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RESEARCH ARTICLE

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Group size influences light-emitting diode light colour and substrate preference of David's Schizothoracin (*Schizothorax davidi*): Relevance for design of fish passage facilities

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Abstract

Fish passage structures have been constructed to facilitate fish movement past barriers, though the effectiveness of passage structures is highly variable. Designing fish passage structures that consider the behavioural preferences of fish under different environmental conditions (e.g., light colour, substrate type) has the potential to improve fish passage success. Similarly, whether a fish encounters a passage facility alone or in a group may influence fish behaviour. In this case, we assessed the preference of different group sizes ($n = 1$, 6 and 12, respectively) of David's Schizothoracin *Schizothorax davidi* under four different light-emitting diode colours and eight different substrate types in the aquaria of the Houziyan Reproduction Station. We found that singletons preferred to visit the white light, cement and fine pebble, while the fish in groups preferred to visit the blue light, fine pebble and cobble. In addition, the total percentage of mobility frequency (18.3 ± 1.8%), movement velocity (20.4 ± 15.9 cm/s) and distance moved (15.8 ± 1.8 m) of singletons in blue light were much lower than that in the others. The movement velocity (3.3 ± 0.6 cm/s) of singletons on cobble was less, but the percentage of total mobility time (162.9 ± 16.0%) and distance moved (153.4 ± 19.6 m) on the cobble were much greater. Our research yielded novel insights for improving passage efficiency for this species. Findings from this study suggest there should be greater consideration of light colour and substrate type when designing fish passage facilities. Because fish almost always experience dynamic hydraulic conditions near and in fishways, additional research is needed to understand the generality of these findings in systems under lotic characteristics.

KEYWORDS
fishway, group size, light, preference, *Schizothorax davidi*, substrate

1 | INTRODUCTION

For centuries, anthropogenic barriers (e.g., dams) have played a large role in human development. Dams are constructed to enable the generation of hydroelectricity, for flood control, and to enable agricultural

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irrigation (Dudgeon et al., 2006). However, this has had negative effects on connectivity in rivers and consequently the fish residing in or migrating through these obstructed habitats (Grill et al., 2019). For instance, fragmented riverine habitats can impede fish migrations, segment fish populations, reduce species diversity and even cause mortality (Xie, 2017; Zhuang et al., 2016). Fishways have been constructed and used in recent decades to facilitate fish migrations beyond barriers (Clay 1995; Shi et al., 2015). Vertical-slot fishways which are estimated to comprise 76% of all fishways in the globe are currently the major model of fishway engineering projects in China. Yet, the efficiency of these structures can often be low (Bao et al., 2019; Mao et al., 2012; Appraisal Center for Environment & Engineering, the Ministry of Environmental Protection, 2012). Most of the fishway research in China is limited to engineering aspects of the fishway facilities, often neglecting the biological requirements of fishes (Mao, 2018).

In order to pass a fishway, migratory organisms need to first find and enter the fishway and then successfully ascend the fishway. Therefore, attracting fish to the entrance is the first step to improving overall passage success (Castro-Santos et al., 2017; Cooke & Hinch, 2013). Fish tend to be attracted to the rapid flows from hydropower stations and often ignore the relatively low volumes of water that are released from fishways (Green et al., 2011). That makes it challenging for fish to locate fishway entrances. If the fish cannot be lured into the fishway, even if there are good conditions inside the fishway, the efficiency of the fishway will be low. Thus, the attraction ability of fishways is essential for ensuring that a fishway is fully functional. Many fish species are rheotactic, so auxiliary (or attraction) flows at a fishway entrance can increase fish attraction. Fishways with higher attraction flows can encourage upstream migration (Burnett et al., 2017; Cai et al., 2019); however, high velocities can be energetically costly which could lead to lower passage success (Burnett et al., 2017). On the other hand, low flow velocities may be insufficient to attract fish. For example, at the Zhentouba Dam in Sichuan, China, insufficient flows at the fishway entrance failed to attract fish and reduced overall passage (Bao et al., 2019). Similarly, in the Baguari hydro project, Brazil, the number of fish that gathered around the entrance of the fishway was much lower than that in the spillway (Silva et al., 2012). At present, most research on fishway attraction is focused on flows and configuration of the fishway entrance, while less attention has been paid to the potential for use of light to attract fish to the fishway entrance (Tan et al., 2021).

Recent evidence suggests that vision plays a major role in movement for freshwater fish. Improving light conditions at the entrance is integral to fish passage for light sensitive fish (Ruediger, 2001). Artificial light may be used to assist passage or to improve fish movement (Kemp & Williams, 2009). Light has often been used to guide fish towards bypasses (Marchesan et al., 2005) or as a deterrent to draw them away from dangerous areas such as turbine entrances (Ford et al., 2018). Ford et al. (2018) revealed that green light could guide white sturgeon (*Acipenser transmontanus* Richardson) away from potential entrainment mortality sources. Moreover, walleye (*Sander vitreus*) avoided orange and green light (Ford et al., 2019), adult lake sturgeon avoided blue light strobing at 1 Hz (Elvidge et al., 2019), and juvenile grass carps avoided red light, while preferring blue light (Mu et al., 2019). What is clear from these previous studies is that light preferences (or aversion) are species-specific and generalisations are difficult to make. Further, knowledge of species-specific light preferences for improving passage efficiency is rare for most species, particularly those in China.

Upon entering a fishway, the substrate type can influence passage success (Santos et al., 2014). Substrate type can alter the hydraulic environment and ultimately energy expended by a fish during passage (Santos et al., 2014). Increasing bed roughness through addition of boulders and creation of microhabitats can slow flow velocities and create vortices to the benefit of fish (FAO/DVWK, 2002). Substrate preferences (e.g., boulder size and density) during migration will differ across species. For instance, kaluga (*Huso dauricus*) migration intensity was greater in bare bottom environments compared to rocky bottom environments (Li et al., 2013). It has also been reported that structural enrichment enhances the swimming agility and survival of captive-reared rainbow trout *Oncorhynchus mykiss* (Ahlbeck Bergendahl et al., 2017). As such, it is of utmost importance to incorporate substrate preferences of a species into fishway design to enhance efficiency of the fishway.

Fish may approach fishways in groups or in isolation, which may influence their behavioural decisions at the fishway. It has been suggested that for Pacific salmon, collective migration may drive movement through fishways (Okasaki et al., 2020). Group size might affect some behaviours of fish, including habitat preference, locomotor activity level, and movement distance (Lloren et al., 2019; Rieucau & Giraldeau, 2009; Webster & Hart, 2004). Kunz and Hemelrijk (2003) indicated that group size could change decision making in the fish group. It has been well documented for some species that different animals have different group responses depending on the habitat type (Dupuch et al., 2011; Bonanno et al., 2014).

David's Schizothoracin, *Schizothorax davidi* (Cypriniformes: Cyprinidae) is a short distance migratory and important cold-water economic fish species mainly distributed in the middle and lower layers of main streams and tributaries in the upper reaches of the Yangtze River, China (Ding, 1994). *S. davidi* feeds on aquatic invertebrates and algae and the breeding period is from August to September. They lay eggs in rapids and attain maximum size of ~10 kg. The Daduhe River in Sichuan Province is the largest tributary of the Minjiang River in the Yangtze River, located in the transition zone from the south-eastern edge of the Qinghai-Tibet Plateau to the west of the Sichuan. Total length of the Daduhe River is about 1,062 km, with a basin area of 77,400 km^2. Currently, 15 dams have been built on the Daduhe River, the second tributary of the Yangtze River, with another 12 planned and 2 under construction, which collectively interrupt the fish migration route and dramatically alter fish habitat (Grill et al., 2019; Vörösmarty et al., 2010). As such, the abundance of *S. davidi* has sharply declined and has been listed as an Endangered Protected species on the China Biodiversity Red List-Vertebrates since 1980s (Jiang et al., 2016). In this study, individual and group preferences for light and substrate were tested to determine the effect of population size on preferences of *S. davidi* behaviour in the context of fish passage. The aims of this study were to test three null hypotheses: (a) light colour has no influence on the behaviour of *S. davidi*, (b) substrate type has no influence on the behaviour of *S. davidi* and (c) group size of *S. davidi* does not influence preference for light colours and substrate types.

2 | METHODS

2.1 | Study sites and fish collecting

We performed two laboratory experiments to investigate group size effects on light and substrate preference of *S. davidi*. Experimental fishes were collected by 10 gill nets (length × height: 4.0 m × 1.5 m; mesh size: 1.0 cm) from the upper reaches of the Daduhe River in Sichuan province, China (30°31′05.08″N, 102°03′48.84″E and altitude, 1,715 m). Nets were placed for 12 hr on 15 days of each month from August to September in 2018. Because of the high flow river and the scarce fish abundance, it is difficult to collect fish and only 250 healthy fish was captured [total length = 21.5 ± 0.4 cm (mean ± *SD*), mass = 85.8 ± 2.1 g (mean ± *SD*)]. Fish were then transported to the Houziyan Reproduction Station nearby the Daduhe River (Figure 1) and reared in seven 800 L circular tanks with a housing density of 1 ind./20 L for 2 weeks. Each tank was supplied with continuous, unfiltered flow-through water (ca. 2 L/min) supplied from Daduhe River. The holding water maintained an optimal environmental condition for this species (dissolved oxygen: ≥8.0 mg/L, ammonia ≤ 1.0 mg/L). Fish were fed twice a day with commercial carp floating pellets containing 35% crude protein (5% of biomass) until 24 hr before the trials. The light-emitting diode (LED) light was placed above the tank about 5 m, which light intensity was 100 lx and light period was 12 L:12 D. The light period was controlled by a timing device. A total of 228 healthy fish samples was used in the light and substrate experiment and all fish were tested only once [total length = 21.2 ± 0.1 cm (mean ± *SD*), mass = 84.9 ± 1.3 g (mean ± *SD*)]. Both the light colours (including four lights: white, green, red and blue) and substrate types (including eight substrates: cement, sand, fine pebble, coarse pebble, very coarse pebble, cobble, boulder and mixed substrates) preferences were divided into singleton (n = 1), small group (n = 6) and large group (n = 12) treatments which were repeated six times. Each test was maintained for 24 hr (8:00 a.m.–8:00 a.m. +1) (Table 1).

2.2 | Experiment I: Light colour preference test

The colour experiment was conducted in a rectangular tank (length × width × depth, 2.0 m × 1.0 m × 0.8 m), which was filled to

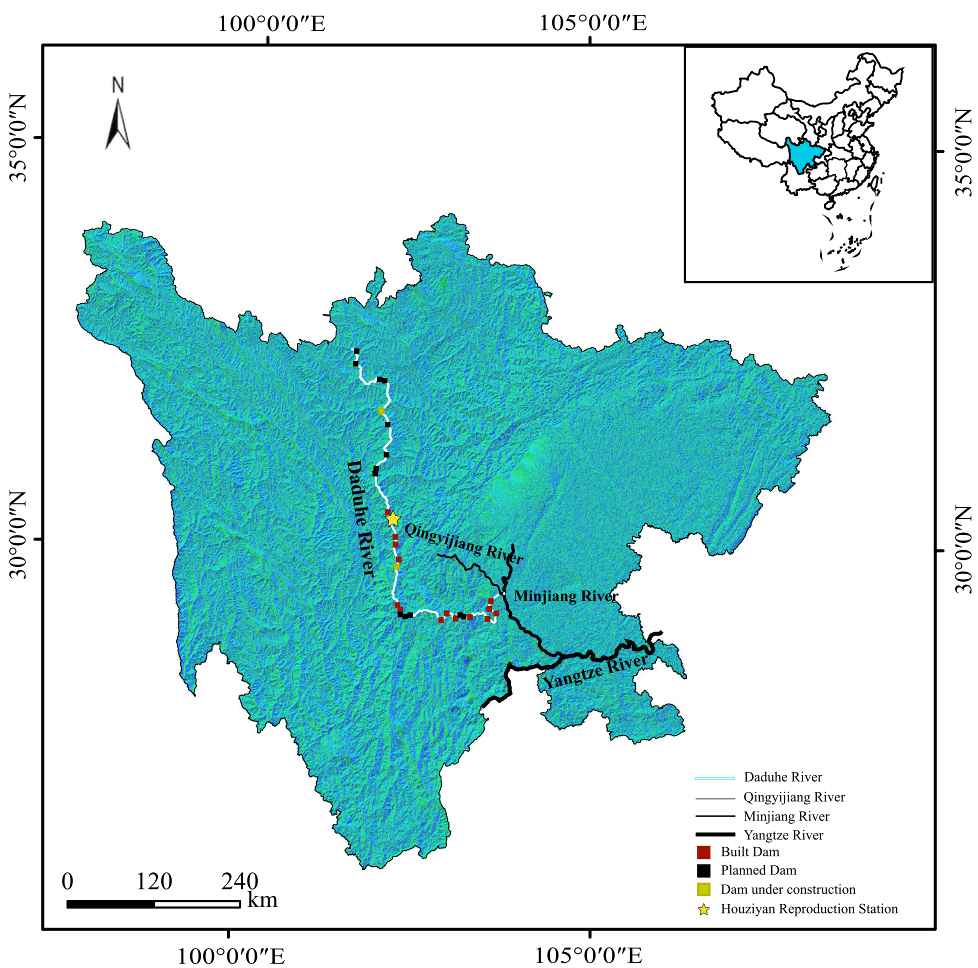

FIGURE 1 Map of the Daduhe River in the Midwest of Sichuan Province, China. Fourteen dams have been built, 13 dams planed and 2 dams under constructed on this river. *Schizothorax davidi* was captured near the Houziyan Reproduction Station (five-pointed star) [Color figure can be viewed at wileyonlinelibrary.com]

a depth of 0.3 m and separated into four equal cells by polyvinyl chloride boards (0.8 m × 1.5 cm × 0.5 m). Four LED light colours were set up above the water surface about 50 cm with the same illumination intensity (i.e., 100 lx) (Figure 2). A lens was arranged under the light source about 25 cm to form a parallel beam. Light intensity at the experimental tank was adjusted and monitored with an AS-823 luxmeter (Shenzhen Sanzer Election Limited Company, Guangdong, China) before the test. The average of light intensity measured under water (each region had nine test counts) was, white (62.22 ± 14.98 lx), green (62.11 ± 10.87 lx), red (51.11 ± 12.15 lx) and blue (63.55 ± 25.97 lx) (Kruskal-Wallis tests, $p > .05$). For the individual ($n = 1$), small group ($n = 6$) and large group ($n = 12$), fish were gently netted from the holding tank into the experimental tank without exposing them to air and exposed to one of the four colour settings randomly. One web camera (TP-link, China) was set above the tank and linked to a DVR (TP-Link, China) that was used to record fish movements. Before and after each test, the main environmental parameters (i.e., temperature, dissolved oxygen and pH) were monitored using a multiparameter meter (YSI Pro20, America) (Table 2) and the light location was changed clockwise to eliminate the impact of the water tank on the fish.

2.3 | Experiment II: Substrate type preference test

The major substrate types in the Daduhe River include cement (0 mm), sand (<1 mm), fine pebble (1–16 mm), coarse pebble (16–32 mm), very coarse pebble (32–64 mm), cobble (64–128 mm) and boulder (>128 mm). We used those substrate types to investigate the habitat preference of *S. davidi*. The substrate experiment was conducted in a circle tank (diameter × depth: 3.5 m × 1.5 m) with a water depth of 0.3 m. The tank (Figure 3) was divided into eight compartments of equal size but with different substrate types. Experimental fish were released at the centre of the experimental tank at the onset of each test. The average temperature, dissolved oxygen and pH were tested before and after each test (Table 2).

TABLE 1 Mean total length (±*SE*) and mean weight (±*SE*) of *Schizothorax davidi* within different trials during the light colour and substrate type experiments in Houziyan Reproduction Station

Experiment	Group	Number of replicates	Totalnumber	Total length (cm) (mean ± *SE*)	Weight (g) (mean ± *SE*)
Light colour	Singleton	6	1	21.18 ± 0.13	80.87 ± 1.83
	Small	6	6	21.31 ± 0.25	86.30 ± 2.84
	Large	6	12	21.38 ± 0.24	87.92 ± 2.30
Substrate type	Singleton	6	1	21.40 ± 0.16	79.19 ± 3.25
	Small	6	6	20.73 ± 0.24	85.25 ± 2.48
	Large	6	12	21.14 ± 0.19	81.78 ± 2.29

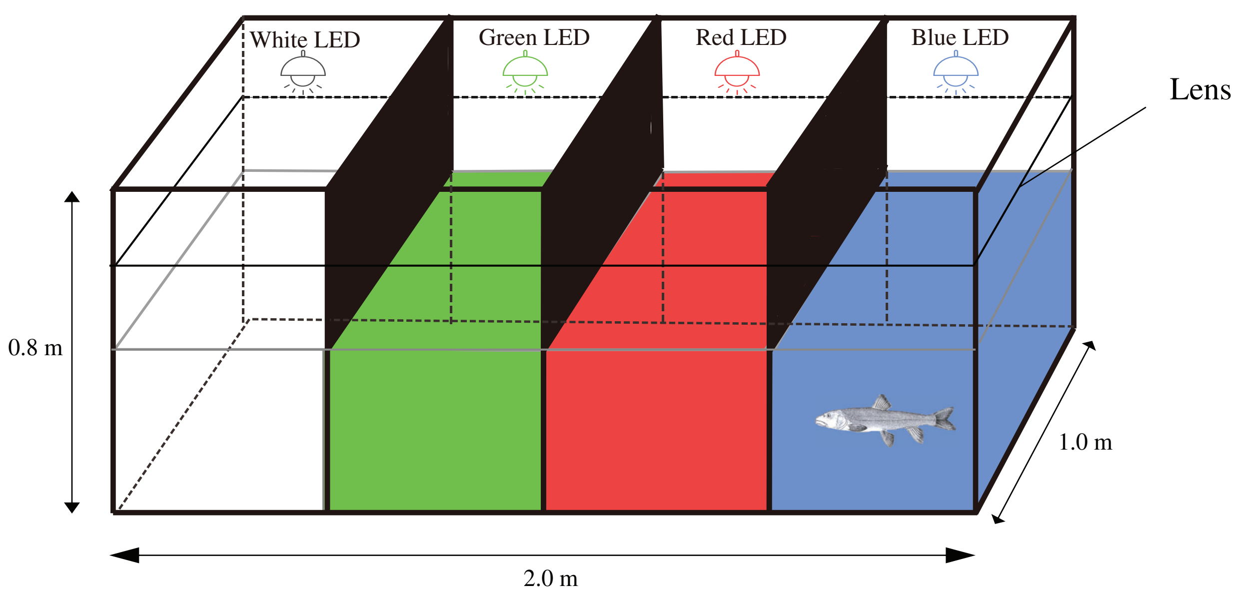

FIGURE 2 Main view of a rectangle light test aquarium in Houziyan Reproduction Station, showing the four same volume compartments. Each compartment was shined with light-emitting diode of different colours (white, green, red, blue) [Color figure can be viewed at wileyonlinelibrary.com]

Experiment	Group	Temperature (°C)	Dissolved oxygen (mg/L)	pH
Light colour	Singleton	8.54 ± 0.04	8.33 ± 0.02	8.33 ± 0.06
	Small	8.58 ± 0.05	8.18 ± 0.02	8.18 ± 0.02
	Large	8.51 ± 0.06	8.12 ± 0.01	8.12 ± 0.05
Substrate type	Singleton	8.47 ± 0.06	7.97 ± 0.05	8.12 ± 0.05
	Small	8.31 ± 0.02	8.20 ± 0.03	8.08 ± 0.02
	Large	8.46 ± 0.03	8.13 ± 0.01	8.05 ± 0.02

TABLE 2 The average temperature, dissolved oxygen and pH (mean ± *SE*) of the experiment water at the light colour and substrate type experiments (averages during the period of experiment ± *SE*) in Houziyan Reproduction Station

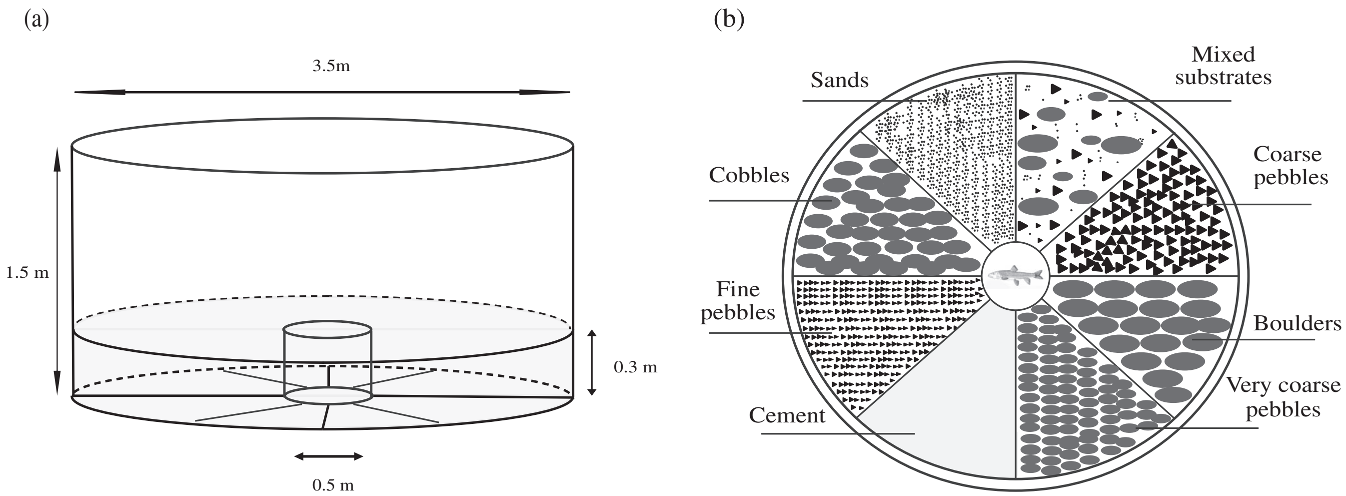

FIGURE 3 The schematic diagram of a circle substrate preference test aquarium in Houziyan Reproduction Station. (a) The sketch map and (b) the top view. Each compartment was putted with different substrate types (cement, sand, fine pebble, coarse pebble, very coarse pebble, cobble, boulder and mixed substrates)

2.4 | Data analysis

The visiting frequency of each individual (as singletons, small groups and large groups) in different light colours and substrate types were recorded over 24 hr. The frequency (*F*) of fish using different light colours or substrate types was calculated as

$$F = f \times \mathrm{N}^{-1}\, 100\%,$$

where *f* was the number of total fish (the number of fishes into one cell was counted each 20 min during the observation 24 hr, summation 72 times) of one region on one observed time, and *N* was the total fish in these experimental regions across all observed times.

For singletons, we used two analysis methods including automatic video-tracking (EthoVision XT 10.1) and manual video-observation. Only manual video-observation was used for group experiments due to limitations of the software package for automated tracking. We digitised 10 min of video images every hour which was imported into the software, which can record the position of a fish every 0.04 s (using dynamic subtraction to differentiate fish from their background and tracking constantly) and calculate activity variables (EthoVision XT 10.1, Noldus et al., 2001). Activity variables that were quantified included: (a) velocity (the swimming distance per unit time in different experimental compartments), (b) movement distance (the swimming distance in different experimental compartments) and (c) mobility state. The mobility state was divided into three items (lowly mobile, mobile and highly mobile) depending on the change in pixels of the detected subject following thresholds (zero mobility: all the pixels are the same, 100% mobility: all the pixels are different) (Noldus et al., 2001):

- Lowly mobile was below 20% mobility.
- Mobile was higher than 20% mobility and lower than 80% mobility.
- Highly mobile was higher than 80% mobility.

Data related to visiting frequency, velocity, movement distance and mobility state (light colours experiment and substrate types experiment: singleton: 6 individuals, small group: 36 individuals, large group: 72 individuals, respectively) were not homogeneously distributed [Lilliefors (Kolmogorov-Smirnov) normality test, $p < .05$). We used a Friedman's test for the comparisons among colours and substrate types followed by Wilcoxon Rank Sum tests to differences between regions when $p < .05$.

Visiting frequency data for the groups in the colour and substrate type test were not homogeneously distributed [Lilliefors (Kolmogorov-Smirnov) normality test, $p < .05$]. We used a Kruskal-Wallis test for comparisons among different group size treatments followed by Wilcoxon Rank Sum tests to comparisons the difference between the different treatments. All analyses were conducted by R 4.0.2 (R Core Team, 2016). All values presented in the text and the plot were untransformed (means ± *SE*).

3 | RESULTS

3.1 | Light colour preference

Visiting frequency in different compartments was significantly influenced by colour (Kruskal-Wallis tests, $p < .05$; Figure 4). For singletons, the average visiting frequency was significantly greater with white (33.8 ± 2.3%) and blue light colours (32.9 ± 2.3%) compared to green (18.8 ± 1.9%) and red light colours (14.6 ± 1.7%) (Friedman tests, $p < .05$). In small group experiments, the distribution of *S. davidi* in blue (38.5 ± 1.5%) was more than the distribution on white (34.8 ± 1.4%), green (15.4 ± 1.1%) and red light colours (11.4 ± 0.9%) (Friedman tests, $p < .05$). In large group experiments, the distribution of *S. davidi* on the blue light colour (41.7 ± 1.3%) was also significantly more than on white (29.8% ± 1.3%), green (17.2 ± 1.0%) and red (11.5 ± 0.6%) light colours (Friedman tests, all $p < .05$).

The activity variables measured for individuals were different in each compartment (Figure 5). The percentage of low mobility time for *S. davidi* in the red (28.9 ± 2.1%), white (29.6 ± 2.4%) and green (23.2 ± 1.8%) compartments were significantly higher than when held in the blue compartment (18.4 ± 1.8%) (Friedman tests, $p < .05$). The mobile time of fish in the red compartment (31.3 ± 2.0%) was significantly higher than white (27.2 ± 2.2%), green (20.2 ± 1.6%) and blue (21.2 ± 1.6%) (Friedman tests, $p < .05$). The highly mobile time of fish in the red compartment (44.1 ± 2.2%) was also significantly higher than that in the white (17.9 ± 1.9%), green (20.5 ± 1.5%) and blue (17.6 ± 1.6%) (Friedman tests, $p < .05$).

The velocity of movement of singletons in the blue compartment (20.4 ± 15.9 cm/s) was lower than that in the white (41.3 ± 21.3 cm/s), green (79.8 ± 15.9 cm/s), and red (56.3 ± 11.3 cm/s) compartments (Friedman tests, $p < .05$) (Figure 6). For distance moved in the light compartment, there was a significant difference in the four compartments (Friedman tests, $p < .05$). Fish in the red (69.0 ± 9.1 m) and green (24.2 ± 3.4 m) compartments moved significantly more than fish in the white (8.8 ± 0.9 m) and blue (15.8 ± 1.8 m) compartments (Friedman tests, $p < .05$).

3.2 | Substrate type preference

The result showed that group size had a significant effect on the substrate preferences of *S. davidi* (Kruskal-Wallis tests, $p < .05$). For singletons, individuals distributed more on cement (30.2 ± 3.8%), fine pebble (26.5 ± 3.7%) and cobble (13.0 ± 2.8%) than other substrates, including sand (8.1 ± 2.3%), coarse pebble (5.3 ± 1.9%), very coarse pebble (5.8 ± 2.0%), boulder (6.5 ± 2.1%) and mixed substrates (4.6 ± 1.8%) (Friedman tests, $p < .05$). There was no significant difference between the average percentage of visiting frequency on cement and fine pebble. In the small group experiment, the average percentage of

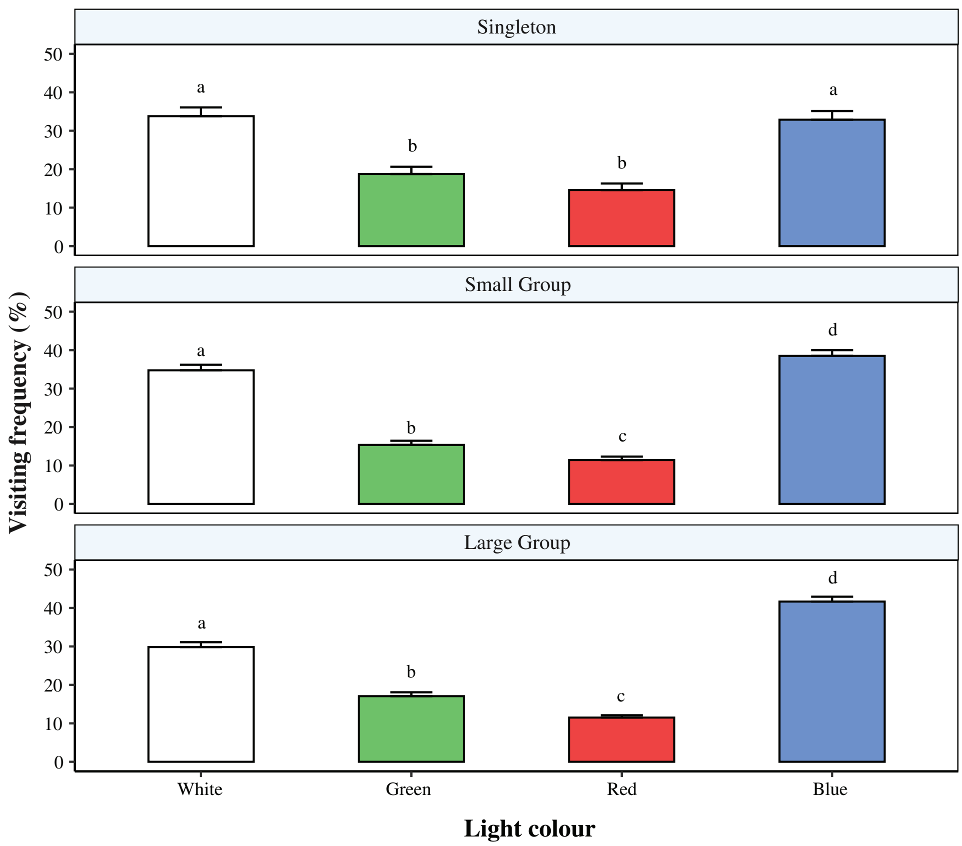

FIGURE 4 Percentage of visiting frequency (mean + *SE*) in different lights (white, green, red and blue) for different groups in *Schizothorax davidi* in rectangle light test aquarium in a laboratory experiment. Different letters indicate significant differences ($p < .05$) between treatments [Color figure can be viewed at wileyonlinelibrary.com]

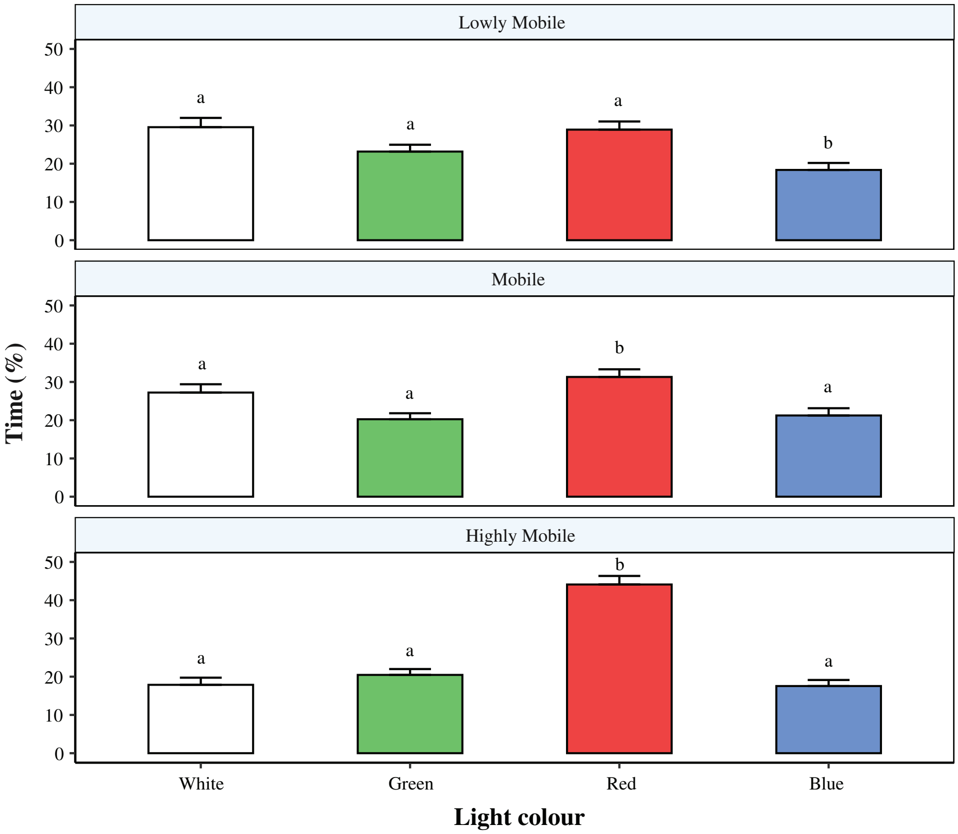

FIGURE 5 The percentage of time (mean + *SE*) in different compartments (white, blue, green and red) with different mobility states in rectangle test aquarium in a laboratory experiment. Different letters indicate significant differences ($p < .05$) between treatments [Color figure can be viewed at wileyonlinelibrary.com]

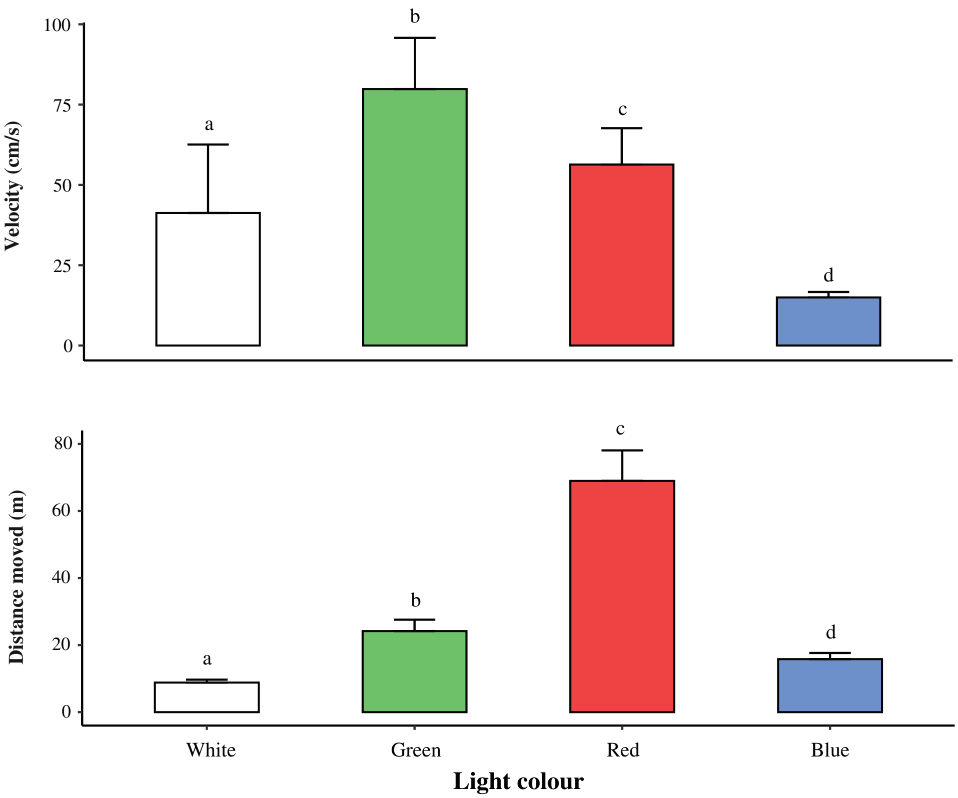

FIGURE 6 The movement velocity (mean + *SE*) and the movement distance (mean + *SE*) to each compartment of singletons in rectangle test aquarium in a laboratory experiment. Different letters indicate significant differences ($p < .05$) between treatments [Color figure can be viewed at wileyonlinelibrary.com]

visiting frequency on fine pebble (17.4 ± 1.5%) and cobble (15.6 ± 1.4%) compartments were significantly higher than the other compartments [i.e., cement (11.6 ± 1.3%), sand (11.0 ± 1.1%), coarse pebble (13.1 ± 1.3%), very coarse pebble (8.7 ± 1.1%), boulder (10.5 ± 1.2%) and mixed substrates (12.2 ± 1.3%)] (Friedman tests, $p < .05$). There was no significant difference in visiting frequency on fine pebble and cobble substrates. In large group experiments, the average of visiting frequency on fine pebble (20.4 ± 1.4%) and cobble (18.8 ± 1.3%) were significantly higher than the others substrate types, which was cement (11.6 ± 1.1%), sand (12.7 ± 1.0%), coarse pebble (8.6 ± 1.0%), very coarse pebble (9.2 ± 1.0%), boulder (9.1 ± 1.1%) and mixed substrates (9.7 ± 1.0%) (Friedman tests, $p < .05$). There was no significant difference between the average percentage of visiting frequency on fine pebbles and cobbles. Note that, all the three group experiments showed a consistent result that the average percentage of visiting frequency on fine pebble (1–16 mm) and cobble (64–128 mm) were relatively higher than that on other substrate types (Friedman tests, $p < .05$) (Figure 7a).

The activity variations of singletons were different in each substrate type compartment. The percentage of lowly mobile time for *S. davidi* on the cement (14.3 ± 2.1%), fine pebble (10.6 ± 1.7%), cobble (25.7 ± 2.6%) and boulder (28.4 ± 2.7%) compartments were significantly higher than that on the others [i.e., sand (7.7 ± 1.1%), coarse pebble (4.9 ± 0.8%), very coarse pebble (3.5 ± 0.8%), mixed substrates (4.9 ± 0.7%)] (Friedman tests, $p < .05$). The percentage of mobile time for the species on the fine pebble (17.6 ± 2.2%) and cobble (38.5 ± 2.9%) compartments were significantly higher than for the other compartments [i.e., cement (10.2 ± 1.6%), sand (4.4 ± 0.8%), coarse pebble (6.7 ± 1.0%), very coarse pebble (5.2 ± 0.7%), boulder (11.3 ± 1.8%) and mixed substrates (6.0 ± 0.8%)] (Friedman tests, $p < .05$). The percentage of highly mobile time for the species in the cobble compartment (44.1 ± 2.2%) was significantly higher than that in the other compartments (i.e., cement (6.8 ± 1.2%), sand (4.8 ± 0.9%), fine pebble (16.7 ± 1.9%), coarse pebble (9.8 ± 1.1%), very coarse pebble (11.3 ± 1.1%), boulder (11.3 ± 1.3%) and mixed substrates (7.6 ± 0.8%) (Friedman tests, $p < .05$) (Figure 7b).

This movement velocity of fish in the singletons on the cement (5.0 ± 0.7 cm/s), sand (5.7 ± 1.0 cm/s), fine pebble (5.0 ± 0.5 cm/s), cobble (3.3 ± 0.6 cm/s) and boulder (2.0 ± 0.3 cm/s) compartments were significantly lower than that on the other compartments (coarse pebble: 6.9 ± 0.8 cm/s; very coarse pebble: 11.8 ± 1.1 cm/s; mixed substrates: 9.1 ± 1.1 cm/s) (Friedman tests, $p < .05$) (Figure 8). This movement distance on cobble (153.4 ± 19.6 m) and boulder (99.6 ± 18.9 m) compartments were significantly higher than in the other compartments (i.e., cement: 40.1 ± 10.4 m; sand: 54.4 ± 12.2 m; fine pebble 64.1 ± 7.9 m; coarse pebble: 52.2 ± 6.0 m; very coarse pebble: 64.7 ± 8.6 m; mixed substrates: 50.9 ± 6.4 m) (Friedman tests, $p < .05$).

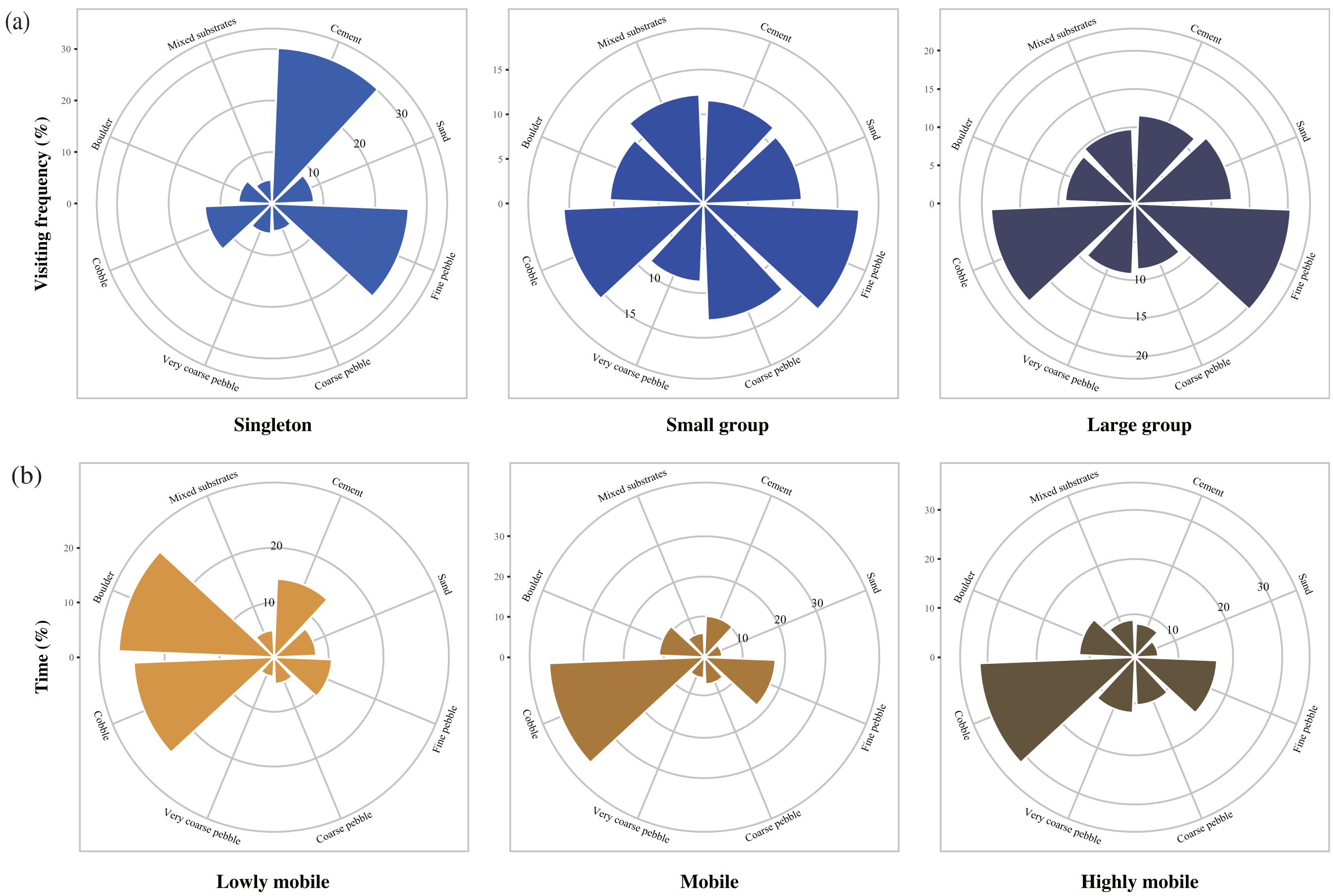

FIGURE 7 (a) Percentage of visiting frequency (mean) for different groups (singleton, small group and large group) of *Schizothorax davidi* on different substrate types (cement: 0 mm, sand: <1 mm, fine pebble: 1–16 mm, coarse pebble: 16–32 mm, very coarse pebble: 32–64 mm, cobble: 64–128 mm, boulder: >128 mm and mixed substrates: 0–160 mm) in circle substrate preference test aquarium in a laboratory experiment; (b) The percentage of time (mean) in different substrate types with different mobility state (lowly mobile, mobile and highly mobile) in circle substrate preference test aquarium in a laboratory experiment [Color figure can be viewed at wileyonlinelibrary.com]

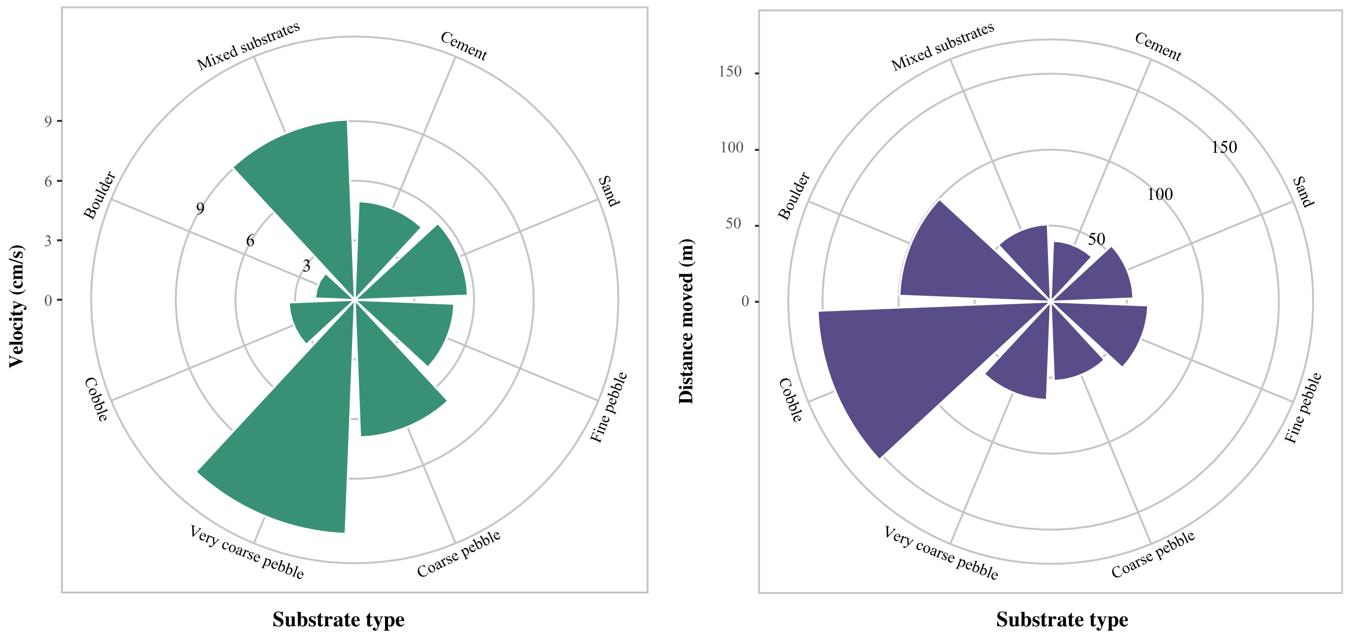

FIGURE 8 The movement velocity (mean) and the movement distance (mean) to each compartment (cement: 0 mm, sand: <1 mm, fine pebble: 1–16 mm, coarse pebble: 16–32 mm, very coarse pebble: 32–64 mm, cobble: 64–128 mm, boulder: >128 mm and mixed substrates: 0–160 mm) of singletons in circle substrate preference test aquarium in a laboratory experiment [Color figure can be viewed at wileyonlinelibrary.com]

4 | DISCUSSION

Migratory fish populations are declining due to dam-induced fragmentation of freshwater habitats. Fishways are intended to make barriers 'transparent' (i.e., allowing fish to move freely and unimpeded past barriers) but rarely achieve that goal (Castro-Santos et al., 2009). Low passage efficiency in fishways may be the result of unsuitable passage environments to facilitate migration (Bunt et al., 2012). We hypothesised that increases in fish passage success could be achieved by altering light colour at the entrance or within the fishway and the substrate type within the fishway. Previously it has been found that fish passage success for some species is influenced by light colour and substrate, as these variables can reduce transit time through a fishway (Mu et al., 2019). Moreover, we tested whether fish group size may interact with light colour and substrate types. Although group size has been widely studied in the context of fundamental behavioural ecology (Hoare et al., 2004), we are unaware of any empirical tests of the influence of group size on aspects of fish passage. We tested the preference of *S. davidi* for light colour and substrate type in a laboratory environment under flow conditions that were rather static. Although some research has shown that water velocity does not influence the light preference of fish (Xu et al., 2020), our results still have some limitations. Future studies should examine if the findings observed here can be generalised across more dynamic flow conditions.

In the present study, group size (from individual fish to large groups) tended to mediate the preference of fish for certain light conditions and substrate types. In this experiment, the preference for light colours and substrate types was influenced by group size. The singled *S. davidi* tended to visit the white light and blue light, while the grouped *S. davidi* were more likely to visit the blue light. Similarly, the singled *S. davidi* visit more frequency in cement, fine pebble and cobble, while the grouped *S. davidi* were more likely to visit the fine pebble and cobble. Specifically, the white light, and cement positively influenced attractivity but negatively influenced the level of inter-attraction between individuals. For instance, the isolated *Periplaneta americana* stay more frequency in vanillin-scented shelter, while animals in groups were more likely to select unscented shelters (Laurent Salazar et al., 2017). Individual and group decision-making yield different behaviours when facing novel environments. Singletons may experience greater uncertainty in a novel environment than fish in groups. Singletons must gather all of the information they need to make a decision for themselves without the social information from group neighbours (Ward et al., 2011). Fish have unique movement profiles when swimming alone, but this individuality disappears in groups as fish tend to coordinate their movement patterns with other group mates (Herbert-Read et al., 2013). The most likely reason for uniform behaviour was group conformity, which showed that an individual performs the same behaviour as most of its group neighbours. In nature, individual members often adapt their behaviour to align with that of the group (Stienessen & Parrish, 2013). Some studies showed that the benefits of shoaling increased for fish that joined larger groups and, indeed, it appeared that larger shoals were more attractive than smaller ones in group choice experiments (Herbert-Read et al., 2013). When fish make behavioural decisions, they often follow the member of the larger groups (Krause et al., 2010). Some research demonstrate that individuals may not show any of their asocial behavioural preferences in larger group sizes (Herbert-Read et al., 2013).

Singletons tended to have different behavioural responses dependent on the ambient light colour conditions. The time spent mobile, movement velocity and movement distance of fish in the red-light condition was higher than the others, and those in blue light was lowest. The photoreceptive cells of the fish retina could perceive the light and dark changes of the optical fibre and distinguish the colour of light such that the fish would have a preference or escape response to some light colours (Elvidge et al., 2019). *S. davidi* strongly preferred a blue light to red light. Light has been used to improve the reproduction and survival rates of fish for many years. For instance, some researches demonstrated the blue light could reduce the stress response and improve the reproduction in Nile tilapia *Oreochromis niloticus* (Maia & Volpato, 2016). In our test, *S. davidi* preferred the blue light, which may be related to the depth selection of the fish. As different wavelengths of light are reflected and absorbed by water, and with the increase of water depth, the red and yellow light waves disappear, leaving only blue light or green light waves that can reach the deeper waters (Bowmaker, 1995). *S. davidi* are benthic and may thus be adapted to environments with blue light. As such, blue light could be placed at the entrance of fish passage structures to attract fish. Given that the *S. davidi* avoided the red light, future studies could consider using red lights to repel fish from dangerous areas (e.g., turbine intakes) or push them towards desirable paths.

For the singletons in the substrate type test, the mobility time of *S. davidi* on the cobble was significantly higher than the others (cement, sand, fine pebble, coarse pebble, very coarse pebble, boulder and mixed substrates), while the cement and fine pebble were lower. Moreover, the velocity of *S. davidi* on the cement, fine pebble and cobble substrates was lower than the others and the distance on the cobble was higher than the others. Considering the contradictory results for cement and fine pebble, it may be that fish were interested in the novel substrate (different from holding tank) but were averse to spending long periods in these unfamiliar compartments. This phenomenon was similar with the sole *Solea senegalensis*, which liked to visit dark plastic but very little time in that compartment (Reig et al., 2010). In addition, the substrate type of the holding tank was cement. When the environment changes, fish may prefer to stay in familiar environments (cement) despite being suboptimal habitat (Jolles et al., 2017). The velocity of movement on the cobbles was lower than the others, while the time of mobility and the distance were longer. Cobbles can be optimal habitat for reproduction, predator avoidance, and feeding (Wu et al., 2020). Cobbles contained devices which provided ambush places for predators before attacking. For example, fish may be able to avoid longitudinal displacement by taking refuge behind substrate or by oral suction. *S. davidi* usually inhabit flowing water and cobbles that may provide lower water velocities and enable rest (Ding, 1994). The preference for cobble by *S. davidi* was presumably not only because of the need for shelter in a flowing current but also due to feeding on organisms that live on the substrate. Considering that the mobility time and move distance of fine pebble were short than cobble, fine pebble could be set within the fishway to increase the attraction rate and increase the migration speed.

While the preference of *S. davidi* on light and substrate were clear in this study, we must also consider how those patterns extend to other contexts. We revealed that *S. davidi* prefer blue light and fine pebble, which was tested in shallow water (30 cm depth) in the absence of flow. To further evaluate the effects of light and substrate on improving fishway attraction, future studies that involve placing LED lights on a fishway entrance and manipulating the substrate in a fishway should be conducted to determine their influence on passage efficiency of *S. davidi*. What is more, fish behaviour in the field can be influenced by many biotic (i.e., presence other conspecifics, predators) and abiotic (i.e., hydraulics, light, temperature, substrate, smell, noise) variables (Santos et al., 2014). As such, future work should examine how the above factors may affect fish pass efficiency.

5 | CONCLUSIONS

In the present study, group size affected fish preference for various light colours and substrate types. To our knowledge, this is one of the first studies to assess the influence of group size on fish passage, which is clearly an important aspect of fish passage science and facility design. Overall, *S. davidi* tended to prefer blue light, and fine pebble, knowledge that could be used to help guide this species during migration through fishways. Blue light could be placed at the entrance of fish passage structures to increase attraction of fishway. Fine pebble could be added to fish passage facilities to create a more 'nature-like' passage environment and encourage movement. We did not test light and substrate type on fish pass efficiency under dynamic hydraulic conditions. Therefore, there is need for additional field research to assess species- and assemblage-specific preferences for different light and substrate near or in fish passage facilities. Furthermore, it is important to consider that (a) the light intensity may have influenced fish preferences, and (b) the colours and shapes of different sizes of the substrate, which varied from a more homogeneous to a more heterogeneous substrate, may have influenced fish preferences. Thus, the relationships among light intensity and colours as well as the types of substrates on the preference response of fish require future study. Further, given the species-specific nature of light colour and substrate preferences, it will be important to take a multi-species approach to ensure that creating the optimal passage conditions for one species (e.g., *S. davidi*) does not decrease the passage success for other species. Indeed, much of the work to date has focused on hydraulic aspects of design (Silva et al., 2018) yet work on other aspects of fish passage design (i.e., light colour and substrate type) may be needed to better emulate natural environments.

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DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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