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Downstream bypass efficiency of Atlantic salmon *Salmo salar* smolts in relation to bypass cobble substrate and flow velocity

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A R T I C L E I N F O

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A B S T R A C T

River connectivity is a major environmental factor affecting fish migration through river systems. Anthropogenic barriers cause substantial delays and mortality to long-migrating diadromous fish, such as salmonids. Downstream bypasses have received little attention over the years and can be constructed in several ways, with bypass acceptance by fish shown to be problematic in many cases. This experiment investigated whether the addition of cobble in the passageway of a surface bypass could facilitate downstream movement of Atlantic salmon (*Salmo salar*) smolts. The experiment also determined if the addition of cobble substrate functioned similarly under five varying flow velocities, as this can directly interact with bypass design and impact bypass acceptance. Surface bypasses were constructed in large experimental flumes, into which the smolts were released and monitored for bypass passage using PIT-telemetry through 3-h night-trials. Behavior was scored using two continuously-recording video cameras at the bypass construction. No clear positive effects on passage efficiency could be detected from the addition of cobble substrate in the passageway of the bypass. Based on these results, the addition of cobble substrate in a surface bypass passageway cannot be recommended as a measure to facilitate the downstream passage performance of Atlantic salmon smolts through surface bypasses. With respect to flow velocity, higher velocities within the tested range (0.48–0.75 m • s^{-1}) led to faster passage.

1. Introduction

River connectivity is a major environmental factor affecting the possibility for fish to migrate through river systems (Reidy Liermann et al., 2012; Reid et al., 2019; Barbarossa et al., 2020). Human-constructed barriers, such as dams and weirs, which fragment rivers into largely discrete sections, disrupt the longitudinal connectivity of river networks (Grill et al., 2019; Belletti et al., 2020). For fish encountering hydropower dams, upstream movement across the barrier is often impossible unless passageways are installed, and while downstream movement is often physically possible, the main flow typically goes through the turbines, which is often associated with high risks of injury and death for the fish following this flow (Schwevers and Adam, 2020). While substantial research efforts have historically been put into making upstream passage possible, particularly for diadromous species, special constructions for downstream passage have received less attention until relatively recently (Larinier and Travade, 2002; Schilt, 2007; Calles and Greenberg, 2009; Calles et al., 2013). Designing and evaluating fish passage across river barriers, both upstream and downstream, is today an important field of research for supporting evidence-based solutions (e.g. Scruton et al., 2008; Nyqvist et al., 2017a; Schwevers and Adam, 2020; Geist, 2021; Tomanova et al., 2021).

Historically, downstream passage across barriers has focused primarily on anadromous salmonid juveniles passing hydropower dams, due to these species' economic importance (Montén, 1985, 1988; Katopodis and Williams, 2012; Algera et al., 2020). Seaward-migrating salmonid juveniles (smolts) are often small enough to pass the turbines with what many consider an acceptable mortality rate (at least from the Swedish perspective: Montén, 1985, 1988; also see e.g. Karppinen et al., 2014). Nevertheless, mortality can in some cases be substantial (Algera et al., 2020; Vikström et al., 2020), especially when accounting for delayed mortality due to internal injury (Mueller et al.,

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2020) and multiplicative loss over consecutive passages (Norrgård et al., 2013). Furthermore, even if the smolts survive passage, their migration can be delayed by barriers (Nettles and Gloss, 1987; Huusko et al., 2018), which may cause the smolts to miss the migration window and de-smoltify (McCormick et al., 1999; Aarestrup and Koed, 2003). For larger fish (e.g. post-spawning adult salmonids, and other species) the injury and mortality rates related to turbine passage can be very high (Vikström et al., 2020).

The subject species of this study is the Atlantic salmon *Salmo salar* L., which is an anadromous salmonid with high economic, cultural and ecological value, and at the same time under substantial pressure within its natural distribution range (e.g. Lehnert et al., 2019; ICES, 2020; Greenberg et al., 2021). The Atlantic salmon is generally similar to other anadromous salmonids in its migratory ecology, although timing of different migratory events differ both among Atlantic salmon populations and among species (McCormick and Saunders, 1987; Fleming, 1998). Anadromous salmonids in general spawn in rivers and spend their initial juvenile stage (the 'parr' stage) in the freshwater environment. When reaching a certain size and the environmental cues (temperature and light-period) are appropriate, these fish typically undergo a physiological transformation (called smoltification), preadapting for a marine environment (McCormick and Saunders, 1987; Björnsson et al., 2011). At this time, the salmon initiate their seaward migratory journey (McCormick and Saunders, 1987). The specific timing of the migration is largely determined by environmental factors such as discharge, water temperature and the diel cycle, although there are some interactive effects between these factors making results from different studies vary (Thorpe and Morgan, 1978; Nettles and Gloss, 1987; Karppinen et al., 2014; Aldvén et al., 2015; Harvey et al., 2020). Discharge (or rather flow velocity, if comparing sites with different river widths; e.g. Harbicht et al., 2021) appears to be one of the key factors, especially during the early period of the smolt migration, with higher discharge generally eliciting and facilitating migration (Aldvén et al., 2015; Persson et al., 2019; but see Jonsson and Ruud-Hansen, 1985; Nettles and Gloss, 1987). After the water temperature reaches ca. 10 degrees in spring, other environmental factors tend to be less important (Mel'nikova, 1970; Nettles and Gloss, 1987; Aldvén et al., 2015).

Some salmonid species, like Atlantic salmon, predominantly have obligate smoltification, while other species show partial smoltification, with some of the juveniles developing into adults within rivers (e.g. brown trout *Salmo trutta* L.) (Hendry et al., 2004). Populations with obligate smolt migration are thereby more sensitive to downstream barriers than partially migrating populations. Populations with obligate migration may therefore require supplemental rearing and stocking below the furthest downstream barrier, when downstream migration is hampered (Montén, 1988; Calles et al., 2013).

Downstream bypasses can be constructed in several ways, e.g. as natural fish ways resembling natural streams, spillway passes (either over the dam crest or through spill gates at the bottom of the dam), or surface bypasses where the fish is guided to a passage that leads the fish to the tailrace (Katopodis et al., 2001; Schilt, 2007). In this study, we focus on a surface bypass into which the fish are guided by an angled screen transversing the river channel. Bypass acceptance by fish individuals has been shown to be problematic in many cases, with fish often showing avoidance behaviors or hesitation at the entrance of bypasses (Nettles and Gloss, 1987; Knott et al., 2020; Schwevers and Adam, 2020). Hence, we investigate whether bypass acceptance can be improved by adding a cobble substrate panel in the bypass. The cobble substrate is hypothesized to increase bypass acceptance by creating a more nature-like environment, which could be less stressful and even attract the fish into the bypass, thereby leading to more rapid bypass passage. The addition of cobble substrate panels is also an inexpensive and easily implementable feature in many existing surface bypass designs. The water discharge in the river and through the bypass can also interact with bypass design with respect to bypass acceptance (Haraldstad et al., 2018; Tomanova et al., 2021), and is the one environmental factor influencing smolt migration and can be adjusted at a hydropower dam. Here, relative bypass acceptance and behavior in the bypass was investigated in relation to presence/absence of a cobble substrate panel, at five different water flow velocities in a large experimental flume, in which a bypass structure was constructed.

2. Materials and methods

2.1. Test species and husbandry

Atlantic salmon smolts ($N = 260$; Fig. 1D), originating from the River Dalälven population, were reared from eggs in the Vattenfall hatchery in Älvkarleby, Sweden. On 7 May 2020 the fish were transported to the Vattenfall Research and Development Laboratory (Älvkarleby, Sweden), where they were split into two equal-sized groups ($n \approx 130$) and maintained separately in two stainless-steel circular vats (3.5 m^3) until the experiments were started. The vats were equipped with bead-filters, UV-filters, chillers, and diffused aeration through three large air stones. They were filled with filtered water from the 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 13.5 ± 4.9 °C (mean ± range). No food was provided during the pre-trial period to reduce risk of fouling the water. Juvenile Atlantic salmon tolerate starvation within the limited timeframe used here (Nicieza and Metcalfe, 1997), although body condition decreases and this decrease is associated with a small but detectable effect on smolt migration speed, where lower condition leads to slightly faster migration speed (Persson et al., 2018). Water was exchanged manually when needed, determined by daily visual inspection. Three days after arrival the fish were sedated with benzocaine (10 ml of 1-g solution per liter), weighed, measured, and tagged with 23-mm passive integrated transponders ('PIT'-tags; Oregon RFID, Portland, USA). Tagging was assumed to have little effect on the performance of the smolts; only a single individual (124 mm) was below the recommended size threshold (131 mm) for tagging with 23-mm PIT-tags (Vollset et al., 2020). A scalpel incision was made on the ventral surface circa 1 cm left of the ventral midline, 2–3 cm in front of the anal opening, and the tags were inserted by hand into the buccal cavity. No sutures were used, as this may increase the risk of inflammation around the incision (Larsen et al., 2013). All smolts survived until the experiment started, and all fish had at least one-week recovery time from tagging until being used in trials. Average body size of the smolts used in the experiment was similar across treatments, without any significant differences (Table 1). No significant differences among treatment groups were detected in either length or mass (linear mixed models; factors: substrate treatment TR, velocity treatment VEL, interaction TR × VEL, and trial group as random intercept; all $p > 0.43$).

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 carried out in the experimental flume 'Laxelerator' at Vattenfall Research and Development, Älvkarleby, Sweden. The circulating flume was divided into two 24 m long, 4 m wide and 2 m deep parallel test arenas (Fig. 1A). Flow of up to 2 $m \cdot s^{-1}$ is provided by four ejector pumps.

Each test arena was split into an upstream and a downstream section by net barriers (1-cm mesh-size nylon net, attached to a removable 6.8 m long and 2 m high steel frame), with a function similar to a guiding β-rack (β-angle: 30°). The net barriers led to surface bypass structures at the left side of the flume in the downstream direction (Fig. 1B). The

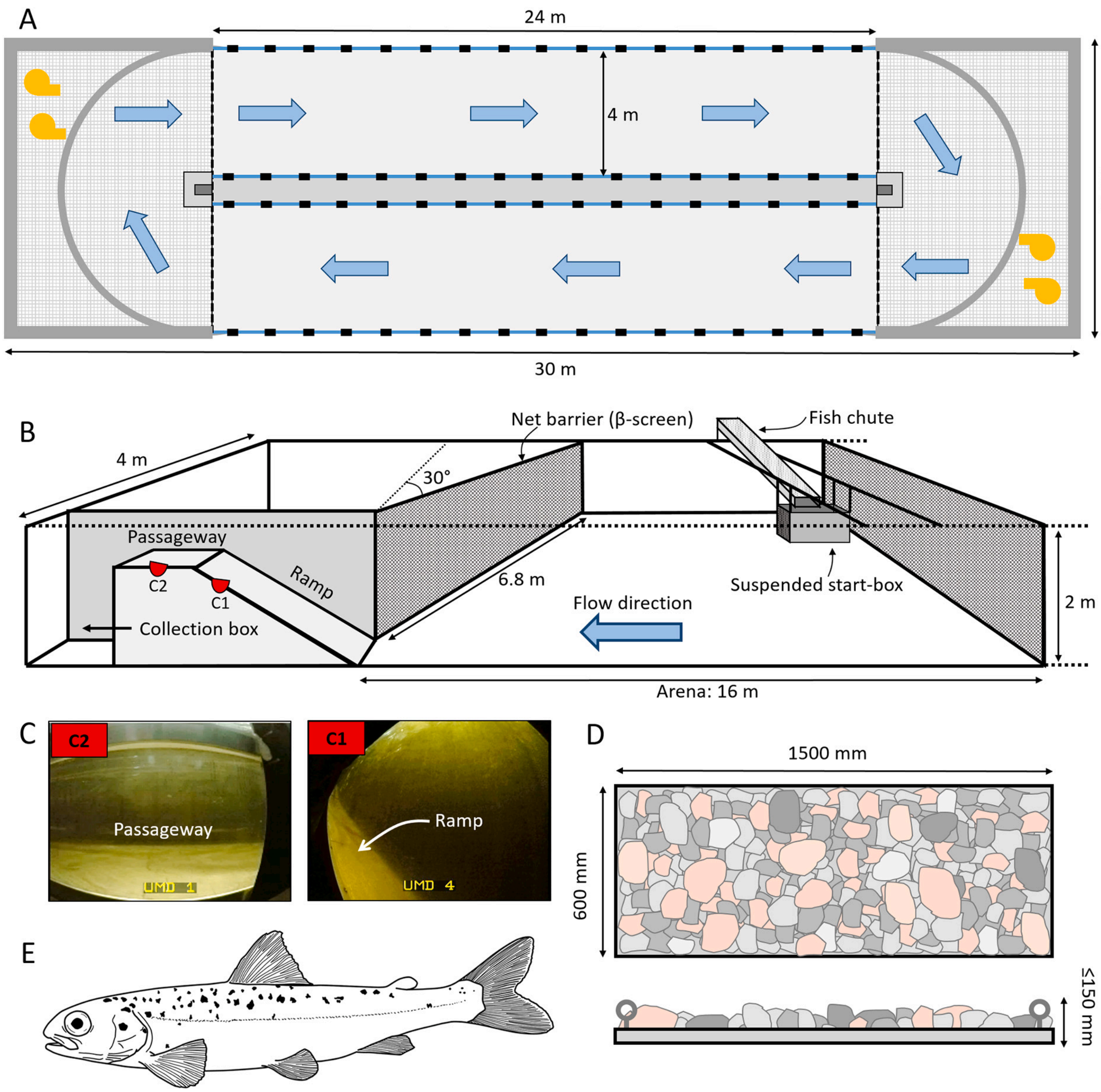

Fig. 1. Overview of the experimental flume, arenas and treatments. A) Top view and dimensions of the experimental flume. Arrows show flow direction; yellow symbols represent the pumps. B) Side view perspective of the experimental arena (note that the length of the arena is not drawn to scale). C) Screen shots from cameras C1–2 (see B for placement). D) Design of the gravel bed treatment, which was placed in the passageway. E) Illustration of an Atlantic salmon (*Salmo salar*) smolt. Parts of this figure (doi: https://doi.org/10.6084/m9.figshare.16635286; license CC-0) are derived from doi:https://doi.org/10.6084/m9.figshare.14672676 (license CC-0). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Table 1
Summary of body sizes of the Atlantic salmon smolts used in the experiment for each treatment combination. SD = standard deviation of the mean; n = sample size, not including individuals not leaving the start-box (n = 14) or with erroneous PIT-data (n = 2). No significant differences among treatment groups were found (all p > 0.43).

	Velocity:	*Vel.48*	*Vel.54*	*Vel.63*	*Vel.67*	*Vel.75*
Total length (mm)						
No substrate	Mean [SD (*n*)]:	162 [10 (23)]	158 [15 (21)]	165 [17 (21)]	159 [13 (22)]	160 [10 (23)]
	Median (range):	162 (141–176)	160 (124–180)	166 (136–200)	156 (142–183)	159 (146–180)
Substrate	Mean [SD (*n*)]:	162 [11 (21)]	163 [13 (22)]	163 [14 (16)]	164 [14 (32)]	158 [10 (23)]
	Median (range):	162 (140–182)	164 (132–183)	164 (135–185)	166 (135–187)	160 (140–172)
Body mass (g)						
No substrate	Mean [SD (*n*)]:	42 [7 (23)]	38 [9 (21)]	43 [13 (21)]	40 [8 (22)]	39 [7 (23)]
	Median (range):	41 (27–54)	39 (19–53)	42 (25–71)	38 (28–58)	39 (29–55)
Substrate	Mean [SD (*n*)]:	40 [8 (21)]	42 [9 (22)]	43 [10 (16)]	43 [10 (32)]	39 [8 (23)]
	Median (range):	40 (26–58)	42 (28–60)	43 (25–61)	42 (26–64)	38 (26–51)

bypass was constructed with an upward ramp terminating in a 0.6 m wide and 0.35 m high (bottom to surface) escape opening, leading to a passageway connected to a collection-box at the end. A steel "start-box", where fish were initially placed for each trial, was situated near the surface in the upstream part of the flume. One PIT-tag antenna (Oregon RFID, Portland, USA) was placed around the opening of the start-box, and one was placed at the exit opening in the bypass, which lead to the collection-box. The floor of the flume was smooth and made of concrete, the sides of the flume were made of acrylic glass and metal brackets, and the bypass structure was made of stainless steel.

Downstream migration was tested in 30 groups of eight fish. For 15 groups, the bypass passageway was equipped with a 60 × 150 cm steel frame, filled with cobble substrate ranging up to 15 cm in diameter ('*Substrate*' treatment; Fig. 1D, photo in Fig. S1). For the other 15 groups, the passageway was devoid of any structures ('*No substrate*' treatment). Two groups were run simultaneously (one for each treatment) using the two test arenas. Assignment of the substrate treatments to the two arenas was determined randomly between trial runs (by coin flip; one of each treatment was run simultaneously). Five average current velocities were used ('*Vel.48*' = 0.48 $m \cdot s^{-1}$; '*Vel.54*' = 0.54 $m \cdot s^{-1}$; '*Vel.63*' = 0.63 $m \cdot s^{-1}$; '*Vel.67*' = 0.67 $m \cdot s^{-1}$; '*Vel.75*' = 0.75 $m \cdot s^{-1}$; see Fig. 2 for flow conditions at the bypass), representing a gradient of reasonable river flow velocities up to a value slightly below the expected swimming velocity of the smolts (ca 0.8 $m \cdot s^{-1}$; Remen et al., 2016). Velocity was set by adjusting the ejector pumps, and velocity values presented above represent average velocities measured throughout the flume for each setting of the pumps (i.e. velocity represents the discharge in the flume, i.e. the approach velocity of the water before reaching the bypass structure; ejector pump settings were identical for both *Substrate*- and *No substrate* treatments).

The trials were filmed with two light sensitive security cameras (Hikvision DS-2CC12D9T-AIT3ZE; Hangzhou Hikvision Digital Technology Co., Ltd., Hangzhou) at the bypass structure (covering the ramp and passageway; Fig. 1B-C), and a wide-angle action camera (GoPro Hero 6; GoPro, Inc., San Mateo, CA) at the start-box. Both security cameras were used to extract data for behavioral analyses (Table 2) and the passageway security camera and the start-box action camera were used to verify the PIT-tag readings.

2.4. Experimental procedures

Trials were run from 18 May to 29 May 2020 during night-time, as the literature indicates that Atlantic salmon smolts predominantly migrate during the dark hours (Thorstad et al., 2012). Four trials were run each night, two in each of the flume channels. A first round of trials started between 19:28 and 20:27, and a second round started between 01:49 and 02:08, depending on logistical factors. The facility was

Table 2
List of behavioral events recorded during the trials.

Behavior	Event	Data type	Values
Entry orientation	Entering camera view	Binomial	Head-first; Tail-first
Exit orientation	Exiting camera view	Binomial	Head-first; Tail-first
Turns	While in view	Count	Turning (change in body orientation; head facing towards/against the current)
Directional change	While in view	Count	Downstream; Upstream
Obs. duration	From entering to exiting camera view	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 camera view	Binomial	Downstream; Upstream

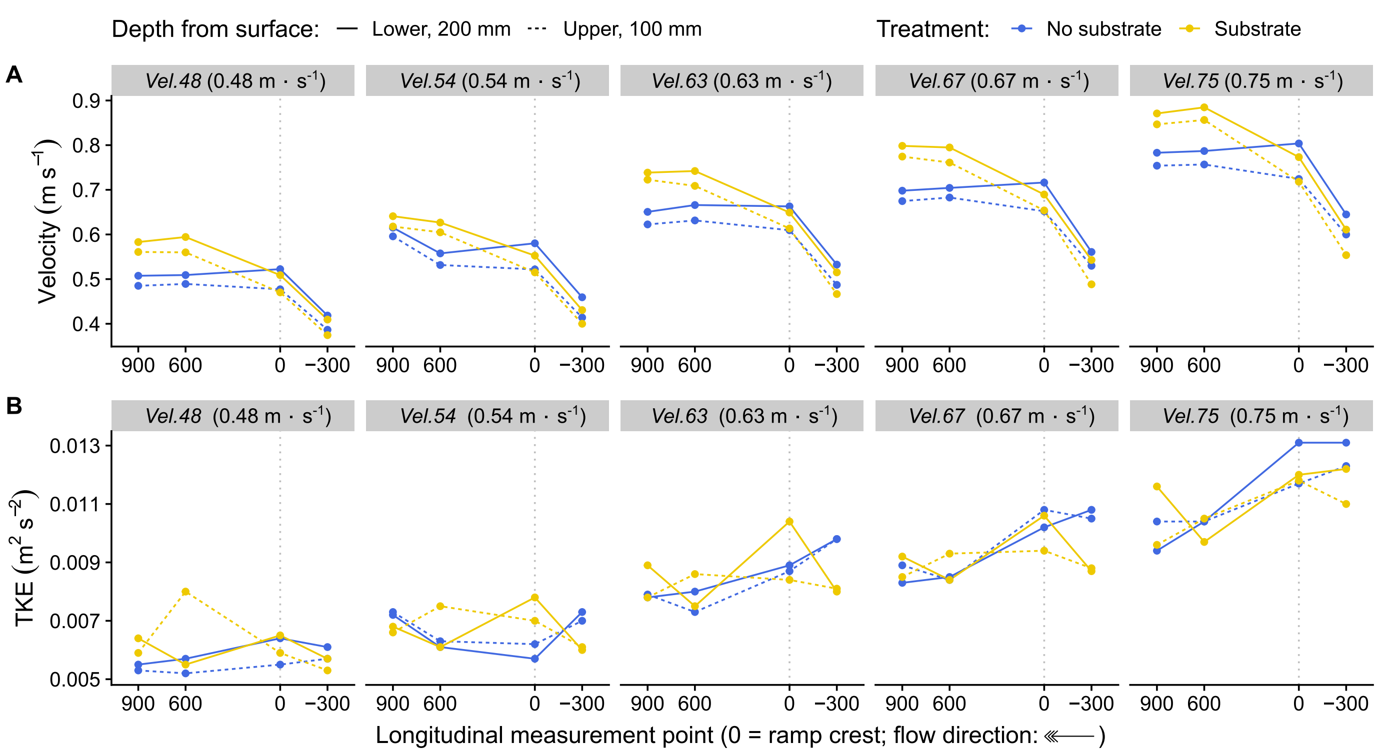

Fig. 2. Flow characteristics at the bypass structure, as measured by acoustic Doppler velocimetry (ADV). Flow and fish migration direction runs from right to left in the graphs; x = 0 is the reference point (the ramp crest); x = −300 is a location at the upper part of the ramp, 300 mm downstream from the crest; x = 600 is a point in the passage way, 600 mm upstream from the crest (by the substrate panel, if part of the setup); x = 900 is a point at the end of the passageway, 900 mm upstream from the crest. For each measurement point, values were derived from two depths (100 mm from the surface and 200 mm from the surface). A) Flow velocity. B) Turbulence kinetic energy.

constantly lit by a weak, diffused light, simulating natural moonlight (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 eight 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 three hours later, at which point cameras were switched off, and the video and PIT-reader data were downloaded. When failure of the PIT-antennas was detected (rendering no or incomplete data), the trial was re-run at a different date using a new batch of fish. In the end, 3 trials were obtained for all substrate treatment × velocity combinations, except *Substrate*:*Vel.63* ($n = 2$; due to corrupted data file) and *Substrate*: *Vel.67* ($n = 4$). While each trial was run with 8 smolt individuals, the final data set contains fewer individuals due to unwillingness by some individuals to leave the start-box ($N = 14$; *No substrate*: *Vel.48*: $n = 1$, *Vel.54*: $n = 1$, *Vel.63*: $n = 3$, *Vel.67*: $n = 2$, *Vel.75*: $n = 1$; *Substrate*: *Vel.48*: $n = 5$, *Vel.75*: $n = 1$) or incorrectly registered PIT-numbers ($N = 2$; *No substrate*: *Vel.54*: $n = 2$). In total, data on bypass performance was obtained for $N = 224$ individual smolts (see Table 1 for sample size per substrate treatment × velocity combination). After each trial the fish were released into River Dalälven, as they were originally reared for this purpose.

2.5. Statistical analyses

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).

Time to pass through the bypass was analyzed using Cox regression (proportional hazards) analyses in the R package *survival* (Therneau, 2020). Passage time for each individual was defined as the time from leaving the start-box to entering the collection-box (as indicated by PIT-antenna registrations). Individuals not passing prior to the end of the trial were censored in the analysis (censor time equaling the time duration from exiting the start-box until the end of the trial; maximum 10,800 s). Two models, one ‘interaction model’ and one ‘additive model’ were used in the analyses (the latter one was added as an alternative ad hoc model after the results of the former were obtained, removing the assumption of interaction effects being possible; i.e. we interpret the significant interaction effect to be spurious). Each model included substrate treatment (TR; categorical fixed factor, two levels: *No substrate* and *Substrate*), flow velocity (VEL; categorical fixed factor, five levels: *Vel.48*, *Vel.54*, *Vel.63*, *Vel.67*, and *Vel.75*), body length (continuous covariate), and paired trials as a random categorical variable (specified as a cluster in the model); the interaction model included the TR × VEL interaction term in addition. Body length was excluded from the models if non-significant at $p > 0.1$, and if the Akaike Information Criterion (corrected for small sample size; AICc) was lower for the reduced model. The interaction model focused specifically on potential interaction effects and was used for constructing descriptive graphs of the experimental results; the additive model focused on main effects and was used as the main model for interpreting the general efficiency of cobble substrate and different velocities on bypass efficiency. Pairwise contrasts were calculated using the *emmeans* package for R (Lenth, 2021).

The assumption of proportional hazards (PH) was evaluated based on scaled Schoenfeld goodness-of-fit tests (Grambsch and Therneau, 1994) and results were plotted using the *survminer* R package (Kassambara et al., 2017). The test suggested that PH was violated for the VEL-factor in both models ($p < 0.001$). Most individuals escaped through the bypass within an hour, so the data were re-analyzed using a 60-min (3600 s) trial duration for the censoring instead. The violation of the proportional hazards remained for VEL, even after shortening the trial window to 30 min. The main problem for PH appeared to be the *Vel.75* treatment, with a very rapid hazard rate; removing this treatment yielded non-significance in the test of PH. With this in mind, the 60-min analysis was retained for interpretation, including the *Vel.75* treatment, noting that results should be interpreted with some caution.

Behavioral variables were analyzed for data where the fish entered the camera view from the arena direction (from upstream), since entry from the collection-box (downstream) direction is a non-feasible scenario in the passageway and not of particular interest at the ramp (descriptive data presented in Table 4). Remaining variables were analyzed only if there was sufficient variation in the data (see Table 4). These criteria limited the analyses to: 1) exit direction at the ramp (exiting camera view upstream or downstream), 2) duration in camera view at the ramp, and 3) duration in camera view in the bypass. Other recorded variables are only reported descriptively. For the three variables analyzed, mixed models and contrast analyses were implemented through the *lme4* (Bates et al., 2020), *lmerTest* (Kuznetsova et al., 2020), and *emmeans* (Lenth, 2021) packages for R. Exit direction was analyzed using a generalized linear mixed model based on the binomial distribution and logit link-function; duration in camera view was analyzed in linear mixed models with the response variable $\log_{10}$-transformed. Models included treatment (‘TR’: fixed factor, two levels: *Substrate* and *No substrate*), flow velocity (‘VEL’: fixed factor, two levels: *Vel.48* and *Vel.75*), the interaction TR × VEL, and trial (random intercept, 13 levels).

2.6. Bypass flow characteristics

Water flow in the bypass was characterized for each substrate- and velocity condition, for descriptive purposes, using acoustic Doppler velocimetry (‘ADV’; Vectrino 3D Fixed Stem G.A., Nortek AS, Rud, Norway). Transects were set up at the transition between the ramp and the passageway (referred to as the reference point), 300 mm upstream of the reference point in the ramp, and 600 mm and 900 mm downstream of the reference point (i.e. over the substrate panels, if present). At each of these four locations, cross-sectional transects were established, with measurement points located 100, 300, and 500 mm from the left (outer) wall, at 100 and 200 mm depth (altogether 24 measurements; see Fig. S2). Measurements were taken for 120 s at each point.

Data were processed in MATLAB (version R2020b; MathWorks, Natick, MA) to filter poor data points based on signal-to-noise ratios following recommendations in the velocimeter manual. Series of velocity measurements at each measurement point were averaged and used to calculate 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):

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

Measurements along the central (300 mm from the outer wall) longitudinal direction are presented in Fig. 2, and data from all measuring points (Fig. S2) are illustrated in Fig. S3A-F. Measured velocity- and TKE values are presented as supporting information to provide information on conditions at the ramp and are not analyzed together with the experimental data.

3. Results

3.1. Downstream passage

The Cox regression models were reduced by removing body length (both with $p > 0.3$, Table S1; for both models the reduced model had the lowest AICc-value, Table S2). In the interaction model the TR × VEL interaction was significant ($\chi^2 = 23.5$, $p < 0.001$; see Table S3 for model summary). Pairwise contrasts relating to TR indicated that there was a difference between the *No substrate* and the *Substrate* treatments in velocity treatments *Vel.48* (*No substrate*:*Substrate*: hazard ratio 2.23, *z*-ratio = 2.9, $p = 0.004$) and *Vel.67* (*No substrate*:*Substrate*: hazard ratio

0.31, z-ratio = −4.0, $p < 0.001$). Contrasts relating to VEL indicated significant differences within the *Substrate* treatment, with *Vel.48* differing from *Vel.67* and *Vel.75* (*Vel.67*:*Vel.75*: hazard ratio 0.30, z-ratio = −3.8, $p = 0.001$; *Vel.48*:*Vel.75*: hazard ratio 0.29, z-ratio = −4.1, $p < 0.001$), *Vel.54* differing from *Vel.75* (*Vel.48*:*Vel.75*: hazard ratio 0.39, z-ratio = −2.8, $p = 0.038$), and *Vel.63* differing from *Vel.67* and *Vel.75* (*Vel.63*:*Vel.67*: hazard ratio 0.54, z-ratio = −3.5, $p = 0.004$; *Vel.63*:*Vel.75*: hazard ratio 0.54, z-ratio = −3.5, $p < 0.001$). All pairwise contrasts are presented in Table S4. A summary of median passage time for each TR × VEL treatment combination (Table 3) and estimated survival curves (Fig. 3) both correspond to the pattern seen in the analysis of the model.

The additive model, which is an ad hoc model based on the suspicion of a spurious interaction effect in the interaction model, indicated no general TR-effect ($\chi^2 = 0.11$, $p = 0.74$) but a significant VEL-effect ($\chi^2 = 16.9$, $p = 0.002$) (see Table S3 for model summary). Pairwise contrasts indicated that *Vel.48* and *Vel.54* had longer passage times than *Vel.75* (*Vel.48*:*Vel.75*: hazard ratio 0.41, z-ratio = −3.6, $p = 0.003$; *Vel.54*:*Vel.75*: hazard ratio 0.41, z-ratio = −3.6, $p = 0.003$). All pairwise contrasts are presented in Table S5 and hazard ratios are visualized in Fig. 4. A summary of median passage times for each velocity (substrate treatments combined) indicate progressively decreasing median values with increasing flow velocity (Table 3).

3.2. Behavior in the bypass

3.2.1. Ramp

The majority of all fish entering the camera view at the ramp from the arena (i.e. from upstream) entered tail-first (Table 4A). In only 4 out of 139 observations (2.9%; all in *Low velocity*; 1 of 77 in *No substrate*; 3 of 62 in *Substrate*) a fish entered the camera view head-first; in all four cases the fish turned its body to swim tail-first and three of these fish proceeded downstream over the crest of the ramp.

After entering from the arena, the probability of exiting camera view in a downstream direction (i.e. towards the passageway and catch-box) differed among the treatment combinations (Table 5A; Fig. 5A). Pairwise contrasts revealed that the probability was lower in low current velocity than in high in the absence of substrate in the passageway [*Low/High* odds ratio: 0.024, $z = -3.536$, $p < 0.001$], but less clear in the presence of the substrate panel (*Low/High* odds ratio: 0.332, $z = -1.723$, $p = 0.085$). Averaging over substrate treatment levels indicated a general effect of current velocity (*Low/High* odds ratio: 0.089, $z = -3.917$, $p < 0.001$). No clear difference was seen in the contrasts focusing on the substrate treatment in either low current velocity (*No substrate/Substrate* odds ratio: 0.518, $z = -1.504$, $p = 0.133$) or high current velocity (*No substrate/Substrate* odds ratio: 7.294, $z = 1.716$, $p = 0.862$). Analysis of duration in camera view at the ramp did not reveal any significant differences among treatments or treatment combinations (Table 5B).

3.2.2. Passageway

All fish entering the camera view in the passageway from the ramp (i.e. from upstream) entered tail-first and none of these fish were observed to turn while observed (Table 4B). In only three observations (all from a single trial; 8% of observations in this trial) the fish entered from the ramp and swam back towards the ramp; in all other observations the fish continued towards the collection-box (Table 4B).

Analysis of duration in camera view in the passageway indicated a clear difference between the velocity treatments ($p = 0.021$), but no difference for substrate treatment ($p = 0.967$) and no interaction effect ($p = 0.817$) (Table 5C; Fig. 5B). Averaging over substrate treatment levels indicated that the duration in camera view was shorter for fish in the higher velocity (*Vel.75*) than in the lower (*Vel.48*) (back-transformed contrast estimate: 2.3 s, $t = 3.982$, $p = 0.004$).

Table 3
Median passage times (in seconds) and inter-quartile range for each combination of substrate and velocity.

Velocity ($m \cdot s^{-1}$)	*No substrate*	*Substrate*	Both treatments
0.48	324 (193–584)	897 (398–2254)	539 (212–1059)
0.54	389 (312–1244)	567 (252–1724)	550 (266–1304)
0.63	350 (127–915)	271 (101–1089)	290 (119–972)
0.67	872 (205–2625)	107 (71–419)	225 (79–783)
0.75	72 (46–131)	80 (53–236)	77 (47–166)
All velocities	319 (92–1004)	272 (79–792)	309 (85–913)

4. Discussion

This experiment investigated whether the presence of cobble substrate in the bypass passageway could improve Atlantic salmon smolts' acceptance of the bypass at five different flow conditions. Contrary to our predictions, no clear substrate effects were detected, but in line with previous observations higher flow velocity generally had a positive effect on the overall passage time.

4.1. Effects of substrate

Based on the model including the TR × VEL interaction, there were differences between the substrate treatments at two flow velocities. At *Vel.48*, the fish in the *No substrate* treatment had shorter passage time than the fish in the *Substrate* treatment and at *Vel.67* the opposite effect was observed. No differences were detected at other flow velocities. The pattern is curious as the effect pattern switches, with no effects seen at intermediate velocities. It could be that there is an antagonistic interaction effect from *Vel.48* to *Vel.67*, where the *Substrate* treatment becomes more favorable for passage with increasing flow velocity, while the *No substrate* becomes less favorable. Then, at some velocity between the *Vel.67* and *Vel.75* treatments, the effect of flow may override any effects of substrate presence/absence at *Vel.75*. However, the observed pattern also raises the question about whether or not these effects could be spurious. An effect at the lowest velocity tested (*Vel.48*) could indicate a threshold effect for the interaction, where substrate has an effect at low velocities which disappears at higher velocities. Another similar experiment run on common roach *Rutilus rutilus* (a cyprinid fish) in the same facility, using the same flume setup at a flow velocity of 48 $m \bullet s^{-1}$, indicated that cobble substrate in the passageway decreased passage efficiency of this species (Bowes et al., 2021). This lends some support for the negative effect of cobble substrate at *Vel.48* being correct. Possibly, cobble substrate may have a negative effect on the flow field experience of the fish at low velocities, which disappears at higher velocities. Nevertheless, behavior and swimming capacity differ between the two species (Tudorache et al., 2008; Peake et al., 1997), and higher velocities were not tested for roach, making it hard to compare the results. The opposite effect at *Vel.67* is harder to explain, unless it is part of an antagonistic effect as discussed above. It may be possible that certain conditions are formed only at this flow velocity, but there are no indications of this from the ADV data (Fig. 2), and no behaviors were recorded at this flow velocity. Fish in the *No substrate* treatment at *Vel.67* also seem to deviate from the general pattern of progressively decreasing passage times with increasing flow velocity (Fig. 3). For this reason, the additive model (excluding the interaction term) is favored for general interpretation. Based on this latter model, no general effects of cobble substrate can be detected.

Our hypothesis was that cobble substrate would make movement through the bypass passageway less stressful and possibly even attract the fish. The fact that smolts have previously been shown mostly to swim in the water column, rather than close to the river bottom, as the younger stages of the species typically do (Thorstad et al., 2012), might make this hypothesis less tenable. While not recorded during behavioral observations, the majority of the fish in this study were observed swimming in the upper section of the water column (R.B. pers. obs.), which could explain the lack of effects of the cobble substrate panels. The use of hatchery-reared salmon may also contribute to the lack of

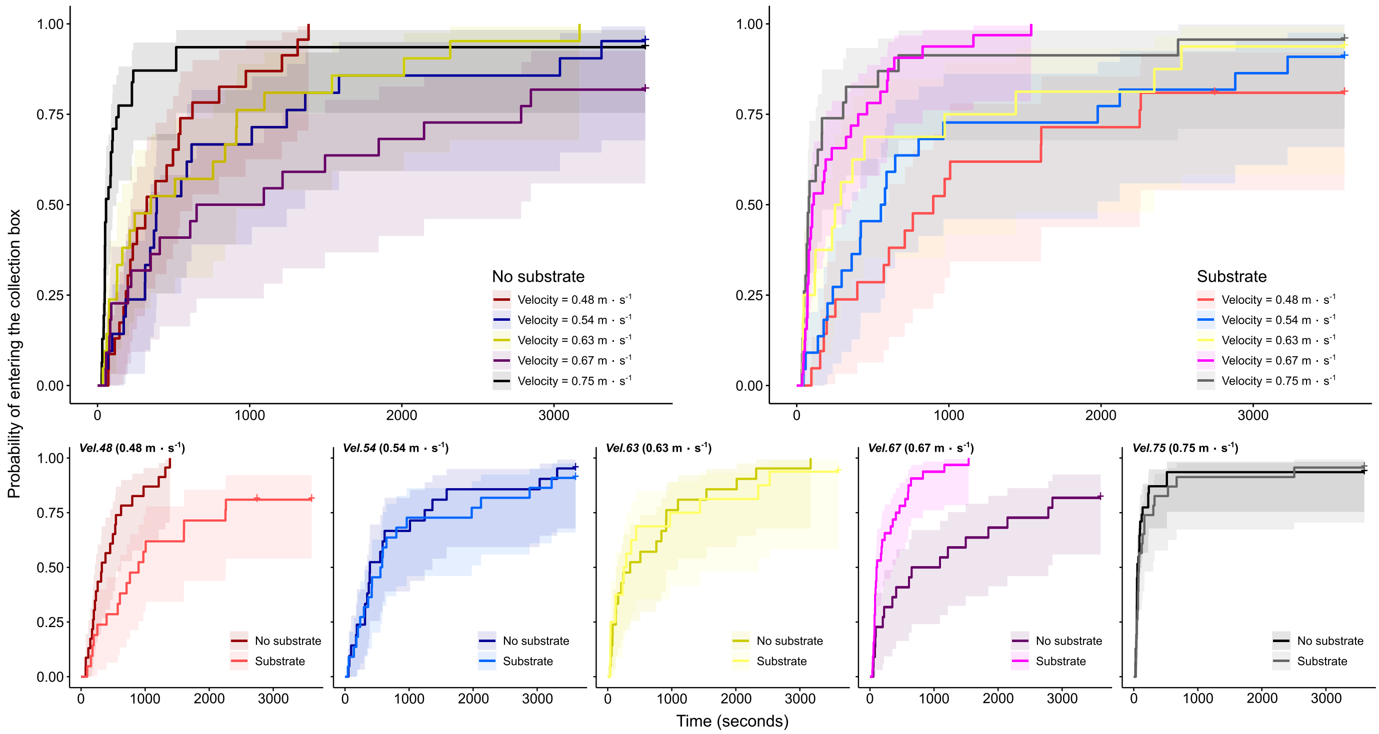

Fig. 3. Time-to-event plots showing time to successful downstream passage in Atlantic salmon smolts (from leaving the start-box to passing the bypass PIT antenna), with 95% confidence bands. Upper panels show comparisons among velocity treatments for each level of substrate treatment, lower panels show comparisons between substrate treatments for each level of velocity treatment. *No substrate* treatments are visualized in darker color and *Substrate* treatment in lighter color. Estimates are based on the interaction model.

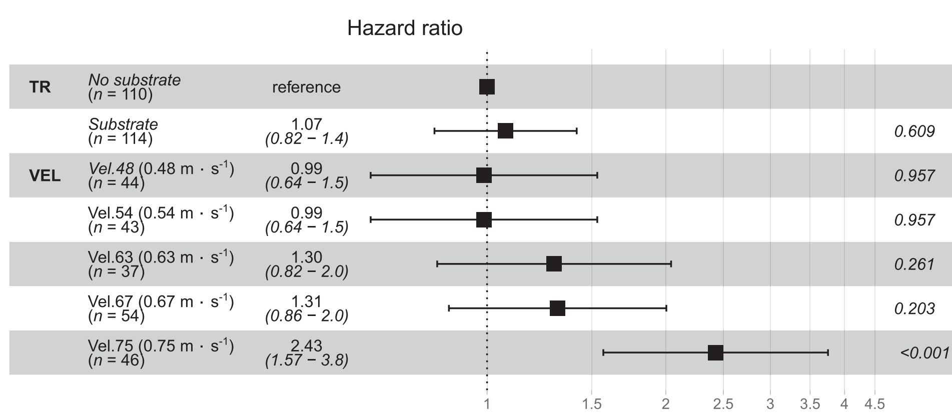

Fig. 4. Hazard ratios from the additive model of passage time (i.e. assuming no interaction effects). Positive hazard ratio indicates shorter passage time. Error bars show the 95% confidence interval.

effects. Since hatchery salmon have no prior experience of nature-like features, such as cobble, in their environment, they may lack any preference for such features, which may affect the behavior of wild salmon (Johnsson et al., 2014).

4.2. Effects of flow velocity

The general effect pattern of flow velocity indicates that passage time through the bypass progressively decreases with increasing flow velocity. From the pairwise contrasts of the interaction model, this pattern is clear for the *Substrate* treatment but not in the *No substrate* treatment. However, as discussed above, the *No substrate* treatment in the *Vel.67* flow treatment deviates from the overall pattern and could be a spurious result. The additive model, which explicitly assumes the same effect of substrate treatment for all flow velocities, lend support for a continuously decreasing passage time with increasing flow velocity. In particular, the highest flow velocity (0.75 m • s^{-1}; *Vel.75*) is clearly leading to faster passage times than the two lowest flow velocity treatments (0.48 and 0.54 m • s^{-1}; *Vel.48* and *Vel.54*, respectively), assuming this model is representing the real effects correctly. In comparison with the highest flow velocity, the lowest flow velocity leads to a median passage time that is 7.0 times slower (combining both substrate treatments; Table 3).

River discharge has previously been shown to be positively associated to approach and passage rates in Atlantic salmon smolts encountering a barrier in a field study (Nyqvist et al., 2017b). A positive association between discharge and bypass passage without hesitation has also been observed in the field (Tomanova et al., 2021). Harbicht et al. (2021) found that discharge had a minor effect on downstream movement speed of Atlantic salmon smolts in a river with multiple

Table 4
Behavioral variables recorded at A) the ramp, and B) the passageway.

Trial	Treatment	Velocity	Enter:A	A:Tail-first	A:Turn	A:A	A:CB	Enter:CB	CB:A	CB:CB
A: Ramp										
1	No substrate*	Low	NA	NA	NA	NA	NA	NA	NA	NA
11	No substrate	Low	15	15	0	8	7	1	1	0
15	No substrate	Low	30	29	1	18	12	8	8	0
			N = 45	*98%*	*2%*	*58%*	*42%*	*N = 9*	*100%*	*0%*
8	No substrate	High	8	8	0	1	7	1	1	0
34	No substrate	High	8	8	0	0	8	0	–	–
35	No substrate	High	8	8	0	0	8	0	–	–
36	No substrate	High	8	8	0	0	8	0	–	–
			N = 32	*100%*	*0%*	*3%*	*97%*	*N = 1*	*100%*	*0%*
10	Substrate	Low	12	12	0	6	6	2	0	2
13	Substrate	Low	5	5	0	3	2	1	1	0
18	Substrate	Low	11	11	0	4	7	3	1	2
38	Substrate	Low	13	10	3	4	9	1	1	0
			N = 41	*93%*	*7%*	*41%*	*59%*	*N = 7*	*43%*	*57%*
3	Substrate	High	6	6	0	0	6	0	–	–
4	Substrate	High	9	9	0	2	7	1	1	0
37	Substrate	High	6	6	0	2	4	0	–	–
			N = 21	*100%*	*0%*	*19%*	*81%*	*N = 1*	*100%*	*0%*
B: Passageway										
Trial	Treatment		Enter:A	A:Tail-first	A:Turn	A:A	A:CB	Enter:CB	CB:A	CB:CB
1	No substrate	Low	8	8	0	0	8	0	–	–
11	No substrate	Low	8	8	0	0	8	6	2	4
15	No substrate	Low	22	22	0	3	19	20	13	7
			N = 38	*100%*	*0%*	*8%*	*92%*	*N = 26*	*58%*	*42%*
8	No substrate	High	8	8	0	0	8	0	–	–
34	No substrate	High	8	8	0	0	8	0	–	–
35	No substrate	High	8	8	0	0	8	0	–	–
36	No substrate	High	8	8	0	0	8	0	–	–
			N = 32	*100%*	*0%*	*0%*	*100%*	*N = 0*	–	–
10	Substrate	Low	6	6	0	0	6	0	–	–
13	Substrate	Low	3	3	0	0	3	1	1	0
18	Substrate	Low	3	3	0	0	3	0	–	–
38	Substrate	Low	8	8	0	0	8	0	–	–
			N = 20	*100%*	*0%*	*0%*	*100%*	*N = 1*	*100%*	*0%*
3	Substrate	High	8	8	0	0	8	4	3	1
4	Substrate	High	9	9	0	0	9	1	1	0
37	Substrate	High	8	8	0	0	8	0	–	–
			N = 25	*100%*	*0%*	*0%*	*100%*	*N = 5*	*80%*	*20%*

Enter: A = Number of fish entering from the A-direction (from upstream; Arena direction); A:Tail-first: number of individuals entering camera view from the A-direction head-first; A:Turn; number of fish turning their body while in view; A:A = number of fish entering camera view from the A-direction and exiting back in the A-direction; A:CB = number of fish entering camera view from the A-direction and exiting downstream towards the collection-box; Enter:CB = number of fish entering from the CB-direction (from downstream; collection-box direction); CB:A = number of fish entering camera view from the CB-direction and exiting upstream in the A-direction; CB:CB = number of fish entering camera view from the CB-direction and exiting back downstream in the CB-direction. Low flow velocity = 0.48 m • s^{-1} (*Vel.48*); High flow velocity = 0.75 m • s^{-1} (*Vel.75*).

* Video too dark to score behaviors.

barriers. However, river width in the system had a negative effect on speed, and assuming that flow velocity is reduced with increased width (i.e. if discharge remains constant and depth is not substantially reduced), flow velocity may still be a driving factor for migration speed.

Approaching a barrier along with a high flow velocity possibly leads to a shorter time for fish to find and assess appropriate safe passage routes across the barrier (Williams et al., 2012). This may cause the fish to go with the main flow of the river and pass through turbines in hydropower plants. However, with a guiding β-rack that diverts the fish away from the turbines and into a bypass (as used in the present study), the short assessment time available may increase the acceptance rate of the bypass as long as no distinctly aversive cues are present (Williams et al., 2012). The results presented here lend support to this latter hypothesis. Measurements of critical swimming speed of hatchery-reared salmon post-smolts, slightly larger in body size (200 mm fork length) than the fish used in the present experiment, in a large swim tunnel suggests that the highest velocity used (0.75 m • s^{-1}) is close to the upper capacity of smolts (ca 0.8 m • s^{-1}; Remen et al., 2016), and at the bypass passageway it reaches or exceeds 0.8 m • s^{-1} when applying the highest velocity. Possibly, this may decrease the passage time through a "flush out" effect when the smolts reach the passageway. Atlantic salmon have the capacity to sustain swimming at near critical speed for substantial time-frames (up to a few hours) (Hvas and Oppedal, 2017), but this will drain energy and might help explain why the passage rate was very fast at the highest velocity. It should be noted that the fish used in both this study and in Remen et al. (2016) were hatchery-reared and may have a lower swimming capacity than wild salmon smolts due to smaller heart size and higher maximum oxygen consumption rates (Hammenstig et al., 2014). Lower swimming capacity in hatchery-reared Atlantic salmon, compared to wild conspecifics, has been observed for the parr life-stage in the Dalälven population (although using fish from a different hatchery), but the effects at the smolt stage were uncertain due to low sample size (Hammenstig et al., 2014).

Importantly, while flow velocity likely has a positive effect on passage efficiency within the tested range (0.48–0.75 m • s^{-1}), it should be noted that high velocity may also cause problems for downstream migrating salmon. For instance, using horizontally inclined metal-bar racks, velocities exceeding 0.5 m • s^{-1} may cause fish impingement as noted by Tomanova et al. (2021).

The turbulence kinetic energy (TKE) increased markedly with

Table 5
Parameter estimates for models used to analyze behavioral variables.

A: Ramp – Exit direction (GLMM; binomial, logit-link)				
Term	Estimate	SE	*z*	*p*
Intercept	−0.313	0.302	−1.039	0.299
VEL (High)	3.748	1.060	3.536	**<0.001**
TR (Substrate)	0.659	0.438	1.504	0.132
VEL (High) × TR (Sub.)	−2.646	1.238	−2.137	**0.033**
B: Ramp – Obs. duration, in camera view (LMM, log10-transf.)				
Term	Estimate	SE	*t*	*p*
Intercept	1.195	0.205	5.826	**<0.001**
VEL (High)	−0.391	0.253	−1.543	0.168
TR (Substrate)	−0.111	0.261	−0.425	0.683
VEL (High) × TR (Sub.)	0.447	0.352	1.270	0.240
C: Passageway: Obs. duration, in camera view (LMM, log10-transf.)				
Term	Estimate	SE	*t*	*p*
Intercept	0.657	0.107	6.147	**<0.001**
VEL (High)	−0.386	0.133	−2.905	**0.021**
TR (Substrate)	−0.006	0.137	−0.043	0.967
VEL (High) × TR (Sub.)	0.044	0.182	0.239	0.817

GLMM: generalized linear mixed model; LMM: linear mixed model. Terms: TR = substrate treatment (*No substrate* vs. *Substrate*); VEL = velocity treatment (*Low*, *Vel.48* vs. *High*, *Vel.75*). SE: standard error; *z*: *z*-value; *t*: *t*-value; *p*: *p*-value.

increasing flow velocity, but was within the range of what has been reported for Atlantic salmon parr in nature (Enders et al., 2009a). As passage success increased with increased flow velocity, the measured increase in turbulence reported from this study did not appear to have negative effects on smolt passage. While smolts, with their more streamlined body, are better adapted to sustained open water swimming than parr (Jobling, 1995), the ability of smolts to handle turbulence within the range measured through the bypass suggests that substantial negative effect on passage would not be expected (Silva et al., 2020). The TKE measured through the bypass was below values that have been shown to constrain swimming performance (> 0.03 $m^2 \bullet s^2$; Silva et al., 2020). If we had used larger cobbles, larger eddies and vortices would have been created, which potentially could induce problems with postural stability for the smolts (Lacey et al., 2012; Cote and Webb, 2015). Hence, the results may depend on the size of the cobbles used in the bypass.

4.3. Behavioral observations at the bypass

Behavior in the bypass was monitored at the highest and the lowest flow velocity, at the upper section of the ramp and in the passageway. In the ramp, the vast majority of all individuals enter the camera view tail-first, i.e. with the head in the upstream direction. The individuals that did not enter tail-first all changed their orientation before reaching the crest between the ramp and the passageway; hence, all fish entered the passageway camera tail-first. This pattern provides a strong indication that Atlantic salmon smolts choose to pass through surface bypasses backwards, suggesting controlled passive drift with the bulk-flow as it accelerates through the bypass structure (Haro et al., 1998; Vowles et al., 2014). Facing the current also likely facilitates quick escape in case cues of potential danger appear along the bypass.

In the low flow velocity, more individuals return towards the experimental arena at the ramp, as compared to the passageway where the vast majority proceeds downstream. No detectable difference between substrate treatments was detected, but the difference between high and low flow velocity was clearer in the *No substrate* treatment than in the *Substrate* treatment. There was also a positive velocity-effect on the passage rate (duration in camera view) in the passageway, independent of substrate treatment. The general pattern of slower passage rate and more returns in lower flow velocity fits with the general finding that passage efficiency is higher when the flow is faster. The lower propensity to pass downstream at the ramp suggests that a lower flow may give the fish more time to assess the suitability of the passage, leading to a higher rate of avoidance behavior. Accelerating flow, which is observed from the ramp section to the crest of the ramp, is known to induce avoidance behavior in salmonids (Haro et al., 1998; Enders et al., 2009b; Vowles et al., 2014). It is possible that the higher flow, close to the estimated critical swimming speed of hatchery-reared smolts (Remen et al., 2016), could make it difficult to escape back upstream even if aversive cues like flow acceleration are present. However, some individuals were observed to travel back upstream after having passed the cameras in the downstream direction (these observations were not counted in the estimation of returns, which was based on observations where the fish enter from upstream), even at the highest velocity (Table 4), possibly after having rested in the collection-box.

4.4. Passage rate compared to field studies

Passage rate in this experiment was fast, with most individuals

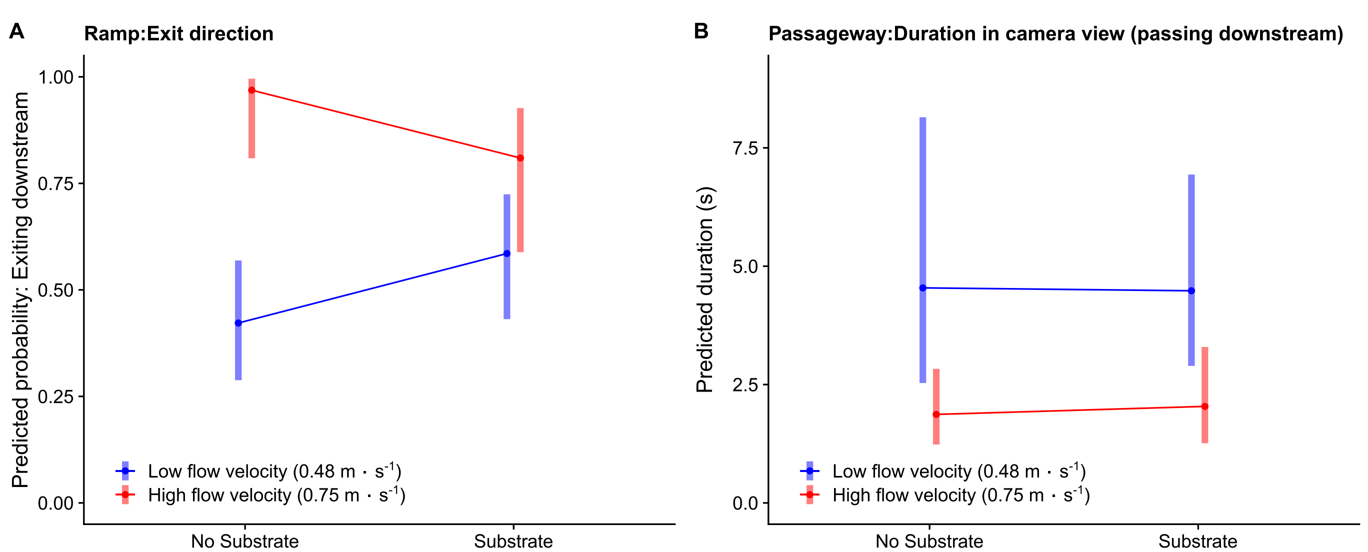

Fig. 5. Behavioral variables with significant effects. A) Predicted probability of exiting the camera view in downstream direction (towards the passageway and catch-box) at the ramp. B) Predicted duration (s) in camera view in the passageway.

passing within one hour after leaving the start-box. Several previous field studies on salmonids encountering barriers suggest that delays at the barrier can last for several days (e.g. Croze and Larinier, 1999; Aarestrup and Koed, 2003). The presence of a guiding β-rack may have facilitated the passage in the experimental setup presented here (Nettles and Gloss, 1987; Nyqvist et al., 2018). A field study where a guidance system was installed to lead salmon smolts to a bypass showed similar delay times in front of the bypass as in the present study, i.e. under one hour for the majority of the fish (Ovidio et al., 2021). It is also possible that the novel environment, which is drastically different from anything previously experienced by the hatchery reared fish used in the trials, could have caused the fish to actively search for an escape route from the arena, but the controlled tail-first movement through the bypass provides, at least speculatively, suggestive evidence against fright-induced escape. Behavior of smolts encountering a barrier after having moved downstream a natural river is likely different than in the present experiment. Hence, delays in a natural system may differ in terms of the delay time in the forebay of a barrier. Nevertheless, the experiment still gives insight into passage acceptance and efficiency.

4.5. Bypass design in a wider context

It is important to note that our results hinge on the fact that there is a guiding β-rack installed that diverges the fish from the main path of the flow when turbines are in operation. Without an angled rack, the discharge through the bypass may have to be substantial compared to the discharge through the turbines, along with relatively low overall discharge in the river, for efficient attraction of the fish to the bypass (Haraldstad et al., 2018). Proportion of inflow to the bypass is in general the most influential parameter for improving bypass efficiency, together with entrance area, according to a meta-analysis (Klopries et al., 2018). An appropriately designed guidance rack can efficiently guide the fish towards a bypass (Fjeldstad et al., 2018), but in such cases the bypass still needs to be accepted by the fish, unless the fish are trapped in a flow exceeding the critical swimming speed, without option for lateral escape out of the current (a scenario which may increase injury rate due to loss of body control).

Trial-and-error approaches are often necessary for finding acceptable downstream passage solutions for human-constructed river barriers (Williams et al., 2012). The present study provides information suggesting that high flow velocity may increase passage efficiency for Atlantic salmon. However, the artificial nature of the experimental setting, where fish placed in a relatively uniform flow in the experimental arena, calls for further validation in field conditions (Johnsson and Näslund, 2018). In nature, fish may avoid the highest flow velocities and thereby delay migration past barriers for this reason. This may be especially true for species that are relatively weaker swimmers as compared to salmonids. Hence, follow-up studies in the field, using a variety of different species, are necessary before recommendations should be made. As discussed in Bowes et al. (2021), which use the same cobble-substrate setup, other implementations of substrate in bypasses could be worth exploring (e.g. Bréton et al., 2013). Furthermore, substrate in other types of bypasses than the one used in this experiment could be beneficial for the fauna of the river. For instance, cobble or gravel substrate dominated nature-like fishways can function well as migration corridors and also be suitable as both habitat and spawning grounds (e.g. Calles and Greenberg, 2007; Gustafsson et al., 2013; Pander et al., 2013).

5. Conclusions

No clear positive effects on passage efficiency could be detected from the addition of cobble substrate in the passageway of the bypass. The possible positive effect detected is, if not spurious, restricted to a very narrow range of water flow, as it was indicated only in the *Vel.67* treatment (0.67 m • s^{-1}). Consequently, our results do not provide support for a positive role of cobble substrate in downstream passage of Atlantic salmon smolts via surface bypass. With respect to flow velocity, higher flow within the tested range (0.48–0.75 m • s^{-1}) led to faster passage, probably due to salmon smolts moving downstream along with the current.

Data availability statement

Data and R-code for analyses are openly available from the figshare repository: https://doi.org/10.6084/m9.figshare.16913044.

CRediT authorship contribution statement

Joacim Näslund: Validation, Formal analysis, Visualization, Data curation, Writing – original draft. **Rachel E. Bowes:** Methodology, Validation, Investigation, Data curation, Writing – review & editing, Supervision, Project administration. **Larry Greenberg:** Conceptualization, Methodology, Writing – review & editing, Supervision, Project administration, Funding acquisition. **Eva Bergman:** Conceptualization, Methodology, Writing – review & editing, Supervision, Project administration, Funding acquisition.

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.2022.106695.

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