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Cobble substrate in a surface bypass reduces bypass acceptance by common roach *Rutilus rutilus*

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ABSTRACT

Historically, ecological engineered solutions for fish passage across anthropogenic barriers in rivers has mainly focused on facilitating upstream passage for long-migrating diadromous fish, such as salmonids. More recently, passage solutions have shifted their focus to a more holistic ecological perspective, allowing passage for species with different swimming capacity, both upstream and downstream. This experiment investigated whether the addition of cobble in the passageway of a surface bypass could facilitate downstream movement of a cyprinid fish, the common roach *Rutilus rutilus*. Surface bypasses were constructed in large experimental flumes and roach were released into the flumes and monitored for bypass passage using PIT-telemetry through 11-h night-trials. Behavior was scored using four continuously-recording video cameras at the bypass construction. There was a negative effect of substrate-treatment on the passage rate through the bypass. The majority of the fish in the *No substrate* treatment had successfully passed within 4 h, while a lesser proportion of the fish in the *Substrate* treatment had done so (additional fish in the latter treatment passed later in the trials). Fish exposed to cobble substrate in the bypass passageway showed more avoidance-like behaviors at the ramp section of the bypass and tended to return back upstream more often than the fish in the no-substrate control trials. When reaching the passageway, the substrate-exposed fish expressed no behaviors that could be indicative of reduced passage success, as compared to controls. We conclude that passage was not hindered by the presence of cobble substrate, but passage was delayed due to avoidance behavior at the bypass ramp when cobble substrate was present. Based on these results, the addition of cobble substrate in a surface bypass cannot be recommended as a measure to facilitate the downstream passage performance of the common roach through surface bypasses.

1. Introduction

A large and increasing number of the world's rivers are not free-flowing, having barriers that fragment the rivers and disrupt longitudinal connectivity (Grill et al., 2019; Belletti et al., 2020). Disrupted connectivity is one of the causes behind the decline of many freshwater fish populations, as it affects their longitudinal movements in rivers (Reidy Liermann et al., 2012; Reid et al., 2019; Barbarossa et al., 2020). Because many dams are used to generate society-sustaining services (e.g. water regulation and hydropower), one solution to this environmental problem is the construction of faunal passageways across the barriers.

Historically, ecological engineering of solutions for fish passage across artificial barriers has focused on facilitating upstream passage for long-migrating diadromous fish, such as salmonids. Hence, the engineered solutions have often been tailored to the capabilities of these species, frequently resulting in steep-sloping ‘fish-ladder’ designs that require strong swimming ability for successful passage (Katopodis et al., 2001). However, many other species, with a large range of swimming capacities, are also moving within rivers as part of their natural behavior (De Leeuw and Winter, 2008; Brönmark et al., 2014; Knott et al., 2020), and may be hindered by human-constructed barriers, even after fishways are installed. More recently, passage solutions have shifted their focus to a more holistic ecological perspective, allowing passage for both strong and weak swimming species. In addition, more focus has also been put on downstream migration (Larinier and Travade, 2002; Schilt, 2007; Calles and Greenberg, 2009; Calles et al., 2013), with solutions

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directed at preventing fish from passing through hydropower turbines, which would otherwise cause a variety of different kinds of injuries or even death (Algera et al., 2020). Lack of attraction to the passage entrance, disorientation, or direct avoidance behaviors have been noted as problems hindering or delaying downstream movement across barriers (Schilt, 2007; Ovidio et al., 2017; Knott et al., 2019). There are also indications that the choice of using a bypass instead of moving through the more risk-associated turbine flow depends on the behavioral phenotype of the individual fish, which means that bypasses could be agents of selection, possibly skewing the population towards certain phenotypes in the long term (Haraldstad et al., 2019). Allowing general dispersal also facilitates gene-flow within the catchment meta-population (Wilkes et al., 2019). It is widely recognized that many fish passage solutions do not work as efficiently as intended, due to e.g. environmental, structural, or behavioral factors (Roscoe and Hinch, 2010; McLaughlin et al., 2013; Birnie-Gauvin et al., 2019). Hence, there is a need to focus research resources on this topic to support evidence-based decisions in the development of environmentally sustainable hydropower production (Geist, 2021). Low-risk downstream passage can be facilitated in several ways, e.g. by constructing nature-like fishways mimicking natural streams, through spillway passage (depending on the spillway construction - spillway passage can be hazardous in several ways; Larinier, 2001), or by using surface bypasses where fish are guided away from the turbines into a bypass structure that leads the fish into the tailrace (Katopodis et al., 2001; Schilt, 2007).

Common roach *R. rutilus* (L.), a cyprinid native to most of Europe and western Asia, is an example of a small-bodied species (common length: 150–300 mm; max length: circa 500 mm; Kullander et al., 2012) that exhibits short-distance spawning migrations in spring, within river systems or between lakes and rivers (Vøllestad and L'Abée-Lund, 1987). They also show partial migration between lakes and rivers for feeding and predator avoidance during other times of the year (L'Abée-Lund and Vøllestad, 1987; Pavlov et al., 2002; Brönmark et al., 2008), with the tendency to migrate being associated with individual behavioral phenotypes (Chapman et al., 2011). In addition, the species shows a generally high activity in river mainstems, with movements covering several kilometers over a fortnight, and there are indications that cyprinids may be relatively free-ranging within river systems, rather than having specific home ranges (Linfield, 1985; Baade and Fredrich, 1998). Roach are not particularly weak swimmers compared to many other freshwater species (Pavlov, 1989; Tudorache et al., 2008), but do not reach the capacity of e.g. salmonids (Peake et al., 1997), for which fishways are often adapted. Roach are commonly encountered at dam bypasses (Knott et al., 2020) and are similar to many other cyprinid species in terms of morphological and ecological traits (Khaval, 1998; Skov et al., 2008), making the species a relevant model for investigating the efficiency of downstream passage.

Acceptance of bypasses by fish is a critical parameter for the efficiency of the bypass, and fish are often observed to hesitate when entering bypasses (Schwevers and Adam, 2020). However, information about how to increase bypass acceptance is currently scarce (Schwevers and Adam, 2020). Here, we compare the relative acceptance of two different bypass designs by roach, using a fish-guiding β-screen (i.e. an angled screen) connected to a surface bypass structure. In half of the trials, a cobble substrate panel was placed on the floor of the bypass passageway, whereas the remaining trials served as controls, without the addition of cobble panels. Cobble substrate was predicted to promote passage across the ramp by creating a more naturalistic and less stressful environment, and by providing sensory stimuli attracting and retaining the fish within the bypass structure, leading to efficient and successful passage. Cobble substrate panels also constitute a cheap and easy-to-implement modification of existing technical bypasses.

Bypass acceptance of roach was investigated by releasing groups of fish in an artificial flume, where the bypass structure was installed, and recording number of successful downstream passages in relation to substrate and local flow velocity conditions. Behavior of the roach at the bypass was recorded using continuous video monitoring.

2. Material and methods

2.1. Test species and husbandry

Common roach ($N = 140$; Fig. 1D) were caught in River Verkmyrån (60°46′02.7″N 17°16′11.8″E) on 5 May 2020, and transported to the Vattenfall Research and Development Laboratories, Älvkarleby, Sweden. Upon arrival, fish were split into 2 equal groups ($n \approx 70$), placed in two circular stainless-steel vats (3.5 m^3 each), where they stayed until experiments started. Each vat was equipped with a bead-filter, a UV-filter, a chiller, and diffused aeration using three large air stones. The vats were filled with filtered water from River Dalälven (pH = 6.4; KH < 3; NO_2 and NO_3 below detection limits), and the water temperature in the vats was kept at 11.0 ± 2.0 °C (mean ± range). The fish were not fed during the experimental period, but activity of roach is not markedly affected by starvation for at least 9 days (van Dijk et al., 2002). The water was changed as needed, based on visual inspection. Three days after arrival the fish were sedated with Benzocaine ($5\ \mathrm{mg} \cdot \mathrm{L}^{-1}$), measured, weighed, and tagged with 23-mm passive integrated transponders (PIT) tags (Oregon RFID, Portland, USA). The scalpel incision was made on the ventral side circa 1 cm to the left from the midline of the ventral surface and 2–3 cm in front of the anal opening, and the tags were inserted into the buccal cavity. No sutures were used, as this may increase mortality (Skov et al., 2005). The 23-mm PIT tags were assumed to have little to no influence on the experimental fish, as their body size was well above the similarly tagged roach in Skov et al., (2005), where no adverse effects were observed. All of the roach survived until the experimental trials started, and there was a period of at least one week between the PIT-tagging and trials. The roach averaged 267 mm (SD: 29.3 mm) in total length (Table 1).

2.2. Ethical note

The experiment was approved by the Ethical Committee for Animal Research in Gothenburg (License 001671; Dnr 5.8.18–03390/2019) and complied with current laws in Sweden and the European Directive 2010/63/EU.

2.3. Experimental design

Experiments were performed at the Laxeleratorn test facility at Vattenfall Research and Development, Älvkarleby, Sweden. Laxeleratorn is an experimental flume, here set up with two 24 m long, 4 m wide and 2 m deep parallel test sections (Fig. 1A). Flow of up to $2\ \mathrm{m} \cdot \mathrm{s}^{-1}$ is provided by four ejector pumps.

The flume was divided into upstream and downstream sections by net barriers (Fig. 1B). At the downstream section of the flume, the net barrier led to an upward ramp and a passageway. This net barrier represented a guiding β-screen (β-angle: 30°) and was made of a 1-cm mesh-size nylon net attached to a removable, 6.8 m long and 2 m high steel frame. The “start-box” was a steel box placed near the surface at the upstream end of the flume. One PIT-tag reader (Oregon RFID, Portland, USA) was placed at the opening of the start box, and one was placed at the end of the passageway leading to a collection box (Fig. 1B).

Downstream migration was tested using 12 groups of 10 fish. For 6 groups, the bypass passageway was equipped with a 60 × 150 cm steel frame, filled with cobbles, ranging up to 15 cm in diameter (‘*Substrate*’ treatment; Fig. 1C). For the other 6 groups, the passageway was devoid of any structures (‘*No substrate*’ treatment). Two groups of fish were run simultaneously (one of each treatment) in the two flume channels, with substrate treatment being switched between the channels after every two trial runs. Current velocity was kept at ~0.5 m/s in all trials.

The trials were filmed with five underwater cameras (GoPro Hero 6; GoPro Inc., San Mateo, USA). The cameras were placed at: i) the upper

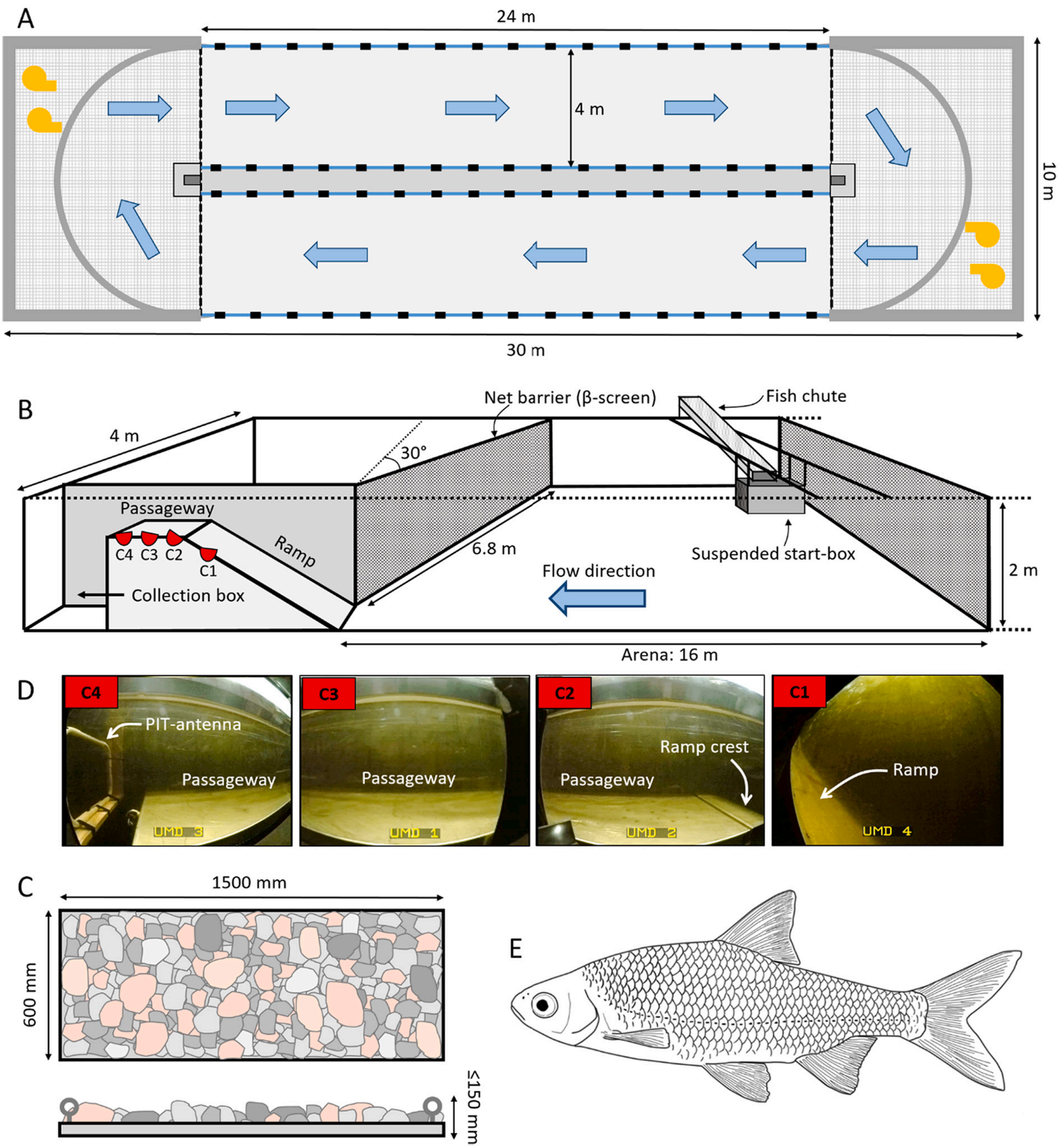

Fig. 1. Overview of the experimental flume, arena and treatment. A) Top view and dimensions of the experimental flume. Arrows show flow direction; yellow symbols represent the ejector pumps. B) Side view perspective of the experimental arena (note that the length of the arena is not drawn to scale). C) Design of the gravel bed treatment, which was placed in the passageway. D) Screen shots from cameras C1-4 (see B for placement). E) Illustration of a roach *Rutilus rutilus*. Figure published under CC-0 license; source: doi:https://doi.org/10.6084/m9.figshare.14672676. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

section of the ramp (C1), ii) the crest at the transition between the ramp and the passageway (C2), iii) the center of the passageway (C3), iv) the end of the passageway by the PIT-tag reader (C4), and v) at the start-box (C5) (cameras C1-4 depicted in Fig. 1B and D). Camera-based observations can be biased under certain conditions, particularly in field studies where e.g. flow and turbidity changes rapidly (Egg et al., 2018). Here, the conditions were relatively stable, and the body size of the subject fish was large enough for good detectability. Nevertheless, recordings are not perfect (e.g. due to dead angles for camera C1; Fig. 1D) and, hence, the estimation of passage efficiency is based on PIT-tag detections while camera recordings are primarily used as a system for direct observations of potential behavioral effects (see list of recorded behaviors in Table 2). However, it was possible to use the filmed material to verify the PIT-tag readings at the antennas, so the combination of PIT-telemetry and camera recordings are complementary.

2.4. Experimental procedures

Experiments were performed every night, from 10 to 15 May 2020. A night schedule was implemented as earlier literature indicated that roach predominantly migrate at night (e.g. Hammer et al., 1994; Baade and Fredrich, 1998), in line with the general pattern for fish (Jonsson, 1991). Two trials were performed each night, one in each of the flume channels. Trials started between 16:34 and 19:57; this variation

Table 1
Body size of the roach individuals used in the bypass acceptance experiment.

	Mean	Median	SD	Min	Max
All experimental fish (N = 120)					
Total length (mm)*	267	265	29.3	204	335
Body height (mm)	67	67	9.2	49	89
Wet body mass (g)	233	217	83.3	93.6	472
Substrate treatment (N = 60)					
Total length (mm)*	269	267	32.3	204	335
Body height (mm)	68	68	10	49	89
Wet body mass (g)	237	216	91.0	93.6	472
No substrate treatment (N = 60)					
Total length (mm)*	266	264	26.2	211	322
Body height (mm)	67	67	8.5	49	81
Wet body mass (g)	229	220	75.3	101	404

* Total length with closed caudal fin.

Table 2
List of behavioral events logged from videos recorded by cameras in the bypass during the experimental trials.

Behavior	Event	Data type	Values
Entry orientation	Entering frame	Binomial	Head first; Tail first
Exit orientation	Exiting frame	Binomial	Head first; Tail first
Turns	While in frame	Count	Turning (change in body orientation; head facing towards/against the current)
Directional change	While in frame	Count	Downstream; Upstream
Obs. duration	From entering frame to exiting frame	Duration	Time spent in view of camera/−s. Used as a proxy for residence time in the different parts of the bypass.
Exit direction	Exiting frame	Binomial	Downstream; Upstream

depended on logistical factors. Trials were run in a constant simulated moonlight environment (circa 2.6 lx; eight 100 W 9000 lm LED-lights over each flume, controlled by an ELG-100 dimmable LED driver; Mean Well Enterprises Co., Ltd., New Taipei City, Taiwan). The cameras were switched on prior to the start of the trial, a group of 10 fish were then transferred to the start-box, and left to acclimate for 10 min. After acclimation, the start-box was opened and the fish could freely enter the flume arena to start their downstream migration towards the bypass. The experiments terminated eleven hours later, at which point cameras were switched off, and the video and PIT-reader data were downloaded. The fish were caught after each trial, and released into new circular stainless-steel vats (same as those described above). When experiments were completed, fish were transported to their native river and released just downstream of their initial catch location.

2.5. *Data analysis*

All statistical analyses were conducted in R (R Core Team, 2020) using RStudio (RStudio, Inc., Boston). Data handling and graphics were done using the *tidyverse* suite of R packages (Wickham et al., 2019).

2.5.1. *Downstream passage*

Survival (time-to-event) analysis was performed to investigate differences in passage hazards (probability of entering the collection box during the eleven-hour experimental period) between the substrate and no substrate treatments. We used proportional hazard Cox models in the R package *survival* (Therneau, 2020). The passage time was defined as the time between leaving the start-box and entering the collection box (data from the PIT-antennas). Individuals that left the start-box but did not pass the collection box PIT antenna were right-censored based on the time they spent outside of the start-box. Individuals not leaving the start-box were removed from the data, as they did not have the chance to enter the bypass. We included substrate treatment as the main predictor of interest, and trial as a random variable (specified as a cluster in the Cox model), thereby accounting for non-independence of observations from the same trial. To allow for potential influence of body size, we initially ran separate models including the covariates length, mass, and height (with and without interaction terms including treatment), with an a priori decision to use the model with the best model fit, as assessed by Akaike Information Criterion (AIC). The final model of choice with the lowest AIC value was a model containing substrate treatment as the only predictor and trial as a random effect (see Supplemental information, Table S1 and Fig. S1). Due to failure of PIT antennas in four trials (two for each treatment), only four trials for each treatment were included in the analysis. As a result, each treatments was overrepresented in either one or the other flume channel (ratio 3:1 for each treatment), which prohibited robust analysis of potential effects of the individual flume channels on the results. The channel effect was therefore investigated graphically, and since no clear pattern emerged, we assume no effects (supplement: Fig. S2).

To evaluate the final model, we plotted the logarithm of the cumulative hazard function in each substrate treatment against the logarithm of time, to investigate the assumption that the hazard ratio is constant over time (proportionality of hazards) (Bradburn et al., 2003). We also ran scaled Schoenfeld goodness of fit tests (Grambsch and Therneau, 1994), and graphed goodness of fit plots using the R package *survminer* (Kassambara et al., 2017). None of these analyses indicated any major violation of the proportionality of hazards assumption, although the goodness-of-fit test was close to significant ($\chi^2 = 3.78, p = 0.052$), which warrants some caution in interpretations with respect to the model parameter estimate values.

Pearson correlation was used to investigate if there was a correlation between the time elapsed from the start of the trial to when the fish left the start-box and passage time.

2.5.2. *Behavior in the bypass*

Recorded videos from four cameras in the bypass were used for behavioral analysis. One camera (C1) focused on the upper section of the ramp and three cameras were placed along the passageway (C2–C4) (Fig. 1B,D). Scoring of behavior was done using the event-logging software BORIS v7.9.19 (Friard and Gamba, 2016). We analyzed six different behavioral variables (Table 2). Each time a fish entered into the view of the cameras a new observation was registered and the behavior was tracked until the fish exited the camera view, i.e. one observation consisted of all behaviors of a single fish from the time it was detected by the camera until it could not be detected anymore (henceforth, this observation time-frame is termed ‘observation duration’). The three cameras in the passageway were scored together, with videos synchronized in time, in effect constituting one camera unit in the subsequent analyses. Camera C1 was oriented so that it filmed the area near the floor of the upper part of the ramp, and could therefore not detect fish swimming close to the surface (Fig. 1D). Hence, the number of observations are sometimes lower for camera C1 than for cameras C2–C4.

Since fish were not visually identifiable or hindered from returning to the arena after passing through the bypass, observations within a treatment:trial-round combination contain non-independent data (several observations can be from the same individual). As a consequence, data are analyzed under the assumption that individual observations represent events as they would play out in a larger statistical population where each observation is independent. To mitigate effects of non-independence, e.g. changed behavior in individuals with prior experience of passing through the bypass, the observations in each treatment:trial-round combination were divided into three observation groups for each trial. The first observation group (G1) contained the first 30 observations where fish enter the camera view from upstream, the second observation group (G2) contained the next 30 observations, and a third observation group (G3) contained the rest of the observations. G1 is thereby likely to contain the highest proportion of unexperienced fish, even if some are certainly included when the number of observations exceed $N = 10$. Analyses focus on G1 and G2, and data from G3 are only presented and interpreted graphically (see Electronic supplement). Observations where fish enter the camera view from downstream direction were excluded from analyses, as these are less relevant from the bypass behavior perspective. A few trials had to be excluded from the analyses due to PIT-antenna or camera failure (Table 3).

Statistical analyses were conducted using Generalized Linear Mixed Models (GLMM) within the *lme4* (models; Bates et al., 2020) and *emmeans* (marginal means; Lenth, 2021) R-packages. Binomial, count, and duration data were analyzed using binomial (logit-link), negative binomial (log-link), and Gaussian (identity-link) GLMMs, respectively. Initial full models and explanation of model terms are presented in *lme4*-syntax (Table 4). Subsequent model reduction was performed if either the interaction between *Treatment* and *Obs.group* (i.e. binned observations) or the covariate *Duration* (representing observation duration) were non-significant ($p < 0.1$).

2.5.3. *Bypass flow characteristics*

Flow characteristics in the bypass were measured using Acoustic Doppler velocimetry (‘ADV’; Vectrino 3D Fixed Stem G.A., Nortek AS, Rud, Norway). Measurements were taken longitudinally at the transition between the ramp and the passageway (referred to as the reference point), 30 cm upstream the reference point in the ramp, and 60 cm and 90 cm downstream of the reference point (i.e. over the substrate panels, if present). At each longitudinal point, measurements were taken 10, 30, and 50 cm from the outer (left-side) wall, at 10 and 20 cm depth (i.e. in total 24 measurement points; see Fig. S9).

Data were processed in MATLAB (version R2020b; MathWorks, Natick, MA) to filter poor data points based on signal to noise ratio as recommended in the manual for the ADV equipment (Nortek, 2018). These velocities were then averaged and used to calculate the turbulence kinetic energy (TKE); the formula is presented below with u', v', and w' being the standard deviation of the velocities in the x, y, and z direction (Pope, 2000):

$$\mathrm{TKE} = \frac{1}{2}\left(\overline{(u')^2} + \overline{(v')^2} + \overline{(w')^2}\right)$$

The average velocities and TKE for all measuring points (Supplementary Fig. S9) are illustrated in Supplementary Figs. S10–S13.

Table 3
Recorded time (decimal hours, h), scored time (decimal hours, h) and recorded observations (number, #), based on the *Ramp* and *Passageway* cameras (fish with *Entry direction* = downstream removed) in each trial for the two treatments (*No substrate* and *Substrate*). Behavioral scoring was terminated after 11 h of recording or when all fish successfully passed the collection box PIT antenna (only Trial 3; No substrate). Scored time indicates the time between trial start and last observation made, and can be less than 11 h if no fish were detected after a certain time point (the full 11 h were still watched).

Trial	Treatment	Recorded time (h)	Scored time (h)	Obs. *Ramp* (#)	Obs. *Passageway* (#)
1	No substrate	Equipment failure	NA	NA	NA
2	No substrate	11.05	9.62	5	10
3	No substrate	10.44	1.21	18	18
4	No substrate	12.17	11.00	21	24
5	No substrate	13.31	5.96	62	160
6	No substrate	Equipment failure	NA	NA	NA
1	Substrate	Equipment failure	NA	NA	NA
2	Substrate	11.06	10.39	67	54
3	Substrate	11.61	9.72	107	140
4	Substrate	Equipment failure	NA	NA	NA
5	Substrate	13.34	11.00	247	217
6	Substrate	2.52	2.39	31	30

Table 4
Description of the full generalized linear mixed models (lme4 model syntax; Bates et al., 2020) used for analyses of roach behavior in the bypass. Presence of interaction terms (i.e. ‘*treatment* × *obs.group*’) implicitly indicate that the main effects of the factors are also included in the model.

Response variable	Model	Family (link-function)
Entry orientation	$\sim$ *treatment* × *obs.group* + (1|*trial*)	Binomial (logit)
Exit orientation*	$\sim$ *treatment* × *obs.group* + (1|*trial*)	Binomial (logit)
Turns	$\sim$ *duration* + *treatment* × *obs.group* + *exit* + (1|*trial*)	Negative binomial (log)
Directional change	$\sim$ *duration* + *treatment* × *obs.group* + *exit* + (1|*trial*)	Negative binomial (log)
Obs. duration ($\log_{10}$)	$\sim$ *treatment* × *obs.group* + *exit* + (1|*trial*)	Gaussian (identity)
Exit direction	$\sim$ *treatment* × *obs.group* + (1|*trial*)	Binomial (logit)

Independent variables: *treatment*: fixed, two levels (No substrate; substrate); *obs. group*: fixed, two levels (G1: Obs. 1–30; G2: Obs. 31–60); *time*: covariate, continuous (observation duration in seconds); *exit*: fixed, 2 levels (exit camera view – US: upstream towards arena; DS: downstream towards collection box); (1|*trial*): random intercept, five levels (Trial 2 to 6).

* Data where fish exit towards the arena excluded (100% exit with head towards the arena).

3. Results

3.1. *Downstream passage*

There was a significant effect of treatment on passage hazard ($N_{\mathrm{observations}} = 79$, $N_{\mathrm{events}} = 68$, hazard ratio = 0.33, $z = -6.80$, $p < 0.001$, Fig. 2A). This result (i.e. a significant hazard ratio < 1) indicates that roach in the *Substrate* treatment had a lower chance of entering the collection box per time unit, as compared to roach in the *No substrate* treatment (*No substrate* – median: 88.6 min, inter-quartile range: 72.1–134.1 min; *Substrate* – median: 210.9 min, inter-quartile range: 140.1–609.4 min; Fig. 2).

Time to exit the start-box was very short on average and similar between the treatment groups (*Substrate*: median = 0.7 min, range = 0.1 to 510 min; *No substrate*: median = 0.7 min, range = 0.1 to 188 min). There was no significant correlation of time between start-box emergence time and passage time ($|t| = 1.09$, df = 69, $r = -0.14$, $p = 0.22$).

3.2. *Behavior in the bypass*

3.2.1. *Model reductions*

Seven out of twelve models were reduced (Table 5). In all cases the AIC-values were lower for the reduced models (Supplementary Table S2). Analysis of deviance (ANODEV) results from the final models are presented in Table 5; ANODEV results for initial full models, and summary tables with parameter estimates for reduced models are found in S3 and S4, respectively.

3.2.2. *Entry orientation*

Accounting for observation group and trial effects, the average estimates of entering head-downstream at the ramp were similar between the treatments [*No substrate*: 59% (95% CI: 50–85%); *Substrate*: 63% (95% CI: 44–79%); Fig. 3A], but for the passageway the estimates deviate more, albeit non-significantly [*No substrate*: 28% (95% CI: 17–42%); *Substrate*: 19% (95% CI: 12–30%); Fig. 3A]. No effects of substrate treatment were detected for this behavioral variable ($p > 0.1$; Table 5 and Supplementary Table S4A–B), but an effect of observation

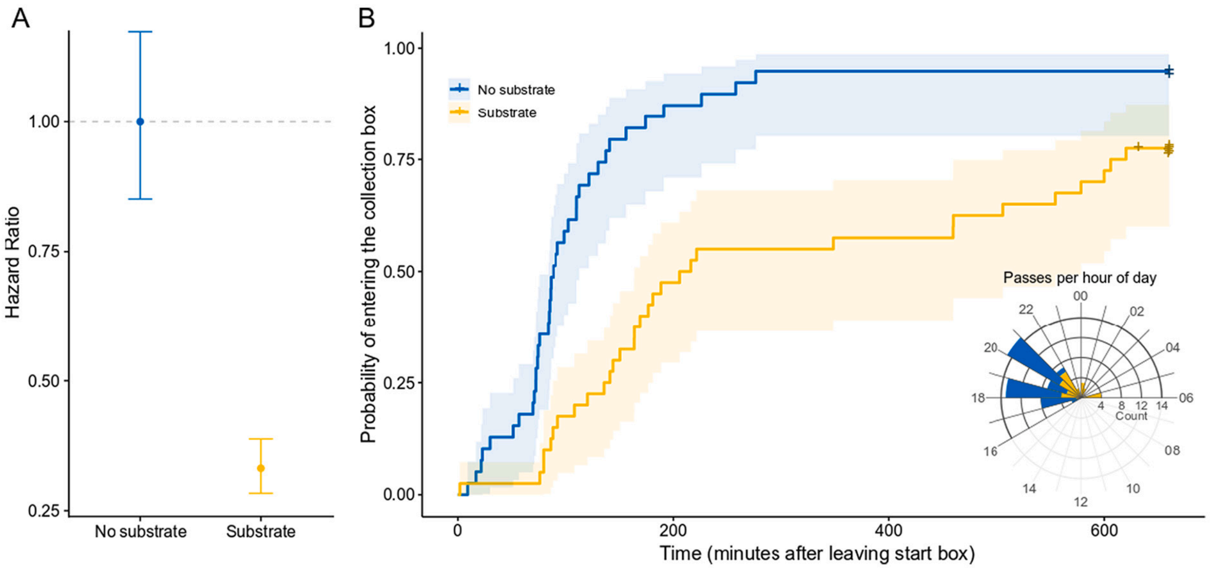

Fig. 2. Analyses of time to successful downstream passage (passing the bypass PIT antenna). A) Hazard ratio ± 95% confidence interval of entering the collection box in the substrate treatment in comparison to the no substrate treatment. B) Reversed survival curves with 95% confidence intervals showing probability of entering the collection box as a function of time in no substrate treatment (blue) and substrate treatment (yellow). Inlay shows passes per hour of day (but note that starting time differed among trials). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

group (G1 vs. G2) was seen in the ramp area, with observations 31 to 60 (G2) having 26% more individuals entering head-downstream than observations 1 to 30 (G1) (Fig. 3A). For the remainder of the observations (>60; not analyzed), this pattern is even more pronounced (illustrated graphically, Supplementary Fig. S3).

3.2.3. Exit orientation

All fish that left the camera view in an upstream direction did so with their heads facing upstream (positive rheotaxis; Supplementary Fig. S4), both at the ramp and in the passageway, which is a natural orientation for swimming directionally upstream (and hence not analyzed further). For exits in the downstream direction, no effects of substrate treatment or observation group on orientation were detected at the passageway (Table 5 and Supplementary Table S4), but model-based estimates of fish exiting head-downstream were generally very low [*No substrate*: 4% (95% CI: 1–15%); *Substrate*: 3% (95% CI: 1–7%); Fig. 3B]. At the ramp, the picture was more complex, with a significant interaction effect between treatment and observation group ($p = 0.028$; Table 5 and Supplementary Table S4). Observation group G2 had a higher proportion of individuals exiting with their head pointed downstream than observation group G1 in the *No substrate* treatment [*G1*: 18% (95% CI: 4–54%); *G2*: 65% (95% CI: 26–91%)], while no differences could be detected for the *Substrate* treatment [*G1*: 30% (95% CI: 9–66%); *G2*: 38% (95% CI: 12–73%)] (Fig. 3B). A lower proportion of exits with the fish facing the upstream direction can be seen for the remainder of the observations (observations >60; illustrated graphically in Supplementary Fig. S4).

3.2.4. Turns

Few turns were generally noted during observations (Supplementary Fig. S5) and appeared independent of individual observation durations (initial models: $p > 0.2$; Supplementary Table S3), suggesting that turns were not just randomly performed by the fish. In the ramp area, an interaction between treatment and observation group was detected ($p = 0.009$; Table 5), with the average number of turns being markedly higher in the *Substrate* treatment than in the *No substrate* treatment in G2, but less so in G1 [*No Substrate*:*G1*: 0.31 (95% CI: 0.21–0.48); *Substrate*:*G1*: 0.49 (95% CI: 0.37–0.65); *No Substrate*:*G2*: 0.13 (95% CI: 0.05–0.31); *Substrate*:*G2*: 0.71 (95% CI: 0.53–0.96)] (Fig. 3C; Supplementary Table S4E). The number of turns was also higher on average in the *Substrate* treatment (Supplementary Table S4E, Fig. 3C), but the estimated difference was not significant ($p = 0.067$; Table 5). In the passageway, all model terms except the intercept were non-significant ($p > 0.1$; Table 5) and while point estimates of average number of turns differed between treatments, the confidence intervals were largely overlapping [*No substrate*: 0.29 (95% CI: 0.18–0.49); *Substrate*: 0.40 (95% CI: 0.26–0.63); Fig. 3C].

3.2.5. Directional changes

The number of directional changes in swimming was strongly positively dependent on observation duration, both at the ramp and in the passageway ($p < 0.001$; Table 5, Supplementary Table S4G–H). Observation group had a significant influence at the ramp, with number of direction changes per second being lower in G2 than in G1 ($p = 0.009$; Table 5; Supplementary Fig. S6). Whether the fish exited upstream or downstream predicted the directional change in the passageway, with fish exiting upstream (towards the arena) changing direction more often ($p < 0.001$; Table 5). The general pattern related to exit direction was similar at the ramp, but non-significant (Table 5; Supplementary Fig. S6). No significant effects of treatment were detected, but at the ramp the *p*-value was 0.052, with the *Substrate* treatment having a slightly higher point estimates for number of directional changes (Table 5; Fig. 3D). Point estimates for number of changes at the mean observation duration were slightly higher for the *Substrate* treatment than for the *No substrate* treatment at the ramp [*No substrate*: 0.59 (95% CI: 0.44–0.80); *Substrate*: 0.79 (95% CI: 0.67–0.94)], but at the passageway they were very similar [*No substrate*: 0.95 (95% CI: 0.69–1.32); *Substrate*: 0.91 (95% CI: 0.68–1.22)]. Point estimates should not be compared between ramp and passageway as mean observation durations differ.

3.2.6. Observation duration

Duration of individual observations (from entering to exiting camera view; proxy for residence time in a given section of the bypass) was significantly predicted by exit direction (Table 5; Fig. 3E). At the ramp, fish exiting downstream (DS; towards collection box) had longer average observation duration than fish exiting upstream (US; towards the arena) [US: 6.1 s (95% CI: 4.1–9.1 s); DS: 3.9 s (95% CI: 2.6–5.8 s)]. The pattern was consistent for both treatments (Supplementary Fig. S7). In the passageway, the general pattern was the opposite [US: 8.5 s (95% CI: 7.0–10.2 s); DS: 12.9 s (95% CI: 10.8–15.3 s)] (Fig. 3E). However, at the passageway, the general pattern was not as clear looking at raw data

Table 5

Analysis of deviance tables for final reduced models used in behavioral analyses of roach in the bypass, based on type III Wald χ^2 tests. For comparisons of model fit (AIC) between reduced and full models, see Supplementary Table S3. Statistically significant terms ($p < 0.05$) indicated with bold text.

	Ramp		Passageway	
Model terms	χ^2	p	χ^2	p
Entry orientation				
intercept	1.411	0.235	8.372	**0.004**
treatment	1.238	0.266	2.122	0.145
obs. group	7.2144	**0.007**	<0.001	0.986
treatment × obs. group	–	–	–	–
Exit orientation				
intercept	3.185	0.074	16.753	**<0.001**
treatment	0.953	0.329	0.164	0.686
obs. group	9.726	**0.002**	2.174	0.140
treatment × obs. group	4.827	**0.028**	–	–
Turns				
intercept	22.011	**<0.001**	26.599	**<0.001**
duration	–	–	–	–
exit	0.274	0.601	2.544	0.111
treatment	3.366	0.067	1.378	0.241
obs. group	3.781	0.052	0.032	0.857
treatment × obs. group	6.806	**0.009**	–	–
Directional changes				
intercept	14.464	**<0.001**	3.140	0.076
duration	148.893	**<0.001**	240.434	**<0.001**
exit	2.006	0.157	57.741	**<0.001**
treatment	3.776	0.052	0.088	0.767
obs. group	6.832	**0.009**	0.902	0.342
treatment × obs. group	–	–	–	–
Obs. duration				
intercept	113.363	**<0.001**	476.656	**<0.001**
exit	16.868	**<0.001**	20.361	**<0.001**
treatment	0.008	0.928	0.579	0.447
obs. group	23.785	**<0.001**	3.706	0.054
treatment × obs. group	17.434	**<0.001**	5.204	**0.023**
Exit direction				
intercept	28.524	**<0.001**	0.386	0.534
treatment	12.685	**<0.001**	4.617	**0.032**
obs. group	0.053	0.818	1.808	0.179
treatment × obs. group	6.062	**0.014**	11.880	**<0.001**

(Supplementary Fig. S7). The a priori specified model did not include exit direction in the interactions. Hence, a post-hoc model was constructed including an exit direction × treatment interaction term, which was found to be significant ($\chi^2 = 11.6$, $p < 0.001$; Supplementary Table S5). The effect seen in the simpler a priori model was retained for the *Substrate* treatment, but no differences could be demonstrated for *No substrate* treatment. The new model affected *p*-values of other terms but only marginally affected the treatment × observation group interaction (Supplementary Table S5). Since this is the main term of interest, we retain the original model as representing the results here.

At both the ramp and the passageway, observation duration was predicted by the treatment × observation group interaction terms (Table 5; Fig. 3E). In both cases, no effects were detected in the first observation group, as indicated by largely overlapping confidence intervals [Ramp:G1 – *No substrate*: 6.0 s (95% CI: 4.0–9.0 s); *Substrate*: 6.1 s (95% CI: 4.1–9.1 s); Passageway:G1 – *No substrate*: 9.6 s (95% CI: 8.0–11.5 s); *Substrate*: 10.4 s (95% CI: 8.9–12.2 s); Fig. 3E]. For the second observation group, the *Substrate* treatment had longer average observation duration at the ramp, and the *No substrate* treatment had longer average observation duration at the passageway [Ramp:G2 – *No substrate*: 2.5 s (95% CI: 1.6–3.9 s); *Substrate*: 6.2 s (95% CI: 4.1–9.3 s); Passageway:G2 – *No substrate*: 13.1 s (95% CI: 9.3–18.3 s); *Substrate*: 9.1 (95% CI: 7.4–11.1 s); Fig. 3E].

3.2.7. Exit direction

At the ramp, the majority of the fish exited downstream, towards the collection box. The *Substrate* treatment had lower predicted probability to exit downstream in the first observation group than other observation group:treatment combinations (G1; significant interaction effect: $p = 0.014$; Table 5) [G1 – *No substrate*: 85% (95% CI: 75–92%); *Substrate*: 60% (95% CI: 51–68%); G2 – *No substrate*: 83% (95% CI: 66–93%); *Substrate*: 88% (95% CI: 80–93%); Fig. 3F, S8, Supplementary Table S4K]. In the passageway, the overall pattern is different, with the majority of fish in the *Substrate* treatment swimming downstream (71%), while the majority of the fish in the *No substrate* treatment swam upstream (38% downstream). Based on the models, a similar pattern was detected in the second observation group (G2), but not in the first (G1) (significant interaction term: $p < 0.001$; Table 5) [G1 – *No substrate*: 43% (95% CI: 25–64%); *Substrate*: 62% (95% CI: 42–79%); G2 – *No substrate*: 27% (95% CI: 10–55%); *Substrate*: 90% (95% CI: 76–96%); Fig. 3F, Supplementary Table S4L].

3.3. Bypass flow characteristics

ADV-data indicate accelerating flow velocity from the crest to the last measuring point in the passageway (Table 6; Supplementary Figs. S9–S13). The *Substrate* treatment has a slightly lower velocity than the *No substrate* treatment at the end of the ramp and the crest, but higher velocity through the passageway, indicating a higher flow acceleration through the bypass (Table 6). Turbulence in the *Substrate* treatment was lower at the end of the ramp, as compared to the *No substrate* treatment, but increased to similar or higher levels at the crest and passageway (Table 6). The very high value in the upper section at cross-section 3 for the *Substrate* treatment could to be an outlier data point, as data from other velocity settings in the same flume do not indicate the same effect (data not presented here).

4. Discussion

4.1. Prolonged downstream passage time with substrate

This experiment investigated whether addition of a cobble substrate panel in the passageway of a surface bypass could facilitate downstream movement of common roach through the bypass. Contrary to our predictions, we found that the substrate panels did not facilitate downstream passage; instead, the presence of substrate prolonged the passage time.

The time-to-event analysis (Cox regression) indicated that roach in the *Substrate* treatment were less likely to enter the collection box than conspecifics subjected to the *No substrate* treatment within the 11-h trials. However, a substantial number did successfully pass through the bypass and, overall, the cobble substrate panels seem to delay passage rather than hindering it, since individuals continue to pass the bypass throughout the trial. Median passage time with added cobble substrate was more than twice as long as when cobbles were absent. Consequently, there is no evidence for cobble substrate panels improving passage rate or success for roach.

Water flow and temperature are two factors not investigated here which may affect behavior of migration (Jonsson, 1991). For logistical reasons, we used a single velocity across all trials and the temperature range was narrow. Any interactive effects between flow or temperature and cobble substrate presence are therefore unknown.

4.2. Timing of the passage

The fact that few individuals moved immediately downstream after start-box emergence, suggests that fish were actively moving through the bypass, and not swept along with the current. In general, the majority of the passage through the bypass occurred within 4 h after the fish emerged from the start-box. Fish in the *No substrate* treatment had a

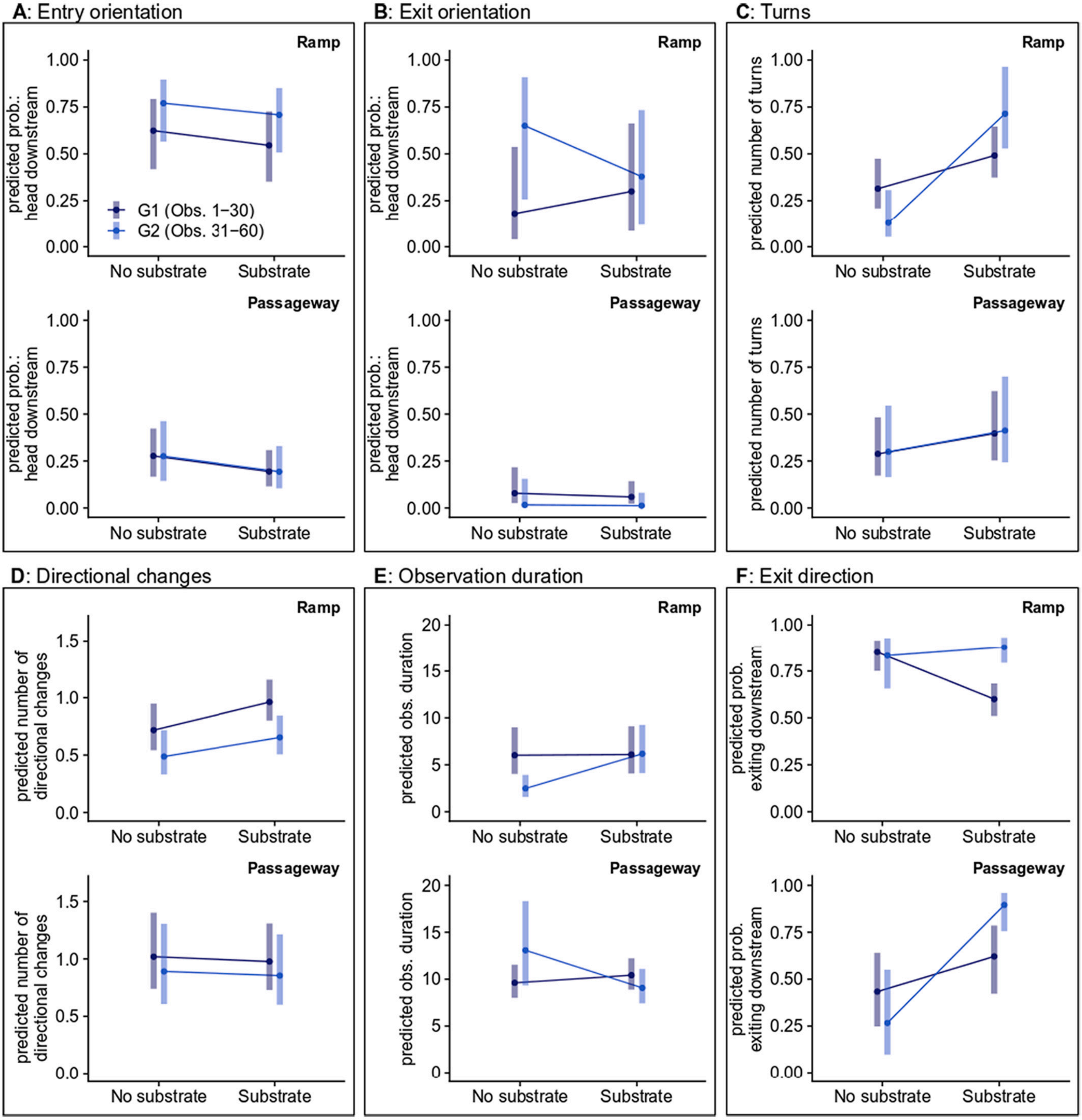

Fig. 3. Estimates of behavioral variables recorded in the ramp and passageway, with or without the presence of a substrate panel in the passageway. A) Probability of orienting with head facing downstream when entering the camera view. B) Probability of orienting with head facing downstream when exiting camera view in downstream direction. C) Number of turns per observation. D) Number of directional changes for an average observation duration. E) Observation duration in seconds (i.e. time in camera view). F) Probability of exiting camera view in a downstream direction. Dots show average estimates and bars indicate the 95% confidence interval of the average for observation groups G1 (obs. 1–30; dark blue) and G2 (obs. 31–60; light blue), see legend in A. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

substantially higher passage rate in the first 2 h as compared to the fish in the *Substrate* treatment. For the *Substrate* treatment, a period of relative inactivity in downstream movements were seen after circa 4 h, and the passage rate at the PIT-antenna in the bypass did not increase again until a couple of hours later (mainly in the morning hours). Given that most individuals emerged from the start-box soon after it was opened, this pattern suggests that the movement could be associated to the circadian rhythm of the roach, with the main activity peak associated to the period between dusk and midnight and, to a lesser extent, dawn (Hammer et al., 1994; van Dijk et al., 2002). However, a recent report of roach catches in direct association with use of bypasses indicates that the downstream passage occurs during both day and night, at relatively similar frequencies (Knott et al., 2020). Whether the bypass behavior of roach in the context of the present study depends on light or the circadian rhythm of the roach remains unknown.

Table 6
Mean velocity and mean turbulence kinetic energy (TKE) as estimated by acoustic Doppler velocimetry, taken 300 mm from the outer wall of the bypass. Comparisons (%) indicate whether the *Substrate* treatment has higher (>100%), lower (<100%) or equal (=100%) values to the *No substrate* treatment. Measurement points (cross-sections of the bypass; C-S) in the bypass are visualized in Fig. S9; C-S 1 is the upstream-most cross-section, just before the ramp crest; C-S 2, C-S 3 and C-S 4 are located in the upstream-, center- and downstream parts of the passageway, respectively.

Velocity ($m \cdot s^{-1}$)	C-S 4	C-S 3	C-S 2	C-S 1
No substrate (upper)	0.4850	0.4892	0.4772	0.3865
No substrate (lower)	0.5075	0.5091	0.5223	0.4184
Substrate (upper)	0.5608	0.5599	0.4703	0.3745
Substrate (lower)	0.5830	0.5943	0.5089	0.4094
Comparison (*Sub./No sub.*, upper), %	115.62%	114.45%	98.55%	96.91%
Comparison (*Sub./No sub.*, lower), %	114.89%	116.74%	97.43%	97.86%
Turbulence (TKE; $m^2 \cdot s^{-2}$)	**C-S 4**	**C-S 3**	**C-S 2**	**C-S 1**
No substrate (upper)	0.0053	0.0052	0.0055	0.0057
No substrate (lower)	0.0055	0.0057	0.0064	0.0061
Substrate (upper)	0.0059	0.0080	0.0059	0.0053
Substrate (lower)	0.0064	0.0055	0.0065	0.0057
Comparison (*Sub./No sub.*, upper), %	112.30%	153.38%	108.40%	92.43%
Comparison (*Sub./No sub.*, lower), %	116.57%	97.85%	100.91%	93.27%

4.3. Behavioral observations at the bypass

A hypothetical cause for the differences in passage between the two treatments is the observed differences in flow pattern created by substrate differences in the passageway (i.e. steeper velocity gradient and higher turbulence as compared to the barren passageway; Table 6 and Supplementary Figs. S10–S13). Fish have sensitive lateral line organs that can detect minor changes in water velocity around their body based on local pressure gradients, which likely affects navigation and whether fish accept or reject certain routes of movement (Montgomery et al., 1997; Liao, 2007; Mogdans and Bleckmann, 2012). Active selection of optimal water flow conditions for downstream movement has also been observed in several species (Jansen et al., 2007; Enders et al., 2009). In particular, turbulence and rapid changes in flow have been shown to be avoided by several species (Enders et al., 2009; Silva et al., 2012, 2016; Li et al., 2021), possibly due to such flow characteristics being associated with sections of rivers with high risks of injury and mortality, e.g. constriction zones and waterfalls. The typical avoidance behavior for several species entering a zone of accelerating flow is a rapid shift to positive rheotaxis, followed by escape upstream (Enders et al., 2009; Li et al., 2021).

Our study indicates that fish orient to face the current (i.e. a positive rheotactic orientation) as they enter the passageway from the ramp, a behavior also seen in salmonids and other species of cyprinids when they encounter a threshold velocity gradient (Enders et al., 2009; Li et al., 2021). Positive rheotaxis may allow for more control of body movements as the current velocity increases when the bypass becomes shallower, and it allows for quick escape upstream if needed.

In terms of treatment effects on behavior, the strongest evidence for avoidance behaviors associated with the *Substrate* treatments comes from the analysis of exit direction at the ramp, which shows that roach in the *Substrate* treatment more often turn back upstream, towards the arena, as compared to the fish in the *No substrate* treatment. In contrast, in the passageway the tendency was that fish in the *Substrate* treatment swim through the passageway downstream to a higher extent than fish in the *No substrate* treatment (significantly so only in the second observation group). This could indicate a possible positive effect of cobble substrate, but only after the roach has passed the ramp section. The number of turns per observation were also higher in the ramp area when the substrate was present than when it was absent, but this effect was significant only in the second observation group (G2; obs. 31–60 within each trial). Nevertheless, as number of turns can be indicative of general hesitation, the pattern suggests that avoidance behaviors may be triggered on the ramp in the *Substrate* trials (Vowles et al., 2014; Li et al., 2021). However, directional changes (switches from downstream movement to upstream movement and vice versa; not necessarily including changed body orientation) per time unit, which also could indicate hesitation, did not differ between treatments. Longer observation durations (time in camera view) could also be indicative of hesitance, and in the second observation group observation durations were longer for the *Substrate* treatment. Overall, the analyses suggest that the transition between the ramp and the passageway is the problem area. This is a bit surprising given that it is located upstream from the substrate panels, but the ADV-measurements suggest that the current characteristics are affected by the substrate, even at the ramp. Furthermore, rheosensation in fish is multisensorial and could be affected by more stimuli than just flow patterns in the vicinity of the fish body (Coombs et al., 2020).

Avoidance behaviors by downstream-moving cyprinids entering bypasses have been observed in other studies. In a study on the riverine Lhasa naked carp *Schizopygopsis younghusbandi* circa 20–40% (depending on flow regime) of individuals repeatedly turned and burst swam upstream when entering a bypass ramp in a circulating flume (Li et al., 2021). The majority of the turns occurred in the upward-sloping section of the ramp, where velocity increases, as also indicated in the present study. Studies on Iberian barbel *Luciobarbus bocagei* have provided indications that high flow velocities can hamper downstream passage, in particular when associated with narrow weir crests that concentrate the current (Silva et al., 2016; Amaral et al., 2018). Avoidance of accelerating flow and turbulence is also seen in other fish species, such as salmonids (Enders et al., 2009; Vowles et al., 2014). In the present study, accelerating flow over the ramp is a feature in both treatments, but apparently the cobble substrate panels introduce additional flow features of the current which increases avoidance behavior.

A problem that occurred in the present study was the upstream movement of fish from the collection box back into the bypass and the arena. This would not be seen in a bypass in a river and it inflated the number of camera observations since returning fish could not be identified. There were indications of changes in behavior across observation groups, suggesting that experience of passing the bypass may alter subsequent behavior, as seen in field studies (Hagelin et al., 2021). Future studies of similar design should consider implementing features that reduce the risk of fish from returning back after successfully passing through the bypass. It should also be pointed out that the flume environment is not perfectly reflecting a natural river environment. The bottom of the test arena is smooth, which reduces turbulence in the section upstream of the bypass ramp. A more varied bottom topography in the flume may propagate turbulence and lead to changes in flow characteristics associated to the bypass less detectable by the fish. Under more turbulent flow, the substrate in the passageway may be less influential on roach behavior.

4.4. Bypass design in a wider context

When abundant in a river system, roach can be one of the more common species using bypasses, as the frequency by which it is encountered moving downstream through bypasses tend to be proportional to the abundance upstream of the bypass (Knott et al., 2020). Hence, the species is an important target species to investigate when it comes to bypass design. While the passage of roach may be delayed as a consequence of the presence of cobble substrate in the bypass, it is not completely hindered. Hence, the relative success of other species passing a cobble-structure bypass may need to be incorporated into final evaluations of this design. Delay is problematic, but bypass designs need to consider passage efficiency at the community level (Silva et al., 2018).

To date, there are few, if any, surface bypass designs that generally function well across multiple sites and species (Klopries et al., 2018), so more investigations are needed from a multi-species perspective (Geist, 2021). The cobble substrate panels tried in this experiment constitute an attempt at a simple and cheap solution to apply in the rather narrow passageways of existing surface bypasses, but has to be considered unsuccessful in the present context. Other implementations of cobble substrate in bypasses could still be worth exploring, e.g. cobble substrate in the ramp section, screens with more sparsely spaced boulders which the fish can swim between (e.g. Bréton et al., 2013), or applying cobble substrate by the entrance to the ramp. It should also be noted that placing natural substrate in other types of bypass channels (e.g. nature-like fishways) should not be discouraged, as it can have several positive effects, including providing habitat for a multitude of aquatic species (e.g. Gustafsson et al., 2013; Pander et al., 2013, 2021).

5. Conclusions

Based on the presented experimental data, addition of cobble substrate in a surface bypass cannot be recommended as a measure to increase the downstream passage performance of the common roach. Passage is not hindered by the presence of cobble substrate, but it is delayed due to avoidance behavior. Differences in avoidance of the bypass between the two setups could be due to differences in bypass flow patterns associated with the cobble substrate.

Data availability statement

Data and R-code for analyses are openly available from the figshare repository: https://doi.org/10.6084/m9.figshare.14695281.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecoleng.2021.106402.

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