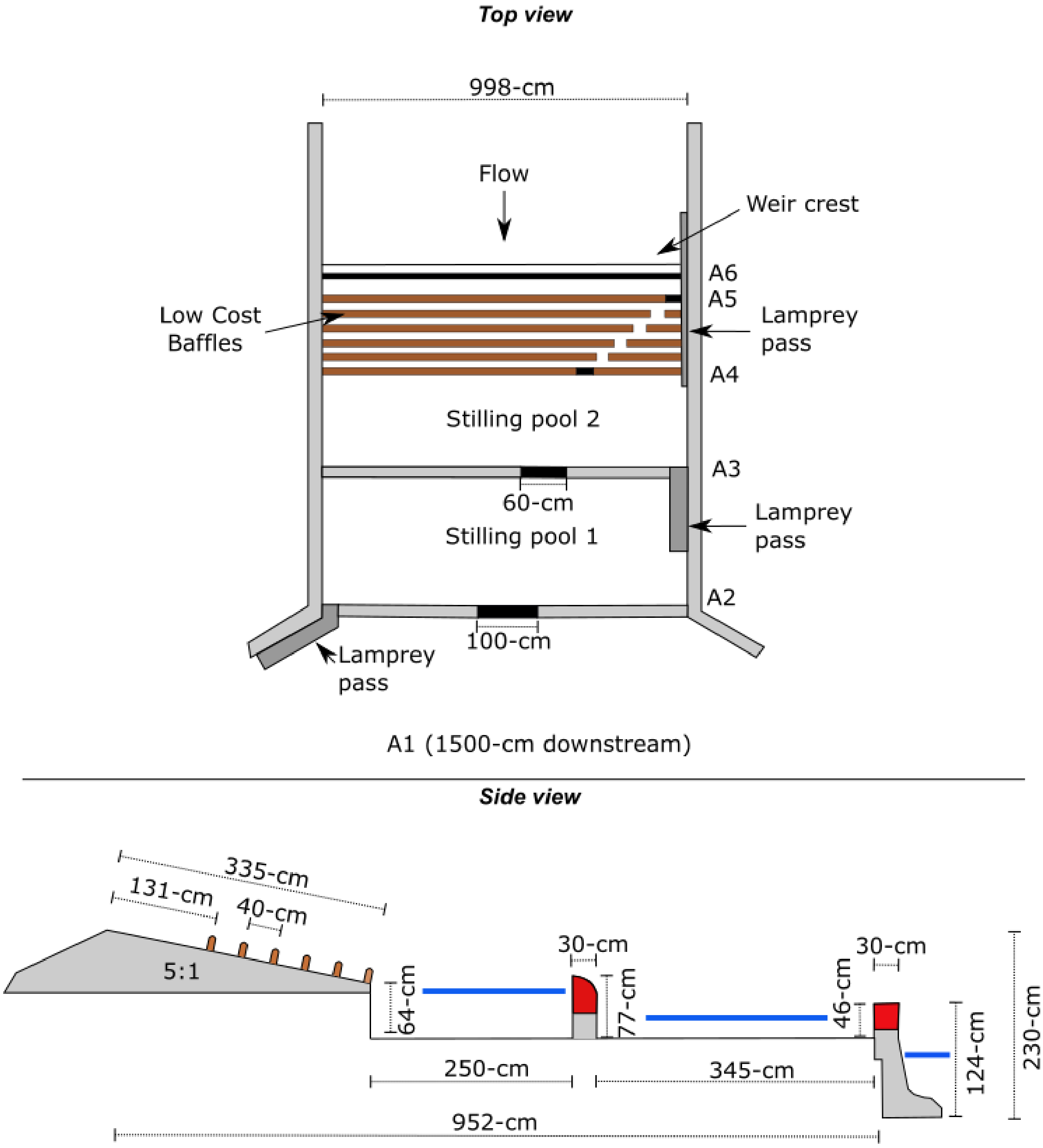

Figure 2. The top and side view of Mallorie Weir, including the location of the Low Cost Baffles (LCB; brown), Passive Integrated Transponder antennas (black filled boxes), stilling pools (including notch depths – red filled boxes), lamprey passes, and river level at Q_{90} (annual flow; blue line).

2.2 Sampling and tagging procedure

Wild riverine brown trout (not sea trout, based on size and colouration; Jonsson and Jonsson, 2011) were captured from reaches directly upstream (*n* = 123; 127 – 326 mm; 0 – 150 m) and downstream (*n* = 77; 133 – 359 mm; 0 – 250 m) of Mallorie Weir on 17 October 2016. Fish were caught whilst wading with a single anode using pulsed DC (200 V, 50 Hz, ~ 1.5 A) electrofishing equipment, powered by a 2 kVA generator. Fish caught from each location were initially monitored for any signs of abnormal behaviour (maintain balance, unresponsive to touch) and/or injury before transported in a river water filled container to an aerated holding tank set up at the impediment. Fish were monitored for a period of one hour to ensure normal behaviour before undergoing surgery. Prior to tagging in the field, fish were anaesthetised using buffered tricaine methanesulphonate (MS-222; 0.8g per 10L). Once anaesthetised the fork length was measured (mm) and recorded. During surgery fish were placed ventral side up in a clean V-shaped foam support. All brown trout >127-mm were tagged with 23-mm (half-duplex, 23.0 mm long x 3.4 mm diameter, 0.6 g weight in air: Oregon RFID, Portland, Oregon) PIT tags. Larsen *et al*. (2013) reported a 100% survival and tag retention rate for >90-mm Atlantic salmon (*Salmo salar* L.) tagged with 23-mm PIT tags. Tags were tested with a hand held detector, disinfected with betadine and rinsed with saline solution before being inserted into the body cavity through a 5-mm long ventro-lateral incision made with a scalpel, anterior to the muscle bed of the pelvic fins. After the surgery, fish were continuously monitored in a well-aerated tank of fresh river water until they were fully recovered. All fish were released in the middle of the sampling reach downstream of the impediment; 150-m downstream of Mallorie Weir (54.132701, -001.535707) and ~200-m upstream of the confluence with the River Skell.

2.3 Monitoring

Monitoring occurred between 17 October and 21 November 2016, which coincided with the brown trout spawning period, using six half-duplex PIT telemetry antennas connected to an Oregon RFID multiple or single antenna reader. Each reader was powered by four 120-Ah, deep-cycle, AGM batteries connected in parallel. The tag horizontal/vertical detection range (30-40cm away from the vertical plane) was tested during initial set-up and each site visit (every 6 days) to ensure the read range of the interrogated water column had not decreased. Antenna 1 (A1) (flat-bed) spanned the width of the river 15-m downstream of the impediment, was constructed from multiple turns of 6-mm copper cable, connected to a single Oregon RFID reader, and the read range from this antenna was ~0.40 m in the vertical plane. Antennas 2 and 3 (A2 & A3) (swim-through) were located on the upstream side of each stilling pool notch, were constructed from multiple turns of 4-mm copper cable, were connected to a multiple antenna logger, and had a read range ~0.30 m each side of the vertical plane. Antennas 4 and 5 (A4 & A5) (flat-bed) were positioned in the gaps in the most downstream and upstream baffles, constructed from multiple turns of single core 2-mm copper cable, connected to an Oregon RFID multiple antenna reader, and had a read range of ~0.30 m in the vertical plane. Antenna 6 (A6) (flat-bed) spanned the width of the river at the crest of the impediment, was constructed from multiple turns of 6-mm copper cable, connected to an Oregon RFID multiple antenna reader and had a read range of ~0.40 m in the vertical plane.

All antennae were fully operational throughout the study. Antennae A1, A2 and A3 had a 99% (95-100% CI, n = 115/116), 97% (88 – 99%CI, n = 56/58) and 93% (83 – 97%CI, n = 51/55) detection efficiency, respectively, based on known location (tagging location or previous and subsequent antenna record) of tagged fish. Detection efficiency could not be calculated for A4 and A5 because fish could ascend over the baffles and A6 because it was the most upstream antenna and no attempt was made to recapture fish above the impediment.

2.4 Data analysis

To evaluate the difference between translocated and non-translocated fish the following fish pass efficiency metrics were used: Available fish was calculated as the number of fish detected on the most downstream antenna (A1) as a proportion of the total number of fish tagged. Entrance efficiency was calculated as the number of fish that entered the pass (A2-A6) as a proportion of the available fish (A1). Fish passage efficiency was calculated as the number of fish that ascended the impediment (last detected on A6) as a proportion of those that entered the pass (A3-A5). Overall passage efficiency was calculated as the number of fish that ascended the impediment (last detected on A6) as a proportion of the available fish (A1).

LCB entrance was the number of fish detected on the downstream baffle notch (A4) as a proportion of those detected or know to have passed A3 during ascent. LCB exit was defined as the number of fish detected on the upstream baffle notch as a proportion of those detected or known to have passed A3 during ascent. LCB passage was defined as the proportion of fish that exited the fish pass through the LCBs top notch after being detected entering the bottom notch during the ascent.

Time to approach was calculated as the difference in time between release and first detection on the most downstream antenna (A1). Overall passage time was calculated as the difference between first detection on A1 and first detection on the most upstream antenna (A6). Time to pass was calculated as the difference between the last detection on A1 to the first detection on A6. To understand the difference in motivation, new approaches to the weir were calculated for each group based on a lapse in time between two subsequent detections on A1 (Castro-Santos and Perry, 2012; Goerig and Castro-Santos, 2017). The threshold used to determine a new approach was calculated as 1100 seconds between detections (Appendix 1).

The length (mm) of brown trout caught upstream and downstream of the impediment were comparable (Mann-Whitney *U* test: $Z = 0.975$, $n = 200$, $P > 0.05$) and thus comparison of fish length between fish from different capture locations was deemed acceptable. Binary logistic regression was used to test the effect of body length on availability at the impediment (detection on A1), fish pass entrance (detection on A3) and passage (detection on A6) for each capture location. Models were tested for significance against the null model. When the null model was not significant or passage efficiency was 100%, i.e. complete separation in binary data, the regression was not performed.

Flow (m^3s^{-1}) at the study site were recorded every 15-min (by the Environment Agency); river flow are presented as exceedance values (Q_x) of the annual flows (2016; median = 0.42 m^3s^{-1}, min-max = 0.13-26.50 m^3s^{-1}), and were between $Q_{0.3}$ and $Q_{96.3}$ during the study period. The flow exceedance value indicates the percentage of time that a given flow value is equal to or exceeded.

Time-to-event analysis (Therneau, 2015) was fitted to determine the influence of release group (capture location, i.e., translocated or non-translocated), flow during approach, total approaches (number up to that approach), time from release to approach, time from last approach and fish size during each successful (i.e., passage) and unsuccessful (i.e., retreat) approach. A variance inflation factor (VIF) was performed to assess potential multicollinearity among the primary covariates. The predictor variables were all entered into the Cox model to test for their coefficient and their importance, with tag number used as a random effect. A Schoenfeld residuals test was then used to assess non-proportionality in the model. Hazard ratios (HRs), which represent the instantaneous rate at which an event (i.e., successful or unsuccessful approach) occurs, were obtained by exponentiating the coefficients estimated for each of the remaining covariates in the cox model.

Chi-squared, Mann-Whitney *U* and Independent-Sample Kolmogrov-Smirnov tests were conducted using SPSS 22 and binary logistic regression and time to event analysis was conducted using R version 4.2.0 (R Core Team 2022).

3 RESULTS

Significantly more translocated (76%, n = 94/123) than non-translocated fish (29%, n = 22/77) approached the impediment, i.e., available fish (χ^2 contingency test: χ^2 = 44.512, *d.f.* = 1, $P <$ 0.01) (Table 1). Likewise, a significantly higher proportion of translocated fish (59%, n = 55/94) than non-translocated fish (14%, n = 3/22) that approached the impediment entered the fish pass, i.e., entrance efficiency (χ^2 contingency test: χ^2 = 14.36, *d.f.* = 1, $P <$ 0.01). A high proportion of both translocated (95%, n = 52/55) and non-translocated (100%, n = 3/3) fish that entered the pass ascended the impediment, i.e., passage efficiency, although there were too few non-translocated fish to compare statistically. The number of translocated fish that ascended the impediment (n = 55) was sufficient to quantify route choice in the fish pass, with 13 (24%) and 33 (60%) detected on the most downstream (PIT antenna A4) and upstream (PIT antenna A5) gaps in the baffles, respectively, and 9 (16%) were detected on both during ascent. The number of fish that ascended the impediment as a proportion of the available fish, i.e. overall passage efficiency, was also significantly higher for translocated (55%, n = 52/94) than non-translocated fish (14%, n = 3/22) (χ^2 contingency test: χ^2 = 12.423, *d.f.* = 1, $P <$ 0.01).

Table 1: Summary of brown trout fish pass efficiency metrics (%, confidence interval (CI), sample size (*n*)), time (days, median (range)), fish fork length (mm, median (range)) and flow (Q, median (range)) for non-translocated and translocated fish (**bold** denotes significantly higher value and - denotes too few fish to compare statistically (Pearson's chi-squared test/Mann-Whitney *U* tests)).

Metric	**Non-translocated**	**Translocated**	**Sig.**
Available fish (%)	29 (20 – 40 CI, n = 22/77)	**76** (68 – 83 CI, n = 94/123)	**P < 0.01**
Entrance efficiency (%)	14 (5 – 34 CI, n = 3/22)	**59** (48 – 68 CI, n = 55/94)	**P < 0.01**
Fish pass efficiency (%)	100 (40 – 100 CI, n = 3/3)	95 (85 – 98 CI, n = 52/55)	-
Overall passage efficiency (%)	14 (5 – 34 CI, n = 3/22)	**55** (45 – 65 CI, n = 52/94)	**P < 0.01**
Approaches	**10.00** (1 – 40, n = 22)	6.72 (1 – 62, n = 93)	**P < 0.05**
Passage fish approaches	2.00 (1 – 3, n = 3)	4.09 (1 – 51, n = 51)	-
Non-passage fish approaches	11.26 (1 – 40, n = 19)	9.90 (1 – 62, n = 42)	P > 0.05
Time from release to first approach (days)	0.70 (0.08 – 4.49)	0.62 (0.04 – 30.37)	P > 0.05
Overall passage time (days)	4.12 (1.94 – 25.54)	0.17 (0.01 – 30.90)	-
Time to pass (days)	1.93 (1.66 – 19.14)	0.06 (0.01 – 22.31)	-
Fish captured (mm)	197 (133 – 359)	212 (127 – 326)	P > 0.05
Size of available fish (mm)	185 (142 – 290)	213 (135 – 326)	P > 0.05
Size of fish that entered (mm)	213 (192 – 254)	229 (147 – 303)	P > 0.05
Size of fish that passed (mm)	213 (192 – 254)	228 (147 – 303)	-
Approach flow (annual Q)	Q68.1 (Q65.3 – Q72.9)	Q67.6 (Q24.6– Q87.5)	P > 0.05
Entrance flow (annual Q)	Q66.8 (Q55.6 – Q72.0)	Q68.7 (Q26.3 – Q87.5)	-
Passage flow (annual Q)	Q66.8 (Q55.6 – Q72.9)	Q68.7 (Q26.9 – Q87.5)	-

Fish that passed the weir approached on significantly less occasions (*median* = 2; IQR = 1.0-5.0) than those that did not (*median* = 7; IQR = 3.0-11.0; Mann-Whitney *U* test: $Z = 4.933$, $n = 115$, $P < 0.001$). In addition, translocated fish approached the weir on significantly less occasions (*median* = 3; IQR = 1.0-8.0) than non-translocated individuals (*median* =7.5; IQR = 3.5-10.5 Mann-Whitney *U* test: $Z = -2.337$, $n = 115$, $P < 0.05$). Too few non-translocated fish passed to allow comparison between passage groups. However, there was no significant difference between number of approaches for translocated (*median* = 5.5; IQR = 3.0-11.0) and non-translocated (*median* = 8; IQR = 3.5-10.5) fish that did not ascend the weir (Mann-Whitney *U* test: $Z = -1.274$, $n = 61$, $P > 0.05$).

The median time between release and first approach to the impediment (i.e. first detection on A1) were similar for translocated (0.62 days, 0.04 – 30.37) and non-translocated fish (0.70 days, 0.08 – 4.49) (Mann-Whitney *U* test: $Z = -0.754$, $n = 115$, $P > 0.05$). Of the available fish, 59% ($n = 13/22$) and 100% ($n = 22/22$) of the non-translocated fish first approached the impediment within 24-h and a week of release, respectively, in contrast to 53% ($n = 50/94$) and 93% ($n = 87/94$) for translocated fish (Fig. 3). The median overall passage time and time to pass was shorter for translocated (0.17 and 0.06 days, respectively) than non-translocated (4.12 and 1.93 days, respectively) fish (Table 1), although there were too few non-translocated fish to compare statistically.

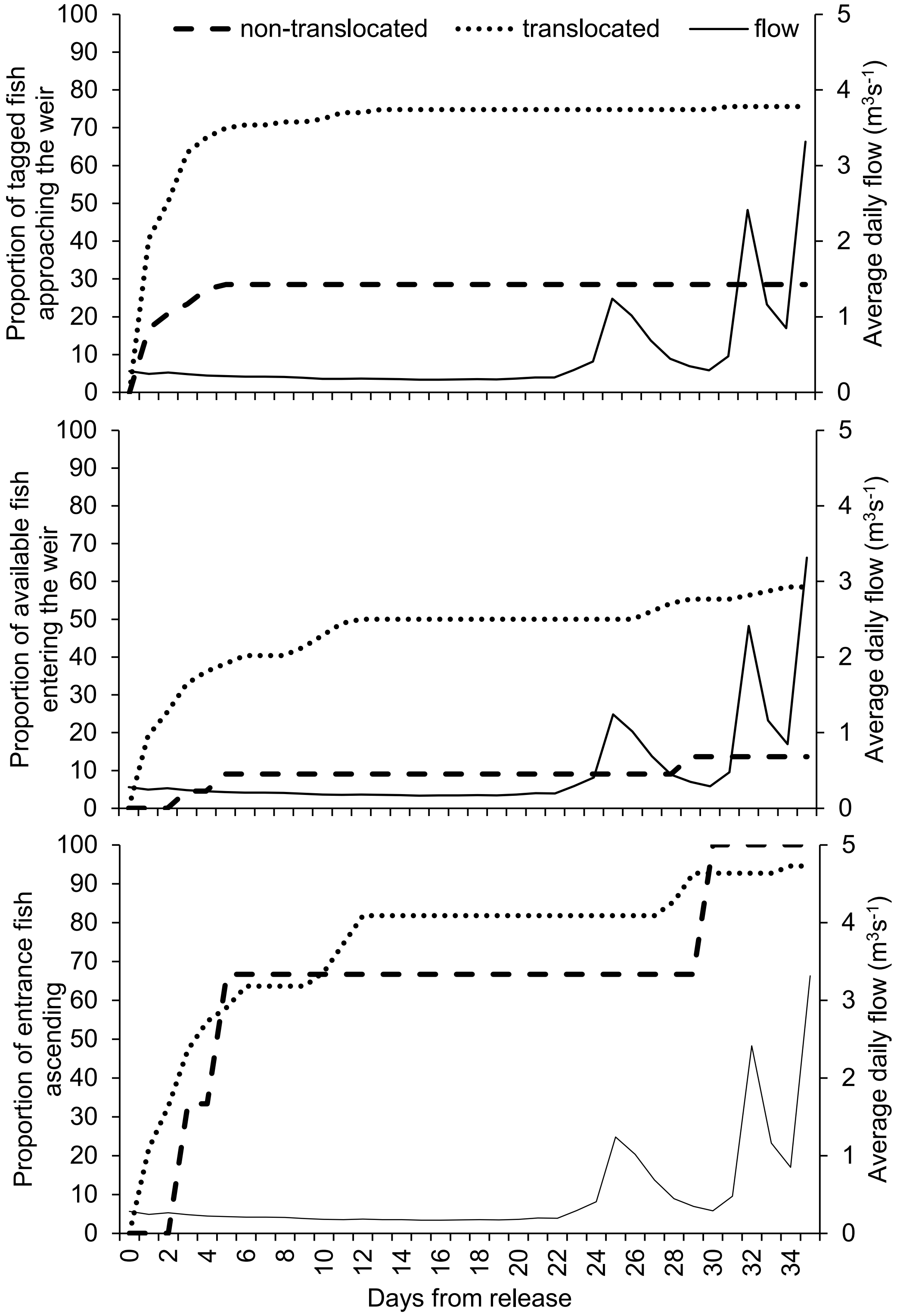

Figure 3. The proportions of tagged brown trout that approached the impediment (top), available fish that entered the fish pass (middle) and entrance fish that ascended the impediment (bottom) with time after release (days), for non-translocated (dashed line) and translocated (dotted line) fish, including mean daily flow (m^3s^{-1}; solid line).

Table 2: Summary of binary logistic regression models for fish length and successful approach, entrance or passage (**bold** donates significant binary logistic regression model). All null models were significant *P* <0.05. Note, too few non-translocated fish passed the impediment (*n* = 3) to perform a regression on passage and overall passage.

Binary Logistic Regression model	Coefficient	Std. Error	Z statistic	P =
Non-translocated approach	-0.008	0.006	-1.383	0.167
Translocated approach	0.005	0.005	0.899	0.369
Non-translocated entrance	0.007	0.012	0.544	0.586
Translocated entrance	**0.018**	**0.006**	**3.130**	**0.002**
Translocated passage	0.012	0.016	0.765	0.444
Translocated overall passage	**0.018**	**0.006**	**3.153**	**0.002**

The size of non-translocated fish that did (median = 185 mm, range = 142–290 mm) and did not (205 mm, 133–359 mm) approach the impediment were comparable (Mann Whitney U-test: *Z* = -0.627, *n* = 77, *P* > 0.05) and the binary logistic regression was insignificant (Coefficient = -0.008, Std. Error = 0.005, z statistic = -1.383, *P* > 0.05; Fig. 4; Table 2). Likewise, the size of translocated fish that approached (213 mm, 135–326 mm) and did not approach (197 mm, 127–294 mm) the impediment were also comparable (Mann Whitney U-test: *Z* = 1.079, *n* = 123, *P* > 0.05) and the binary logistic regression was insignificant (Coefficient = 0.004, Std. Error = 0.005, z statistic = 0.899, *P* > 0.05; Fig. 4; Table 2). The size of translocated and non-translocated (185 mm, 142–290 mm) fish that approached the impediment was also comparable (Mann Whitney U-test: *Z* = 1.908, *n* = 116, *P* > 0.05). Only three non-translocated fish that approached the impediment entered the fish pass (192, 213 and 254-mm), which prevented statistical comparison to non-translocated fish that approached but did not enter, and the binary logistic regression for entry was insignificant (Coefficient = 0.013, Std. Error = 0.014, z statistic = 0.941, *P* > 0.05; Fig. 4).

The translocated fish that entered the fish pass (229 mm, 147–303 mm) were significantly larger than translocated fish that approached but did not enter (193 mm, 135-326 mm) (Mann-Whitney *U* test: *Z* = 3.477, *n* = 94, *P* < 0.01) and the binary logistic regression was highly significant (Coefficient = 0.017, Std. Error = 0.005, z statistic = 3.130, $P < 0.001$; Fig. 4); 90% probability of entrance was 315 mm. All three non-translocated fish that entered the fish pass passed. Only three translocated fish that entered the pass did not pass (171, 259 and 274-mm), which prevented statistical comparison to those that passed, and the binary logistic regression was insignificant (Coefficient = -0.004, Std. Error = 0.015, z statistic = -0.265, $P > 0.05$; Fig. 4; Table 2). Translocated fish that passed the weir were significantly larger than those that approached (Mann-Whitney *U* test: $Z = 3.421$, $n = 91$, $P < 0.01$) and the binary logistic regression was highly significant (Coefficient = 0.018, Std. Error = 0.006, z statistic = 3.153, $P = 0.002$).

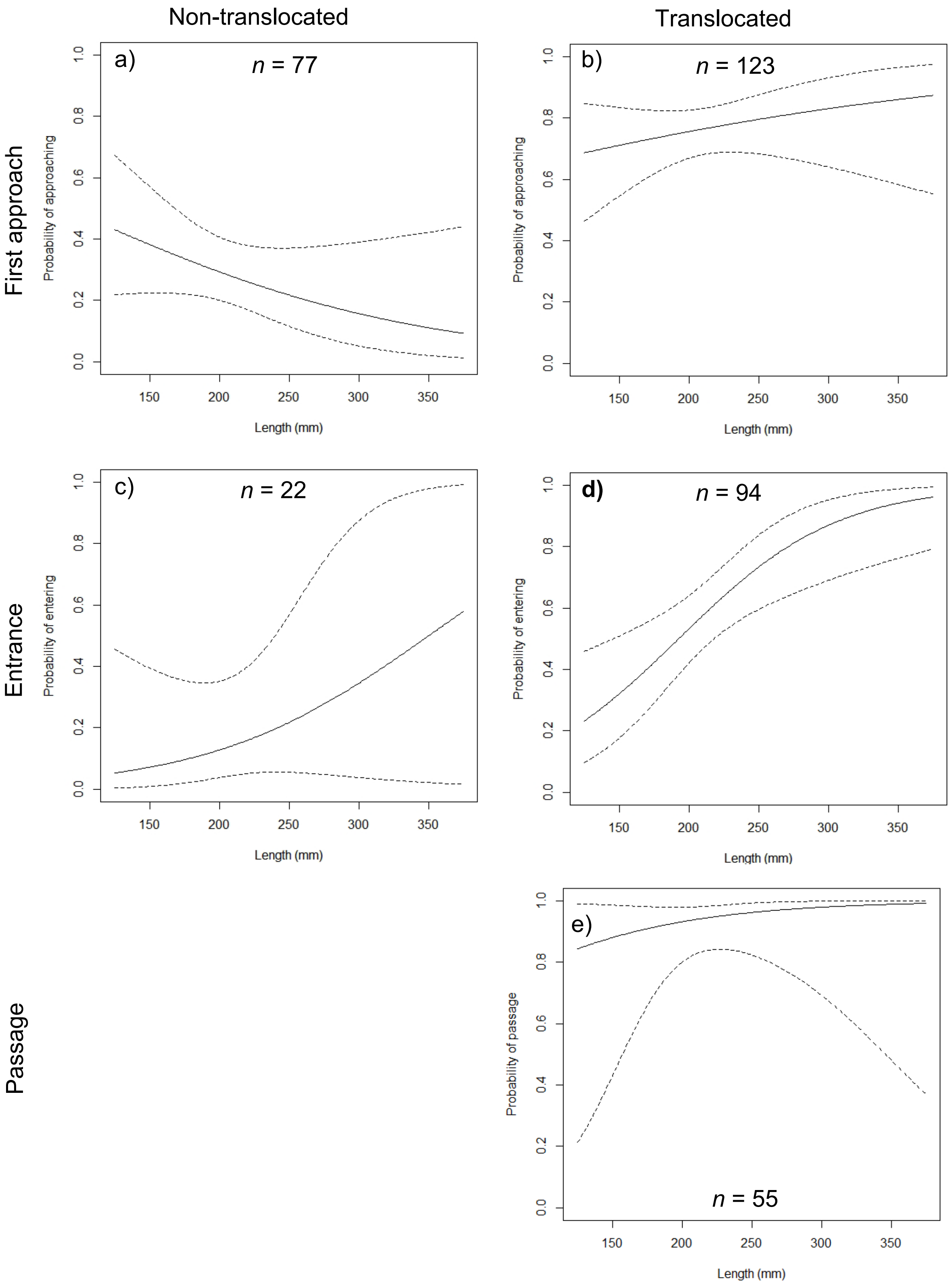

Figure 4. Binary logistic regression on the probability of first approach (a, b), entrance (c, **d**) and passage (e) for non-translocated (left) and translocated (right) fish in relation to fish size (mm) with 95% confidence intervals (dotted lines) (**bold** denotes significant binary logistic regression model). All null models were significant *P* <0.05. Note, too few non-translocated passed (*n* = 3) to perform a regression.

Translocated fish first approached ($Q_{65.3}$ – $Q_{72.9}$ compared to $Q_{24.6}$– $Q_{87.5}$), entered ($Q_{55.6}$ – $Q_{72.0}$ compared to $Q_{26.3}$ – $Q_{87.5}$) and passed ($Q_{55.6}$ – $Q_{72.9}$ compared to $Q_{26.9}$ – $Q_{87.5}$) the impediment on a wider range of flows than non-translocated fish (Table 1; Fig. 5). The median flow when non-translocated ($Q_{68.1}$) and translocated ($Q_{67.6}$) fish first approached was comparable (Mann Whitney U-test: $Z = -0.908$, $n = 116$, $P > 0.05$), and too few non-translocated fish entered and passed to compare statistically. The flow when translocated fish entered the pass ($Q_{26.3}$ – $Q_{87.5}$) was comparable to when translocated fish approached but did not enter ($Q_{65.3}$ – $Q_{87.5}$) (Mann-Whitney U test: $Z = 1.633$, $n = 93$, $P > 0.05$). The highest proportion of translocated fish approached (95%), entered (72%) and passed (67%) through the fish pass during 0.2-0.4 m^3s^{-1} flow band, which was also the most frequent flow band during the study period (39%) (Fig. 6). In addition, all (100%) non-translocated fish approached, entered and passed through the fish pass on the same flow band.

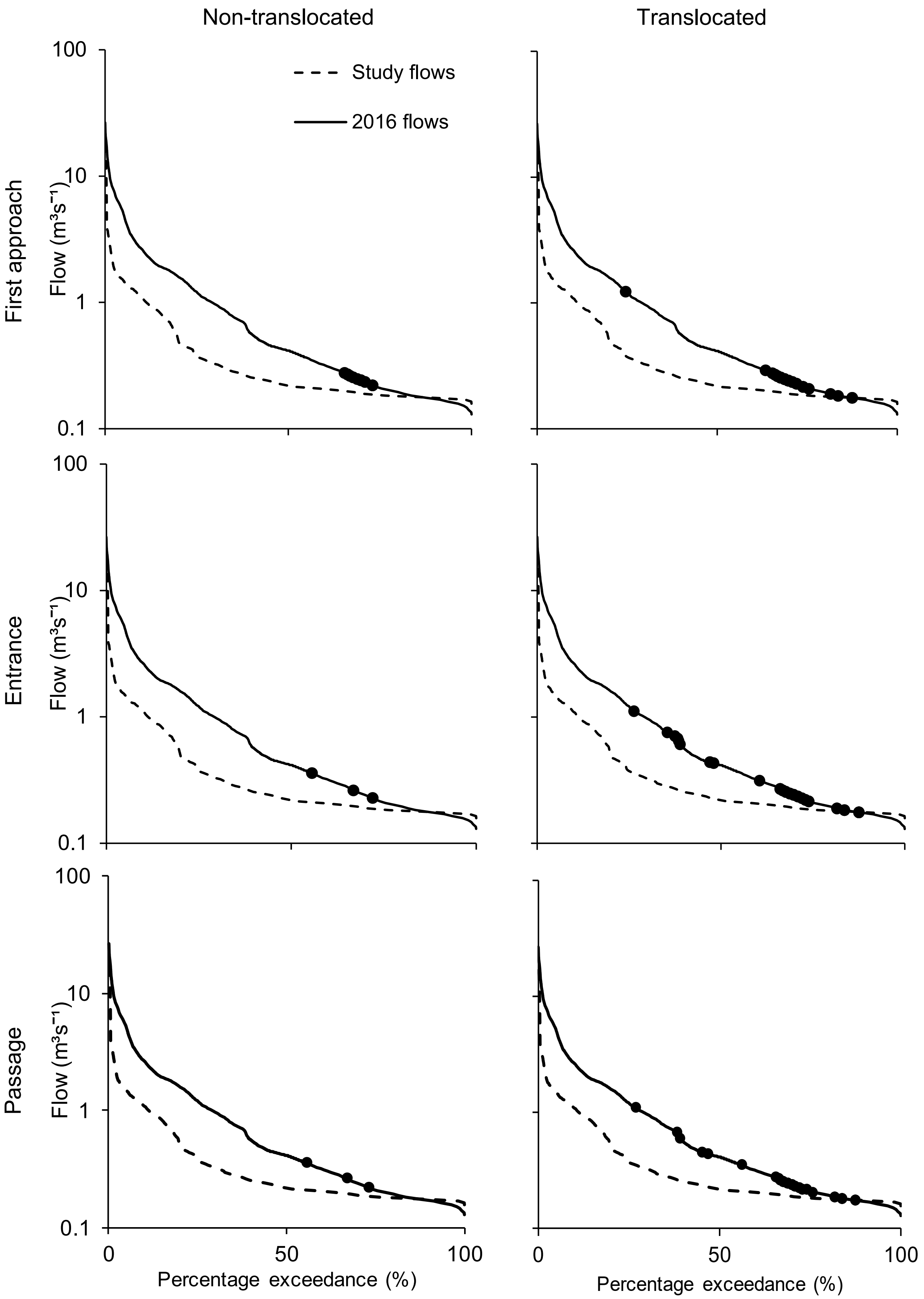

Figure 5. First approach (top), entrance (middle) and passage (bottom) flows (m3s-1; black dots) of non-translocated (left) and translocated fish (right); flow exceedance curve for 2016 (solid) and during the study (17th October – 21st November 2016; dashed).

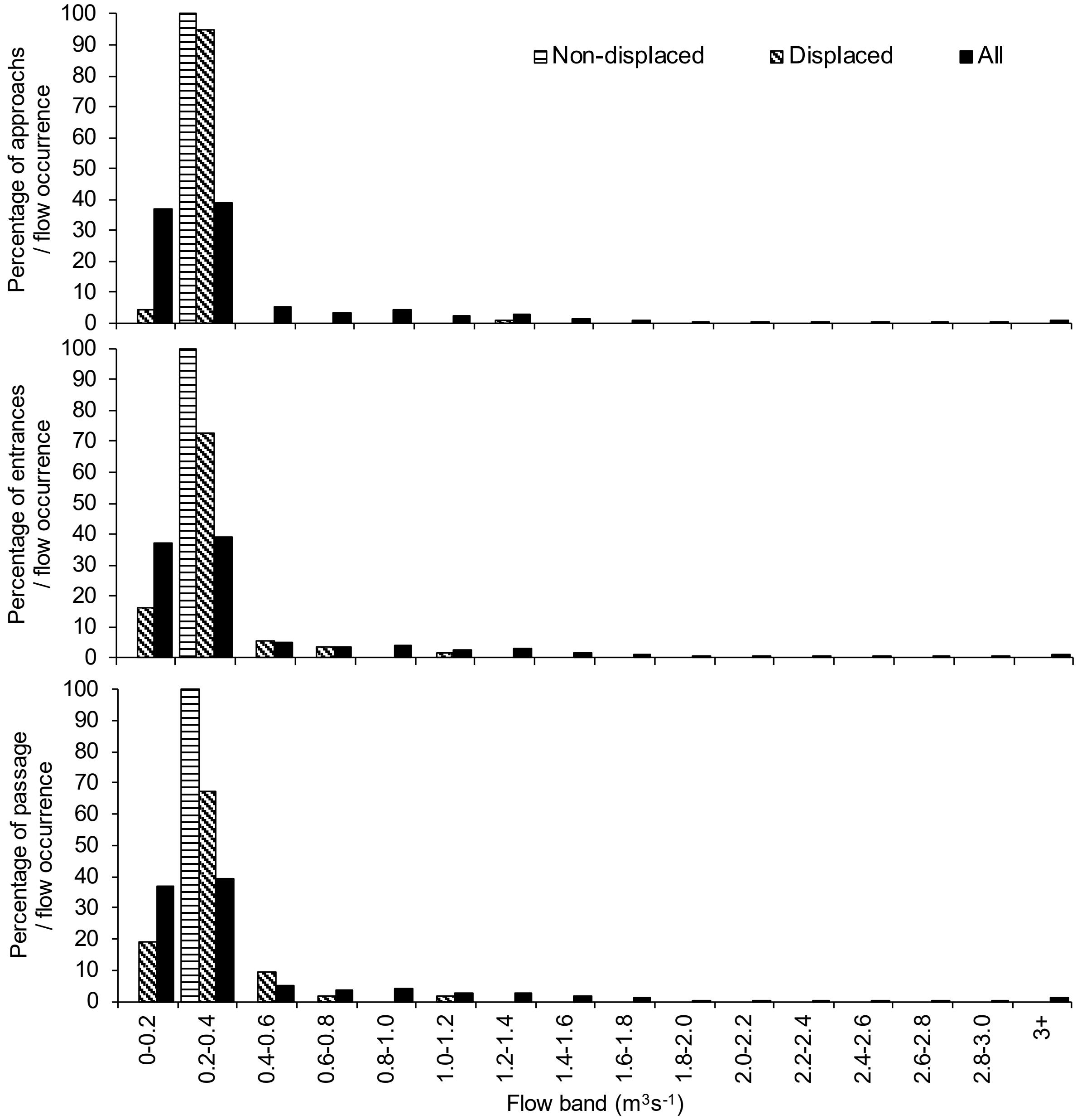

Figure 6. Percentage of first approach (top), entrance (middle) and passage (bottom) during flow bands (m^3s^{-1}) for non-translocated (horizontal) and translocated (diagonal) fish during flow occurrences (0.2 m^3s^{-1} band).

Table 3: Estimation of variables used in the cox regression analysis.

	coef	*HR*	*se(coef)*	*z*	*P*
Release group	4.109	60.894	1.407	2.92	**0.003**
Fish length	0.031	1.0320	0.010	3.10	**0.001**
Flow	-5.165	0.006	1.869	-2.72	**0.005**
Total approaches	-0.321	0.725	0.084	-3.81	**<0.001**
Time from last approach	-0.001	0.999	0.001	-3.04	**0.002**
Random effect	SD		Variance		
Tag number	3.34		11.19		
Number of approaches:	946				
Number of events:	54				

The VIF indicated that multicollinearity was not a significant concern (all values <1.3). The Schoenfeld residuals test indicated that “time from release to approach” was found to violate the proportional hazard assumption, so this variable was removed from the final model. All other variables had a significant influence on passage (Table 3). Research group (i.e., capture location) was found to have the greatest influence on the probability of passage (OR = 60.89), with translocated fish having a 60 times higher probability of passage than non-translocated fish. Fish size was the only other variable to have a positive influence, with a 1cm increase in length estimated to increase passage by 3%. Flow was indicated to have the largest negative influence on the probability of passage with an increase of 1 m^3s^{-1} predicted to reduce probability of passage by 99%. Subsequent approaches were also predicted to reduce the chance of passage by 27.5%.

4 DISCUSSION

Accurate assessments of mitigation measures aimed at improving connectivity are imperative to determine whether target species can successfully reach habitats to meet ecological, management, policy and conservation goals (Cooke and Hinch 2013; Ovidio et al. 2017). Sub-optimal fishways, i.e. those that only allow passage for a select range of species or sizes, are often recommended for alteration, which can come at a huge expense (Schmutz et al. 1998; Roscoe and Hinch 2010; Steffensen et al. 2013; Kim et al. 2016). This investigation helps to support that translocated riverine fish can provide a quicker, more accurate and robust assessment of fish passes designed to improve river connectivity than non-translocated fish (Forty et al. 2016). Indeed, by translocating fish it was possible to understand whether riverine fish *can't pass* through the remediation measure for behavioural or physiological reasons or *won't pass* due to a lack of motivation.

During this investigation, a significantly higher proportion of translocated than non-translocated fish approached the impediment (i.e., available fish), entered the fish pass (i.e., entrance efficiency) and passed the impediment (i.e., overall passage efficiency). Given extrinsic factors were comparable for both groups of fish during the investigation; it is argued that intrinsic factors caused the differences in fish pass performance. Consequently, it is hypothesized that translocated brown trout were more motivated to pass the impediment because they were performing a homing movement (Harcup et al. 1984; Armstrong and Herbert 1997). In contrast, the majority of non-translocated fish *won't pass* due to lack of motivation, instead they remained in their existing home range with non-passage approaches to the impediment likely attributed to exploratory movements after release (Höjesjö et al. 2015) rather than an attempt to pass. With all key life-stage habitats present downstream of the weir (e.g., refuge, feeding and spawning habitat), over time the fish population may have increased in residency, similar to those in other studies (Branco et al. 2017, Bravo-Córdoba et al. 2018). Conversely, the small fraction (14%) of non-translocated fish that passed the impediment likely represent partial migration within the downstream population (Brodersen et al., 2008; Skov et al., 2010; Chapman et al., 2012a, b).

Others have reported a low proportion (<30%) of non-translocated fish approached an impediment, probably because passage was also not obligatory to complete their lifecycle (e.g., Lucas et al. 1999; Calles and Greenberg 2007; Stuart et al. 2008; Bravo-Córdoba et al. 2018; Kucukali et al. 2019; Lothian et al. 2020). In such studies, it could be assumed that if fish approached the impediment they were motivated to pass, and thus all other results (e.g., entrance efficiency) were a consequence of fish pass design. The findings of this investigation imply this may be an erroneous assumption with unknown impacts on findings. Furthermore, others have used number of approaches or attempts as a proxy for motivation to pass, predicated on the assumption that fish with more failed attempts are more motivated to pass (e.g. Goerig and Castro-Santos, 2017). By contrast, we found translocated fish approached the weir significantly fewer times than non-translocated fish. This was seemingly caused by translocated fish ascending the weir during initial approaches while the non-translocated fish would appear to be approaching the weir during their regular movements within their home range, and thus were not attempting to pass the weir. Ultimately, fish passage solutions should be effective for both motivated and unmotivated fish to fit within the principles of the "ideal fishway dichotomy" set out by Castro-santos *et al.,* (2009), where the dammed reach of the river is made transparent to the movement of native species with no negative effects (e.g., delay, energetic costs, stress or injury). However, as demonstrated here, when a fish pass does not render an impediment completely transparent, non-translocated fish may not provide an accurate portrayal of fish pass performance.

Understanding how the capacity of individual fish (i.e., fish size) and external factors (i.e., prevailing flow) affect the movement through fish passes is fundamental to understanding pass performance (Bourne et al. 2011). Significantly larger translocated fish entered and passed the fish pass, in comparison to those that approached, and thus it is hypothesized that smaller translocated fish *can't pass* due to their physiological capability. Others have reported similar findings for anadromous salmonids (Noonan et al. 2012), and modifications to the fish pass entrance may be required to enable smaller fish to enter. It must be noted, only three non-translocated fish entered the fish pass; too few to enable the influence of fish size on fish pass performance to be statistically assessed. Further, translocated fish approached, entered and passed the impediment over a far wider range of flows than non-translocated fish allowing a more accurate portrayal of the flow conditions when the pass functions effectively. Such information is also important when comparing to national guidance. For example, Armstrong et al. (2010) states that a fish pass should be effective between flows that are exceeded 95% of the time (Q_{95}) and up to 5% of the time (Q_5).

In an ideal world, all fish used to investigate fishway performance would be naïve to the weir (Hagelin et al. 2021) both before and after fishway construction to ensure previously learnt behaviours do not influence the likelihood to approach or pass the impediment. At the very least, fish passage solutions should be studied when first opened to assess performance when first encountered. However, as with the vast majority of fish pass investigations on riverine fish, this was not possible here. Indeed, it was entirely plausible that both non-translocated and translocated fish had prior experience of the weir and / or the fish pass, either in an upstream and / or downstream direction, and may even encompass an individual's home range (Dodd et al., 2017). For example, the natal origin of translocated fish may have been in the reach downstream of the weir and moved upstream pre- or post-fish pass construction. Conversely, the natal origin of non-translocated fish may have been upstream of the weir and moved downstream by choice or displaced during elevated flow events (Ferguson et al., 2019; Yamada and Wada, 2021). These unknowns may account for differences in approach, entrance and passage efficiencies within and between non-translocated and translocated fish.

Management implications

There is an urgent need to assess the fishways performance (i.e., the proportion of fish, size classes and environmental conditions) for riverine fish species globally to 1) ensure compliance with local legislation (e.g. WFD (EC; 2000/60/EEC)), 2) identify reasons for passage failure and address them through physical alternations, and 3) inform the design of future fish passage solutions. Our study showed that fish pass performance assessed using non-translocated riverine fish provided a very different outcome when compared with performance using translocated fish. If non-translocated fish were studied in isolation, the low passage efficiencies would have been erroneously attributed to poor fish pass performance, which may have led to non-compliance with local legislation, expensive remediation works could have been performed and/or elements of the fish pass design (i.e., low cost baffle with pre-barrages) disregarded. It is hence recommended that both non-translocated and translocated fish should become an integral component of future fish passage investigations for riverine species. Doing so will enhance our understanding of intrinsic and extrinsic influences on fish movements and ultimately enable the most accurate and robust assessment of fish pass performance to be performed.

Fish pass efficiency investigations are technically challenging, typically involve tagging large numbers of fish to account for unmotivated individuals and losses (e.g., emigration, natural mortality and predation), are potentially performed over a long time period, and are generally expensive (though not relative to the pass itself). Incorporating translocated fish which are motivated to perform a homing movement will enable fewer fish to be tagged, with both practical and ethical benefits (i.e., the reduction principle of animal research; Metcalfe and Craig 2011), while reducing both study duration and cost. Standardised and accurate approaches to fish pass monitoring will enable reliable assessments of legislation compliance and direct comparisons between datasets, which will lead to improvements in fish pass designs (European committee for standardisation, 2021, Hershey 2021). The findings presented are also transferable to conservation management actions that require the dispersal of territorial terrestrial animals, such as habitat creation or reductions in fragmentation.

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Conflict of interest

The authors declare that they have no conflict of interest and the views in this paper are the views of the authors.

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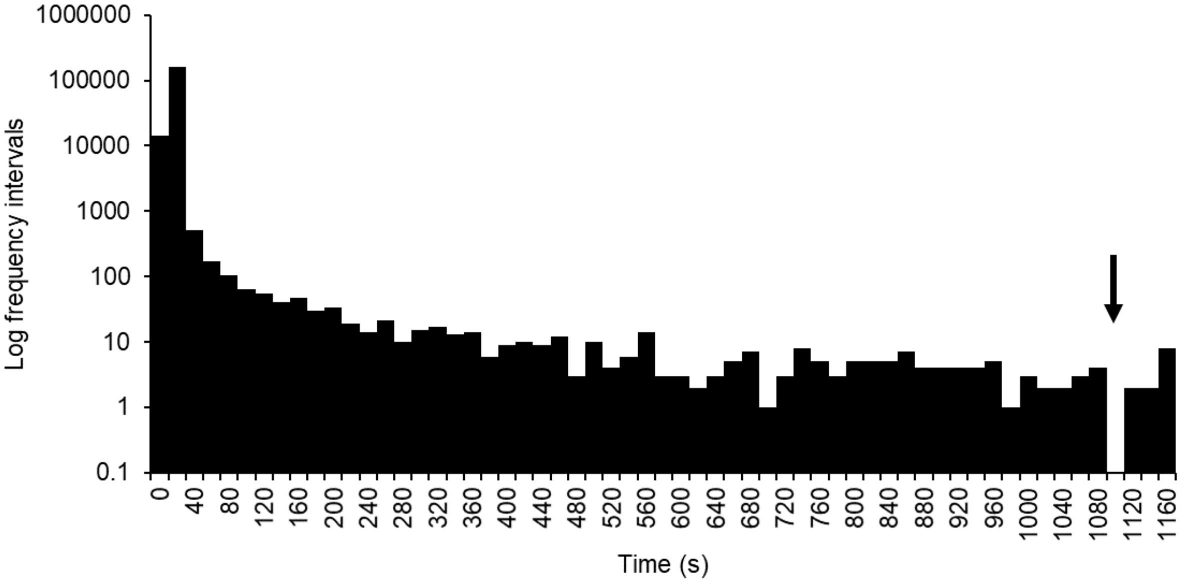

Appendix 1: Frequency (log transformed) of lapse in time between two subsequent detections on A1 to identify inflection point (black arrow), which denotes the approach duration.