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Selective effects of small barriers on river-resident fish

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Abstract

1. Habitat fragmentation is a principal threat to biodiversity and artificial river barriers are a leading cause of the global decline in freshwater biota. Although the impact of barriers on diadromous fish is well established, impacts on river-resident fish communities remain unclear, especially for low-head barriers.

2. We examined the movement of five contrasting freshwater fish (topmouth gudgeon, European minnow, stone loach, bullhead and brown trout) in an experimental cascade mesocosm with seven pools separated by small vertical barriers.

3. Passage rates differed significantly among species and increased with body size and sustained swimming speed (U_{sus}), ranging from an average of 0.2 passes/hr in topmouth gudgeon to 3.4 passes/hr in brown trout. A random-walk simulation indicated that barriers can result in net downstream movement and shifts in community composition.

4. Passage rates in brown trout were leptokurtic, that is, most individuals were relatively sedentary while a small proportion showed frequent movements. Upstream passage rates of brown trout increased with body length and boldness while fish with lower aerobic scope tended to move downstream. Passage rates showed significant individual repeatability in brown trout, independent of body size, indicating the potential for in-stream barriers to exert selective effects on fish populations.

5. Our results show that barrier effects can be more complex than simply blocking fish passage, and that river-resident fish can be impacted even by very small barriers. We show that fish passage depends on a wide range of morphological, physiological and behavioural drivers, and that barriers can exert selective effects on these traits and cause shifts in community composition.

6. *Policy implications*. Barrier mitigation measures need to embrace interspecific and intraspecific variation in fish passage to avoid inadvertent artificial selection on fish communities. Given the high abundance of low-head structures in river systems worldwide, a paradigm shift is needed to recognise the subtle impacts of small barriers on freshwater biodiversity. Removal of small barriers or nature-like fishways should allow better passage of the wider fish community compared to widely used salmonid-centric fish passage options.

1 | INTRODUCTION

Anthropogenically induced loss of connectivity is a major cause of global biodiversity declines in terrestrial and aquatic systems (Fahrig, 2003; Reid et al., 2019). Two-thirds of rivers worldwide are heavily fragmented by artificial barriers (Grill et al., 2019), an estimate that does not account for low-head structures such as weirs, culverts and bed-sills, which are orders of magnitude more abundant (Belletti et al., 2020; Jones et al., 2019). Barriers can impede fish migrations (McLaughlin et al., 2006), reduce population connectivity (Kelson et al., 2020) and cause habitat fragmentation (Junker et al., 2012), thereby threatening population persistence (Valenzuela-Aguayo et al., 2020). Mitigation options include the prioritisation of problematic barriers for removal (Kemp & O'Hanley, 2010) and the construction of fish passes to facilitate movement (Clay, 1995). However, the success of these remediation measures relies on detailed knowledge of how fish respond to barriers.

Historically, fish passage research has focused on large diadromous fish such as salmon (Silva et al., 2018). This is perhaps due to a common misconception that species which complete their life cycles in freshwater are sedentary (Gerking, 1959), and therefore largely unaffected by barriers. However, most river-resident species are migratory to some extent, regularly undertaking longitudinal movements along river networks to complete their life cycles (e.g. Dudley & Platania, 2007; Fredrich et al., 2003; Schumann et al., 2015). Hence, consideration of the needs of river-resident fish is critical for delivering effective fish passage solutions.

Identifying the factors that influence passage success is essential for effective barrier mitigation. River fish vary widely in physiology, morphology and behaviour, both at the interspecific and intraspecific levels. Passage success often increases with swimming ability (Castro-Santos, 2006), but the role of inter and intraspecific variation in determining fish passage remains unclear (Birnie-Gauvin et al., 2018; Kemp, 2016). For example, while fish may be able to overcome single barriers, passage over multiple barriers is not guaranteed because it is energetically costly (Kemp & O'Hanley, 2010; Thiem et al., 2016). Individuals with higher standard metabolic rate (SMR) and aerobic scope (AS) tend to show higher activity levels, can sustain higher swimming speeds and are often less risk averse (Metcalfe et al., 2016). Hence, one would predict fish showing higher swimming ability and higher metabolic rates to exhibit higher passage success.

Larger fish generally attain higher swimming speeds than smaller-bodied individuals (Plaut, 2001) and more streamlined fish tend to show higher swimming performance than deeper-bodied conspecifics (Baktoft et al., 2016). Pectoral fins are important in holding position and resisting flows (Arnold et al., 1991) and individuals with longer fins relative to their body size can show higher swimming speeds (Ojanguren & Braña, 2003). Fish with high slender caudal fins (high aspect ratio) tend to show higher swimming ability than those with a high surface area relative to height (low aspect ratio; Sambilay, 1990). Therefore, based on empirical evidence, larger, more-streamlined fish, with longer pectoral fins and higher aspect ratios, may be expected to show higher passage rates.

Passage of multiple barriers is contingent on successive behavioural decisions. The role of behavioural traits in determining fish passage success is unclear and has rarely been evaluated. An important behavioural component of fish passage is 'motivation to move'. For example, while fish may be physiologically and morphologically capable of negotiating a barrier, they may behaviourally 'choose' not to do so (Castro-Santos, 2005). Fish often exhibit repeatable behavioural traits, which can be quantified along a 'shy-bold' spectrum (Toms et al., 2010). The 'bold-shy' axis of fish behaviour tends to correlate with 'exploration-avoidance' behaviours and activity levels (Chapman et al., 2011; Conrad et al., 2011), suggesting that bolder individuals may be more likely to pass barriers.

Individual repeatability is a proxy for heritability (Dohm, 2002), that is, the proportion of trait variation that can be attributed to genetic factors, as opposed to environmental factors. Previous studies have identified significant repeatability in swimming ability (Marras et al., 2010), metabolic rate (Norin & Malte, 2011), boldness (Jolles et al., 2016), risk-taking (Roy et al., 2017) and movement (Taylor & Cooke, 2014) in fishes, but repeatability has never been evaluated in fish passage. It is important to evaluate repeatability because by excluding the passage of some individuals while allowing the passage of others, barriers have the potential to exert selective effects on traits within fish populations.

In this study, we aimed to assess potential selective effects of barriers on fish communities and better inform fish passage science regarding the traits that influence passage success. We investigated the response of five river-resident fish species, with contrasting size, morphology and swimming ability, to a series of small vertical barriers in a laboratory-based cascade. We quantified interspecific and intraspecific variability in fishes' ability to pass small barriers, as well as assessing individual repeatability in one species (brown trout). The influence of physiological, morphological and behavioural factors on passage success was assessed. We also used a random-walk simulation model to predict the consequences of barriers for taxonomic composition in a hypothetical river fragmented by multiple barriers.

2 | MATERIALS AND METHODS

2.1 | Study species

We examined barrier impacts on topmouth gudgeon *Psuedorasbora parva*, European minnow *Phoxinus phoxinus*, stone loach *Barbatula*

barbatula, bullhead *Cottus gobio* and non-diadromous brown trout *Salmo trutta*. These species were selected because they are river-resident, and vary widely in body size, shape and swimming mode (Jones, Svendsen, et al., 2020). Information on the passage behaviour of topmouth gudgeon is important because it has invaded large areas of Europe, Asia and Africa with acute ecological impacts (Gozlan et al., 2010), and dispersal along river catchments is a major pathway of secondary introduction (Pinder et al., 2005), with implications for barrier management (Rahel, 2013). Between 30 and 54 individuals of each species were collected by backpack electrofishing (HT-2000, Halltech, Canada) from wild populations in South Wales (Table S1). Following capture, fish were housed in species-specific tanks in a 2,500 L recirculating aquaculture system (TMC System 5000P; Tropical Marine Centre Ltd). A 12-hr light/dark cycle was maintained and housing water was kept at 15 ± 1°C. Fish were fed to satiation on pellet food (Atlantic Gold; Pacific Trading Aquaculture Ltd.), supplemented with live maggots and frozen bloodworms. All fish were marked using unique visual implant elastomer (VIE) tags (Northwest Marine Technology) to allow individual identification for cascade experiments, swimming respirometry, behavioural assays and morphometrics. Fish were left to acclimatise to housing tanks for at least 2 weeks before testing in the cascade setup.

2.2 | Cascade setup

Fish passage was monitored in a cascade setup (185 L) consisting of seven 20-L pools (H: 25 cm, W: 30 cm, L: 38 cm) separated by 7.5 cm vertical waterfalls (Figure 1). A standardised waterfall height of 7.5 cm was chosen to create a selective effect on barrier passage (i.e. allow some individuals/species to pass upstream while excluding others) in the study species, based on available information on jumping ability of similar species (e.g. Holthe et al., 2005; Prenosil et al., 2016; Utzinger et al., 1998). Two tubs downstream of the experimental area acted as sumps. A submersible pump at the downstream end recirculated the water at a rate of 13 L/min. A chiller (TK150 chiller; TECO) maintained temperature to 15 ± 0.5°C and water quality was maintained by daily water changes and UV treatment. Black plastic walls (0.8 m high) and impassable mesh barriers at the downstream end (mesh size 2 mm) limited fish movements to the experimental area (tanks 1–7). A florescent ceiling light positioned above the cascade simulated light intensity on an overcast day (120 lux).

Fish (37–189 mm) were introduced individually to the middle pool (4), which was temporarily fitted with a cover during a 30-min acclimatisation period (Figure 1). The cover was then removed, and the movements were recorded over a 2-hr period using an aerial CCTV camera (ANNKE, Model: C51N). Experiments lasted for 2 hrs to allow fish sufficient time to express innate differences in movement (Amaral et al., 2016; Branco et al., 2013; Poulsen et al., 2010), but not enough time to allow potential learning (i.e. reduce the risk that fish could learn that cascade setup was a small closed system and adopt more sedentary behaviour in response). Videos were played back using VLC media player 3.03 (VideoLAN) and five metrics of passage movement were recorded: downstream pass rate, upstream pass rate, total pass rate and upstream attempt rate (see Figure 1 for definitions). An upstream attempt was defined as fish leaping within 5 cm of the base of a waterfall but failing to pass upstream.
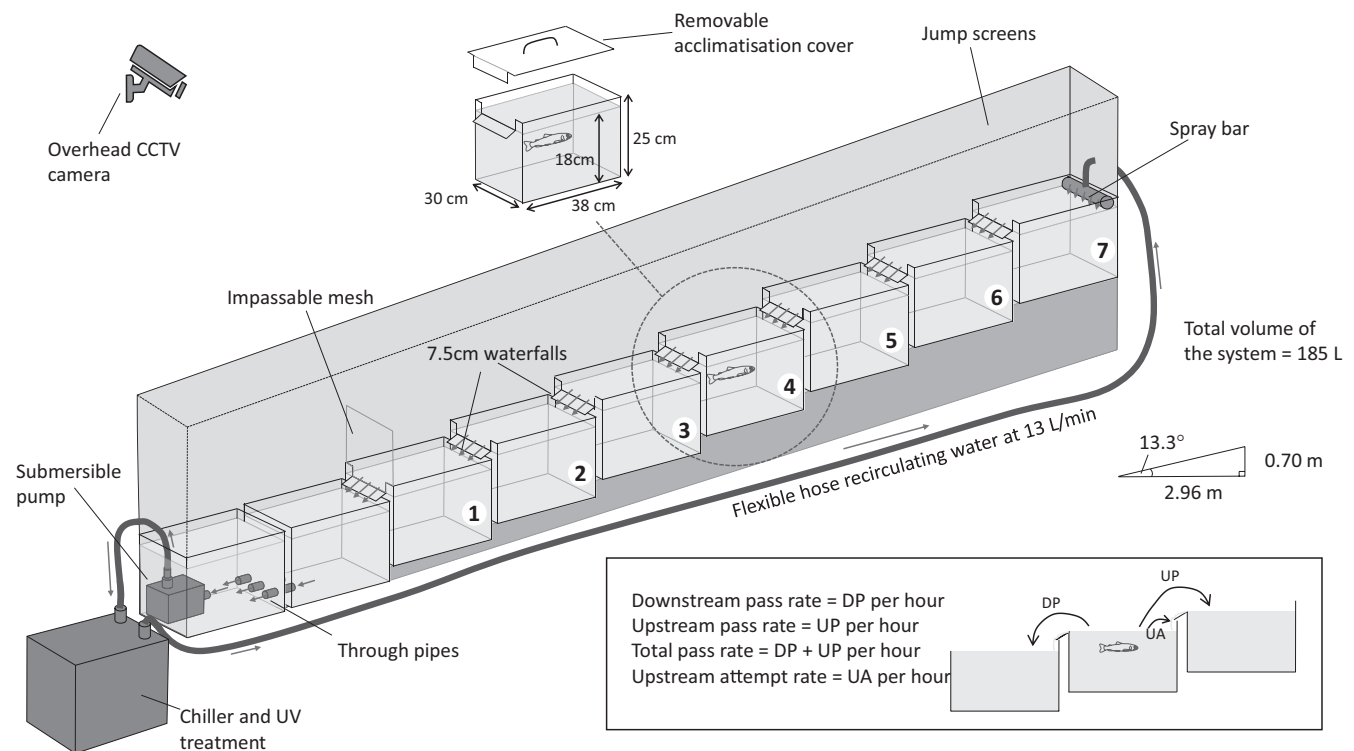

FIGURE 1 Design of experimental cascade setup and the passage metrics measured (inset)

A separate group of 20 brown trout were used to assess repeatability of passage behaviour. Each of these individuals was tested in three replicate trials, allowing 10 days of recovery time between trials. Brown trout were chosen for the repeatability study because they showed the greatest range of individual variation in barrier passage.

2.3 | Intrinsic drivers of fish passage

To assess the potential mechanisms driving interspecific differences in passage rates, physiological (swimming performance and metabolism) and morphological traits were measured in a subsample of fish per species: topmouth gudgeon ($n = 26$), European minnow ($n = 22$), stone loach ($n = 22$), bullhead ($n = 22$) and brown trout ($n = 26$). In addition to the morphological and swimming performance information, boldness was measured in the 26 brown trout.

2.3.1 | Swimming performance and metabolism

The standard metabolic rate (*SMR*), aerobic scope (*AS*) and sustained swimming ability (U_{sus}) were measured in swim tunnel respirometers (Loligo Systems, Viborg, Denmark). Individual fish were introduced to swim tunnel respirometers (current speed set at 1 cm/s) and left to acclimatise overnight (16hrs) while measuring metabolic rate (mgO$_2$ kg^{-1} hr^{-1}) using intermittent flow respirometry (180 s flush, 60 s wait, 420 s measure). The mean of the 10 lowest metabolic rate values over the 16-hr test period was taken as the *SMR* for each individual, similar to previous studies (Svendsen et al., 2014).

After measuring *SMR*, incremental velocity experiments were undertaken to measure *AS* and U_{sus}. To measure U_{sus}, current velocities within the swim tunnels were increased in 5 cm/s increments (from a start velocity of 5 cm/s), at 9-min intervals, until the fish were no longer able to resist the current. The 9-min interval proved suitable to obtain accurate measurements of metabolic rate and U_{sus} across a range of fishes with different body sizes and swimming abilities (Jones, Svendsen, et al., 2020). Sustained swimming ability (U_{sus}) was defined as the maximum flow velocity maintained for an entire 9-min measurement loop. Metabolic rates were measured for the duration of the increased velocity tests and maximum metabolic rate (*MMR*) was taken as the highest value observed (Svendsen et al., 2013). Aerobic scope (*AS*) was calculated as MMR – SMR (Metcalfe et al., 2016).

2.3.2 | Morphology

Standardised photos of each fish were taken at a known scale using an overhead camera (Lumix DMC-G2; Panasonic). Measurements of body length (total length—*BL*), maximum body girth (*MBG*), pectoral fin length (*PL*), caudal fin height (*CH*) and caudal fin area (*CA*) were measured (±1 mm; Figure S1) using measurement tools on ImageJ

(Schneider et al., 2012). Three metrics of body morphology were calculated due to their relevance for swimming ability and therefore barrier passage: Fineness Ratio (FR; Baktoft et al., 2016), Pectoral Fin Length Ratio (PFLR; Danner & Boucher, 2005) and Aspect Ratio (AR; Sambilay, 1990) (Figure S1).

2.3.3 | Boldness

We assessed the extent of scototaxis (preference for dark environments [Maximino et al., 2010; Toms et al., 2010]) as a proxy for boldness in brown trout. The test arena consisted of a 25-L glass tank (H: 20 cm, D: 20 cm, L: 60 cm) filled with 15 L of water from the holding tanks. Each tank was lined with adhesive plastic to create two distinct halves: one black (cover) and one white (exposure) (Figure S2). There was a removable acclimatisation cover (H: 20 cm, D: 20 cm, L: 20 cm) in the middle of the tank (Figure S2).

Brown trout were identified by VIE tags and introduced singly to the acclimatisation zone. The acclimatisation cover was removed after 10 min, allowing fish access to the test arena for 15 min (Maximino et al., 2010). Fish movements during the test period were recorded using an overhead GoPro HERO 5 camera. Videos were processed using VLC media player 3.03 (VideoLAN) and the proportion of time spent in each half of the tank was recorded as a proxy for boldness (BOLDNESS), varying between 0 (shy) and 1 (bold).

2.3.4 | Statistical analysis

All statistical analyses were undertaken using R version 4.0.0. (R Core Team, 2020). We first used random forest regression models, fitted using the R package 'RANDOMFOREST' (Liaw & Weiner, 2002), to select the most important trait covariates out of the potential covariates influencing interspecific differences in total pass rate, as random forest models are robust to situations where there is a large number of covariates compared to the number of data points (Bradter et al., 2013). Total pass rate was the response variable, while *Species*, U_{sus}, *SMR*, *AS*, *BL*, *FR*, *PFLR* and *AR* were explanatory variables, and the importance of each covariate was evaluated by mean squared error and node impurity for each trait, using ntree = 50,000 and a 75% split in training: test data and default values otherwise. The random forest approach consistently identified a reduced set of four influential variables (Figure S3), which were fitted in a classical GLM model with negative binomial distribution, taking advantage of the robustness and interpretability of GLMs in low-dimensional settings (small number of covariates). The GLM was fitted using the *glm.nb* function in the package 'MASS' (Venables & Ripley, 2002) to account for the zero-inflated and over-dispersed count data.

A random-walk simulation model, parameterised using the experimental data, was used to examine how the observed differences in response to barriers might affect the composition and spatial distribution of our fish communities exposed to multiple barriers over a 24-hr period. The R code used was:

```
for (i in 1:1000) {
steps <- sample(c(−3:+3), size = 12, prob = c(0.47,0.09,0.12,0.14,
0.00,0.12,0.06),
replace = TRUE)
FinalDists[i] <- sum(steps)rm(steps)
}
```

where *steps* is number of barriers moved after 24 hr, *sample* is barriers moved upstream (+) or downstream (−) within 2-hr period (experimental time), *size* is the length of time for simulation (12 × 2 = 24 hrs) and *prob* is probability of the species ending in each location after 2 hrs (example shown is probabilities for brown trout). The model was run five times simulating the movement of 1,000 individuals each time, changing *prob* according to the probability data for each species.

A similar method (as per interspecific model) was used to assess the drivers of intraspecific passage variation in brown trout. Passage metrics (total pass rate, upstream attempt rate, upstream pass rate and downstream pass rates) were fitted as response variables, whereas physiological (U_{sus}, *AS* and *SMR*), morphological (*BL*, *FR*, *PFLR* and *AR*) and behavioural (BOLDNESS) traits were explanatory variables. A random forest protocol was used to reduce the intraspecific models (Figure S4), with ntree = 50,000, a 75% training to test data split, and the *glm.nb* function in 'MASS' was used to fit the reduced models. Potential interactions between predictor variables were explored in candidate models and excluded from the final models where non-significant.

To test the statistical significance of repeatability, we used 'rptR' package which uses a GLMM approach to estimate repeatability (*R*) with 95% confidence intervals via parametric bootstrapping (Stoffel et al., 2017). Passage metrics (upstream pass rate, downstream pass rate, total pass rate and upstream attempt rate) were fitted as the response variable using the 'rpt' function, and 'Trout ID' was fitted as a random effect, and *BL* as a fixed effect to control for the effect of body size. Models were run using 1,000 parametric bootstraps and zero permutations. This method accounts for overdispersion in the passage data by internally adding an observation-level random effect to the models (Stoffel et al., 2017).

3 | RESULTS

3.1 | Interspecific variation

Substantial interspecific differences in passage rates were observed (Figure 2a–d). Mean total pass rate ranged from 0.2 per hour in top-mouth gudgeon to 3.4 per hour in brown trout (Figure 2a). Total pass rate differed significantly between species (Deviance$_{4,110}$ = 10.01,
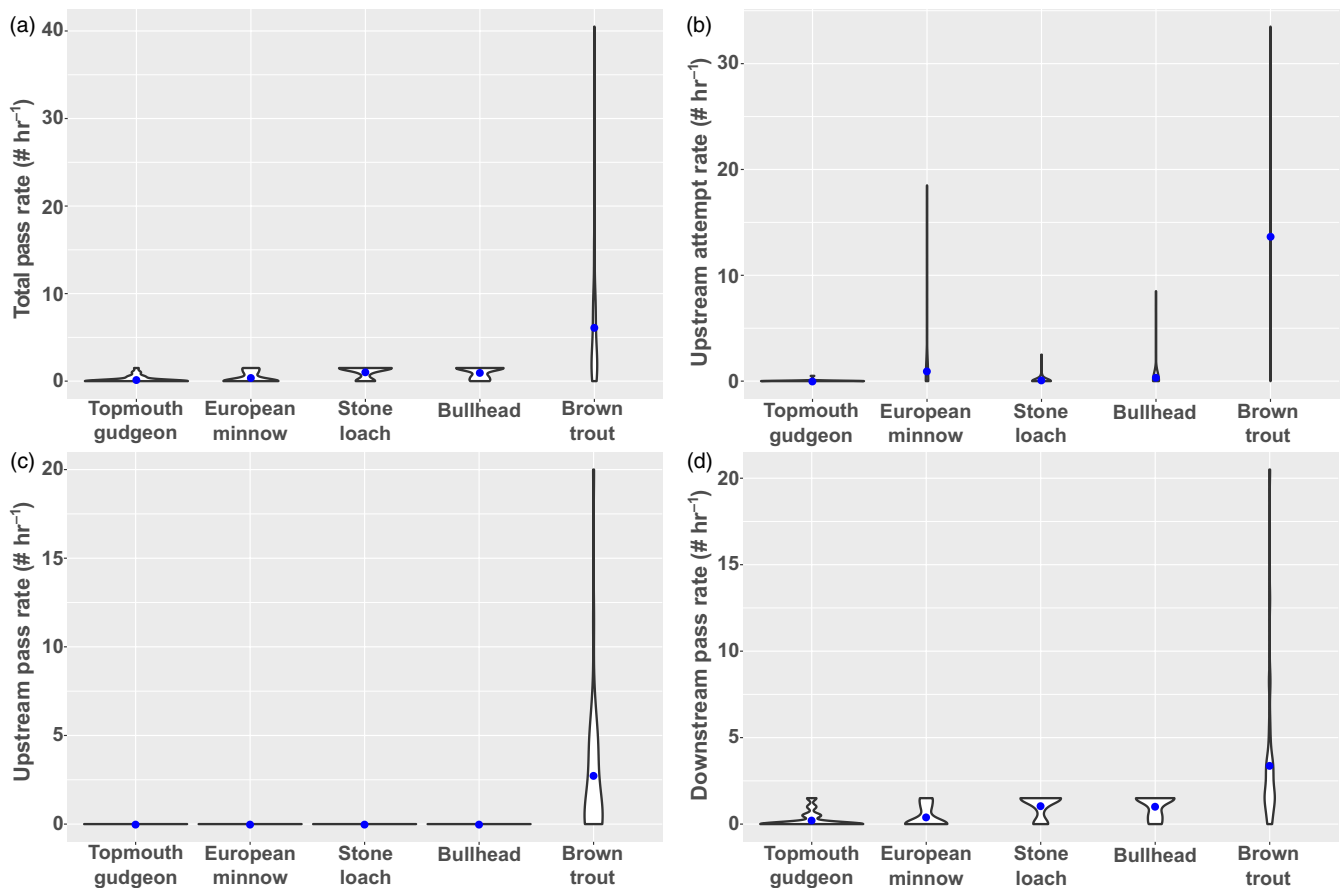

FIGURE 2 Interspecific variation in (a) Total pass rate, (b) upstream attempts rate, (c) upstream pass rate and (d) downstream pass rate. Violin plots show the probability density of passage data at different values. Blue dots show the median value for each species. *n* = 30 for all species except brown trout (*n* = 34)

$p = 0.040$) and showed a positive relationship with *BL* (Deviance$_{1,114}$ = 105.15, $p < 0.001$) and U_{sus} (Deviance$_{1,115}$ = 92.61, $p < 0.001$). Aerobic scope (*AS*) had no significant effect on total passes (Deviance$_{1,116}$ = 0.023, $p = 0.879$) and all other traits had negligible influence (Figure S3). At least some individuals of each species showed upstream attempts (topmouth gudgeon = 3%, European minnow = 17%, stone loach = 10%, bullhead = 20%, brown trout = 82%; Figure 2b), but only brown trout passed upstream (Figure 2c).

The random-walk simulation model, based on the probabilities of each species movement in the cascade, indicated that the presence of multiple barriers would result in a strong net downstream movement for all species (Figure 3). Unequal movement across barriers between species resulted in sorting of the fish community: bullhead and stone loach moved furthest downstream (mean of −25 and −26 barriers, respectively) while topmouth gudgeon and European minnow moved the least (mean of −6 and −10 barriers, respectively). Brown trout showed intermediate movement (mean = −15 barriers) but had a much wider distribution and were the only species for which some individuals showed net upstream movement.

3.2 | Individual variation in brown trout

Brown trout showed substantial intraspecific variation in the various passage metrics (Figure 4a–d): for example, total pass rate ranged from 0 per hour up to a maximum of 40.5 per hour between individuals. Excess kurtosis was evident in total pass rate ($b_2 = 7.62$), upstream pass rate ($b_2 = 7.18$) and downstream pass rate ($b_2 = 7.45$) indicating distributions of these metrics were leptokurtic: that is, most individuals were relatively sedentary but a small number of individuals were highly mobile. In contrast, upstream attempt rate showed no evidence of kurtosis ($b_2 = 0.44$): that is, motivation to move upstream was more normally distributed. Of the 31 (91%) brown trout that made upstream attempts (Figure 4b), only 21 (68%) successfully passed upstream (Figure 4d).

BOLDNESS showed a significant positive relationship with all movement metrics in brown trout (Table 1). Body length (*BL*) had a significant positive effect on total pass rate, upstream pass rate and downstream pass rate but not upstream attempt rate. Aerobic scope was negatively associated with downstream pass rate (i.e. individuals with lower AS were more prone to move downstream). None of the other traits (*SMR*, U_{sus}, *FR*, *PFLR* or *AR*) showed significant relationships with any of the movement metrics (Table 1; Figure S4).

Brown trout showed significant repeatability in movement behaviour across three separate trials (Figure 5a–d). Individuals that moved extensively in the first trial tended to repeat this behaviour in the subsequent two trials, and, vice versa, individuals that moved little during the first trial tended to be sedentary in subsequent trials. Repeatability estimates were statistically significant after controlling for the effect of body size (*BL*): total pass rate (R (±SE) = 0.53 ± 0.15, $p < 0.001$; Figure 5a), upstream pass rate (R (±SE) = 0.69 ± 0.15, $p < 0.001$; Figure 5c) and downstream pass rate
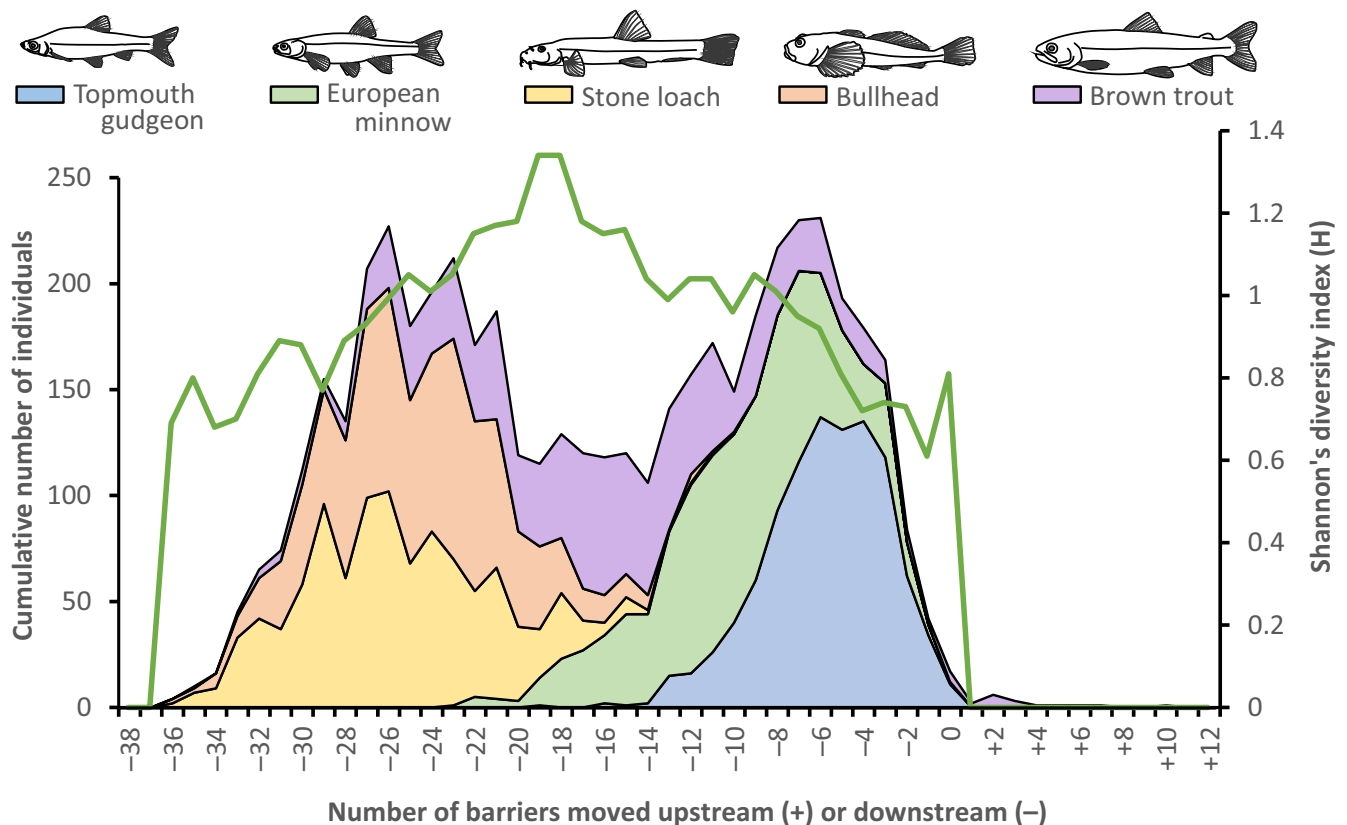

FIGURE 3 Movement of different species after a 24-hr period as estimated by a random-walk simulation model based on the probabilities of movement from cascade experiment
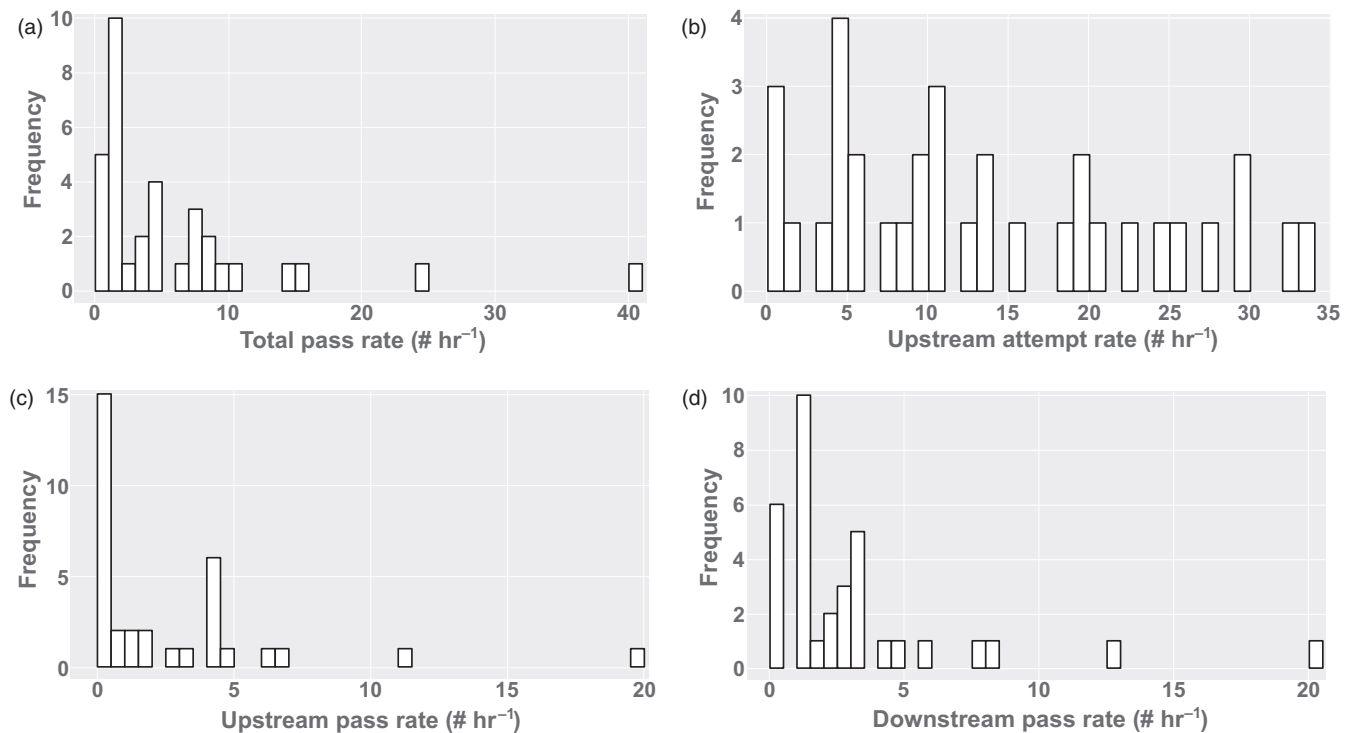
FIGURE 4 Intraspecific variation in movement metrics for the 34 brown trout tested in the cascade: (a) Total pass rate, (b) Upstream attempt rate, (c) Upstream pass rate and d) Downstream pass rate

TABLE 1 Parameter estimates for GLMs predicting relationship between intraspecific variation in movement metrics in brown trout ($n = 26$) and the various morphological, physiological and behavioural traits examined

Metric	Trait	$\beta \pm SE$	z	p
Total pass rate	Boldness	0.48 ± 0.18	2.65	$0.008*$
	BL	0.54 ± 0.24	2.29	$0.022*$
	AS	-0.40 ± 0.21	-1.90	0.057
	PFLR	0.06 ± 0.20	0.31	0.760
	U_{sus}	0.03 ± 0.24	0.128	0.898
Upstream attempt rate	Boldness	0.33 ± 0.15	2.20	$0.028*$
	FR	0.24 ± 0.13	1.85	0.064
	AS	-0.21 ± 0.14	-1.44	0.151
	BL	0.12 ± 0.14	0.82	0.412
Upstream pass rate	BL	0.58 ± 0.23	2.50	$0.012*$
	Boldness	0.61 ± 0.26	2.35	$0.019*$
	AS	-0.36 ± 0.25	-1.45	0.147
Downstream pass rate	BL	0.54 ± 0.20	2.74	$0.006*$
	AS	-0.48 ± 0.19	-2.56	$0.011*$
	Boldness	0.39 ± 0.16	2.43	$0.015*$
	PFLR	0.21 ± 0.18	1.13	0.257
	U_{sus}	0.08 ± 0.21	0.37	0.711

Abbreviations: AS, aerobic scope; BL, body length; FR, fineness ratio; PFLR, pectoral fin length ratio; U_{sus}, sustained swimming speed.
*Highlights statistical significance ($p < 0.05$).

$(R (\pm SE) = 0.42 \pm 0.16, p = 0.002$; Figure 5d). Only upstream attempt rate showed non-significant repeatability ($R (\pm SE) = 0.21 \pm 0.14$, $p = 0.082$; Figure 5b).

4 | DISCUSSION

Our results highlight the potential for small river barriers to have selective effects on fish communities, both at the interspecific and intraspecific levels. While environmental factors such as flow (Knapp et al., 2019), light intensity (Vowles & Kemp, 2012) and temperature (Ficke et al., 2011) can influence barrier passage in the natural environment, removing these confounding factors in the laboratory allowed us to test the effect of intrinsic factors on fishes' responses to barriers. The significant repeatability observed in the movement of brown trout indicated that the movement patterns observed in the cascade setup were more than just experimental 'noise' and that the differences seen were representative of fishes' motivation and ability to move over vertical barriers.

4.1 | Community effects of barriers

At least some individuals of all species showed movements downstream and attempts at jumping upstream: evidence of motivation to move within the cascade system. Yet, despite the low height of the barriers (7.5 cm), only brown trout successfully passed
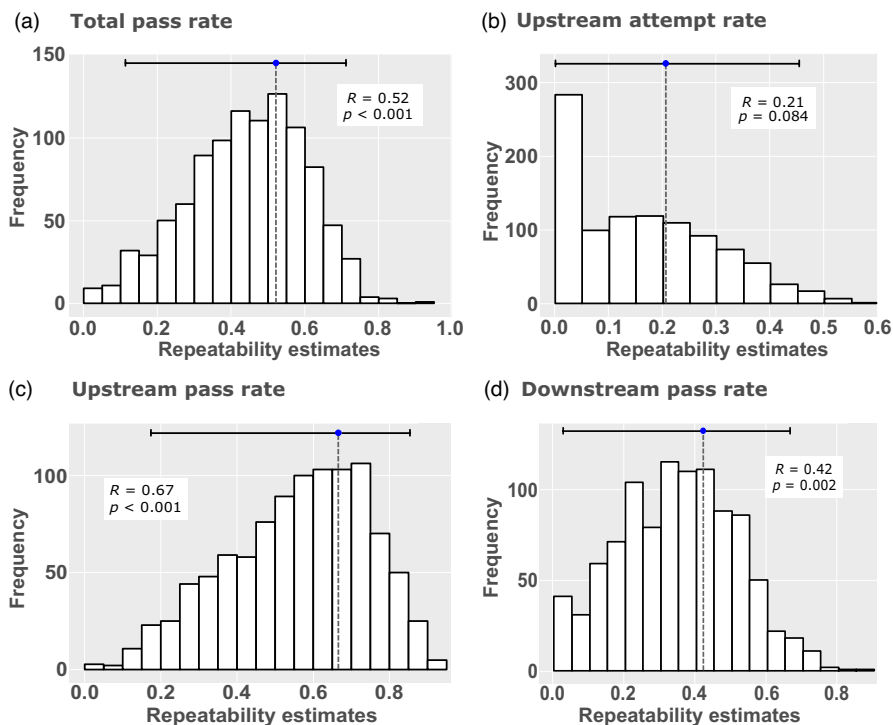
FIGURE 5 Repeatability estimates (±95% CIs) for the 1,000 parametric bootstraps run on the data from the 20 brown trout tested three times each in the cascade: (a) Total pass rate, (b) upstream attempt rate, (c) upstream pass rate and d) downstream pass rate

upstream. In agreement with our results, very small barriers (<5–17 cm) have previously been found to block the upstream passage of a range of cottids and cyprinids with similar morphologies to many of our study species (LeMoine & Bodensteiner, 2014; Prenosil et al., 2016; Utzinger et al., 1998). However, European minnow can jump up to 27 cm (Holthe et al., 2005) and even small trout can jump several times their body length (Brandt et al., 2005; Kondratieff & Myrick, 2006). Hence, it is possible that more fishes would have been able to pass upstream over barriers of the size tested in our cascade given a longer timeframe or where motivational cues were suitable. Still, given the observed attempts (and failures) to move upstream, our results do indicate the potential for small barriers to disrupt upstream movement, by selecting against certain species and individuals, as well as by delaying passage. The barrier height in our cascade was well below the head drop suggested to ensure the passage of 'coarse fish' (any freshwater fish other than salmonids) in the United Kingdom (0.1–0.2 m; Armstrong et al., 2010), suggesting that even fish passes built to best-practice guidelines have the potential to disrupt movements of fish communities.

We found that body size and swimming speed were the main factors determining barrier passage at the interspecific level, consistent with observations elsewhere (e.g. Castro-Santos, 2006; Haro et al., 2004; Noonan et al., 2012). These patterns further highlight the potential for barriers to prevent movements of smaller-bodied and weaker-swimming species. Longitudinal movements are essential for fish to recolonise vacant habitat patches (Schumann et al., 2015), compensate for egg/larval drift (Dudley & Platania, 2007), access spawning grounds (Fredrich et al., 2003), reach refugia (Davey & Kelly, 2007) and they also support gene flow between populations (e.g. Junker et al., 2012). Isolated fish populations are more vulnerable to other anthropogenic stressors and stochastic events (Fausch

et al., 2009; Junker et al., 2012; Radinger et al., 2018) so impeded passage can threaten the long-term persistence of populations.

Our random-walk simulation indicated that differential movement among species could potentially result in effective sorting of fish communities. The trend for net downstream movement in all species indicates that the presence of multiple barriers could result in the loss of fish from upstream areas where reciprocal upstream movement is precluded by the impassability of barriers to most fish. Because this was a laboratory study, these results require field validation: for instance, fish behaviour in situ may be influenced by multiple factors such as habitat suitability, flow dynamics, temporal cues, light conditions, movement of conspecifics or the presence/absence of competitors. Nevertheless, the results of our simulation model suggest that net downstream movement is a strong possibility where multiple barriers are present and upstream passage is challenging. This may have important conservation implications as net downstream movement could be a mechanism by which some fishes with poor jumping ability can become locally extinct above small barriers (Nislow et al., 2011; Schumann et al., 2019; Utzinger et al., 1998). As barriers can be densely distributed in rivers (e.g. 1 barrier every 0.6 km in the United Kingdom; Jones et al., 2019), the selective passage effects observed here could potentially affect river community composition and distribution over the long term. Maximising metrics such as barrier-free length (Jones et al., 2019) and dendritic connectivity index (Cote et al., 2009) could help mitigate these effects.

Invasive topmouth gudgeon were completely blocked by a barrier height of 7.5 cm in our study, although we cannot disregard than given a longer timeframe, or different motivation, some individuals may have been able to pass the barriers. Yet, our results do indicate that barrier designs incorporating small vertical head differences could block their dispersal. However, barriers to restrict invasive

species should aim to provide for passage of native fauna to avoid the harmful effects of isolation (Rahel, 2013), and in this case, the use of even a small barrier would exclude upstream passage of all native fishes except brown trout. This highlights the difficulties of developing selective barriers for invasive species management (Jones, Tummers, et al., 2021; Rahel, 2013).

4.2 | Selective effects in brown trout

The leptokurtic distributions observed in our barrier passage metrics for brown trout show that the presence of barriers may be selecting for the passage of only a small subset of individuals. The repeatability values reported here (e.g. R for upstream pass rate = 0.67) are relatively high for behavioural studies (see Wolak et al., 2012), suggesting innate predisposition to mobile or sedentary behaviour in response to barriers, independent of body size. Significant repeatability may suggest trait heritability (Dohm, 2002) so barriers may have the potential to cause generational effects. In contrast to the patterns observed in passage rates, upstream attempt rate had a more normal distribution and showed non-significant repeatability. This implies that the leptokurtosis observed in the passage rates of brown trout is a barrier effect rather than a reflection of individuals' motivation to move.

Intraspecific passage rates in brown trout showed a positive relationship with body size, which emphasises how small barriers can create size-selective effects on populations (Haugen et al., 2008; Maynard et al., 2017; Noonan et al., 2012). However, significant repeatability was apparent when body size differences were controlled for, indicating other intrinsic factors may also be important. BOLDNESS was a significant predictor of all passage metrics in brown trout. Motivation is widely recognised as an important factor in fish passage (Goerig & Castro-Santos, 2017; Kemp, 2016) and the patterns identified here call for a greater recognition of the influence of behavioural traits. The lack of a significant relationship between any of the brown trout movement metrics and U_{sus} was unexpected given that swimming performance is regarded as a key factor determining fish passage success (Castro-Santos, 2006; Haro et al., 2004). The significant negative relationship between downstream movements and aerobic scope may suggest that holding position within pools was energetically demanding, perhaps explaining why individuals with low aerobic scope were more prone to move downstream. Overall, the intraspecific analysis in brown trout indicates that a wide range of behavioural, morphological and physiological traits drive fish movement over barriers, and highlights the need to move beyond simply assessing body size and swimming speed (Silva et al., 2018).

5 | CONCLUSIONS

Assessing and mitigating the consequences of reduced connectivity for biodiversity and ecological processes is a key management concern and the most striking finding of our study is that even very small barriers have the potential to generate selective effects both at the interspecific and intraspecific levels. Barriers seemed to select for the passage of larger-bodied, faster-swimming, bolder fish. By selectively allowing passage of some species while excluding others, barriers and fish passes have the potential to alter community composition and change species' distributions (Agostinho et al., 2007; McLaughlin et al., 2006), with consequences for wider ecosystem functioning. While many small-bodied river fish were traditionally viewed as sedentary (Gerking, 1959), there has been a paradigm shift (Rodríguez, 2002), and there is an increasing recognition that most species need to move up and downstream to complete various parts of their life cycles (Davey & Kelly, 2007; Dudley & Platania, 2007; Fredrich et al., 2003; Schumann et al., 2015). Even where such movements are infrequent, they are important to support gene flow between populations and avoid the loss of genetic variation (Fagan, 2002). Selective passage may thereby reduce the capacity of populations to adapt to environmental change (Haugen et al., 2008).

Overall, our results support the idea that barrier impacts need to be viewed beyond their effects on migratory fish (Fuller et al., 2015; Jones, Consuegra, et al., 2020; Ogbeibu & Oribhabor, 2002), by showing their potential for causing far-reaching impacts on river-resident fish too (Weibel & Peter, 2013). Given the abundance of small barriers in rivers worldwide (Belletti et al., 2020; Jones et al., 2019), it is important to evaluate their more subtle effects to fully understand the extent and consequences of river fragmentation. Mitigation measures need to account for natural variation at the interspecific and intraspecific levels to maximise passage of the wider fish community. For example, barrier removal tends to focus on large barriers (>1 m) to improve passage of diadromous salmonids, but our results indicate the need to also remove low-head (<1 m) barriers to improve connectivity for river-resident species. Where barrier removal is not possible, effective fish passes are needed. However, there is a general consensus that traditional methods in fish pass design are failing (Birnie-Gauvin et al., 2018; Kemp, 2016; Noonan et al., 2012), and new approaches are needed. Fish passes incorporating minimal vertical head differences and offering diverse flow conditions (e.g. nature-like fish passes; Calles & Greenberg, 2005; Katopodis et al., 2001) offer an option that embraces the natural variation in freshwater fish communities, but one that still requires optimisation to ensure efficacy for non-salmonid fish (Kim et al., 2016; Landsman et al., 2018; Raabe et al., 2019).

AUTHORS' CONTRIBUTIONS

C.G.L., P.E.J. and T.C. conceived the ideas and designed the methodology; T.C., P.E.J. and J.V. collected the data; P.E.J. and L.B. analysed

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.