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# Global and local behaviour of brown trout (*Salmo trutta*, L.) and chub (*Squalius cephalus*, L.) inside a laboratory vertical slot fishway model

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## ABSTRACT

Fish passes are commonly installed to partially reinstate river connectivity for fish species. They are designed according to the hydrological context and the biological features of the target species. Vertical slot fishways (VSF) still need a design optimization for small fish species, potentially relying on a better knowledge of fish behaviour inside the pools. This work studied the behaviour of two common fish species in France rivers: brown trout (*Salmo trutta* L.) and chub (*Squalius cephalus* L.) while passing through a VSF model. Fish movements were recorded by video tracking and analyzed following two steps: (i) global fish passages and (ii) fish behaviour inside one pool (trajectories, use of resting zones, movement patterns, position, and orientation before a successful upstream move). The mean total efficiencies (i.e. number of individuals that managed to pass and stay upstream over the total number of individuals studied) were 23.6 and 35.7% for trout and chub, respectively. Two behaviours were observed: direct passages in the upstream pool and passages with stops in one or more "resting" zones. Direct passages induced short transit times (several seconds) while a resting behaviour induced longer times (up to several minutes). A preferential resting zone, where flow conditions were the least constraining, was highlighted. Finally, the distance of fish from the slot was identified as a key parameter to ensure a successful passage. These results highlight the importance of the presence of resting zones and their hydraulic conditions for small fish passage success in VSF.

## KEYWORDS

Ecohydraulics; vertical slot fishway; fish passage; turbulent flow

## Introduction

To complete their life cycle, fish have to move between different habitat types. The magnitude and the temporality of these movements are highly dependent on the species and the considered life-stages, respect to their needs for nutrition, resting, or reproduction. River fragmentation by weirs and dams limits or stops these displacements and is one of the main causes of the decline in the distribution and abundance of freshwater and diadromous fish species (Katopodis and Williams 2012; Hameed and Hilo 2021; Hershey 2021). In France, more than 100,000 obstacles to flow have been identified throughout the national hydrographic network. Some of them may impede fish movements, depending on the characteristics of the obstacles, the hydrology, and the swimming abilities of the considered species (Jungwirth 1998).

Although they don't solve the ecological problems caused by the habitat alterations due to the presence of obstacles, fish passes are commonly installed to partially reinstate river connectivity for fish species.

Such devices are able to provide a good passage efficiency if they are designed according to the hydrological context and the biological features of the target species (Odeh 1999; Baumgartner et al. 2018; Ahmadi et al. 2022). To optimize the dimensions of fishways and reduce construction costs, their sizing criteria are often based on the critical swimming speed and the maximal endurance of target fish species (Beamish 1978; Peake, Beamish, et al. 1997; Katopodis and Williams 2012; Katopodis et al. 2019). Data on fish swimming abilities are thus important to design fish passage devices, but a better knowledge of fish behaviour (Liao 2007; Enders et al. 2009; Hockley et al. 2014; Kirk et al. 2017; Harding et al. 2019; Erpicum et al. 2022) inside them should also help to optimize the design criteria.

Vertical slot fishways (VSF) can be suitable devices for a wide variety of fish to migrate (DVWK 2002), allowing fish to pass from a pool to another by swimming through the slots anywhere in the water column (Puertas et al. 2012). Many studies were conducted to improve the design of VSF

respect to fish abilities. However, in many cases, fish abilities were simplified to their maximum swimming capabilities (Puertas et al. 2012). Only a few studies tried to relate fish passage efficiency to the geometric characteristics of the VSF, the hydraulic conditions inside the pools, and fish behaviour (Roscoe and Hinch 2010). Fish behaviour inside the fishway is nevertheless an essential step to identify the link between flow conditions in the pool and the crossing success of individuals, requiring detailed information on the behaviour and movement patterns of identifiable individuals (Bunt et al. 2012).

The use of model fishways in laboratory makes it possible to control the hydrodynamic conditions and to observe individual fish in a pool, from its entrance to its potential exit. Therefore, over the last decade, several laboratory experiments have been carried out in VSF to characterize the relationships between fish behaviour and the hydrodynamic conditions inside the pools (Wang et al. 2010; de Freitas Duarte et al. 2012; Cornu, Baran, et al. 2012; Branco et al. 2013; Rodríguez et al. 2015; Romão et al. 2017; Fuentes-Pérez et al. 2018; Li et al. 2019). These studies showed that the passage of small species (e.g. smallest species than the ones for which fishways were initially designed) or juveniles may not only be limited by high flow velocity values in the slots but also, for example, by turbulence characteristics in the pools, such as turbulent kinetic energy, Reynolds shear stress or vorticity (Noonan et al. 2011; de Freitas Duarte et al. 2012; Bao et al. 2019). The cartography of minimal values of those turbulence characteristics led to the definition of potential resting zones (Calluau et al. 2014) which are known to be stable and observed in devices at laboratory scale as well as field scale (Cornu, David, et al. 2012).

We chose to study one salmonid and one cyprinid species, to be representative of the majority of fish populations in mainland France: brown trout (*Salmo trutta* L.) and chub (*Squalius cephalus* L.), which both are known to be good swimmers. Those species allowed to investigate potential interspecies differences in behaviour: trouts have a pronounced migratory behaviour and the chub is a potamodromous species (Rose et al. 2020) with a very wide distribution, from the middle to the downstream parts of rivers. The aim of this work was to better understand the fish behaviour inside a VSF where flow conditions were restrictive in regard to the fish size and swimming capability. To achieve this goal, different points were considered:

- Is our VSF model efficient in regard to the harshness of flow conditions with respect to fish

size and swimming capability?

The local and total efficiencies of our VSF model were analyzed and compared to other studies with laboratory VSF model as well as in-situ VSF.

- How long does it take for a fish to pass through a pool and how long resting periods could be during a passage?

The transit and holding times inside the pool have been measured. The ratio of resting behaviour durations compared to those of direct passages was analyzed.

- Which zones of a pool are the most occupied? Do fish have a preferential route?

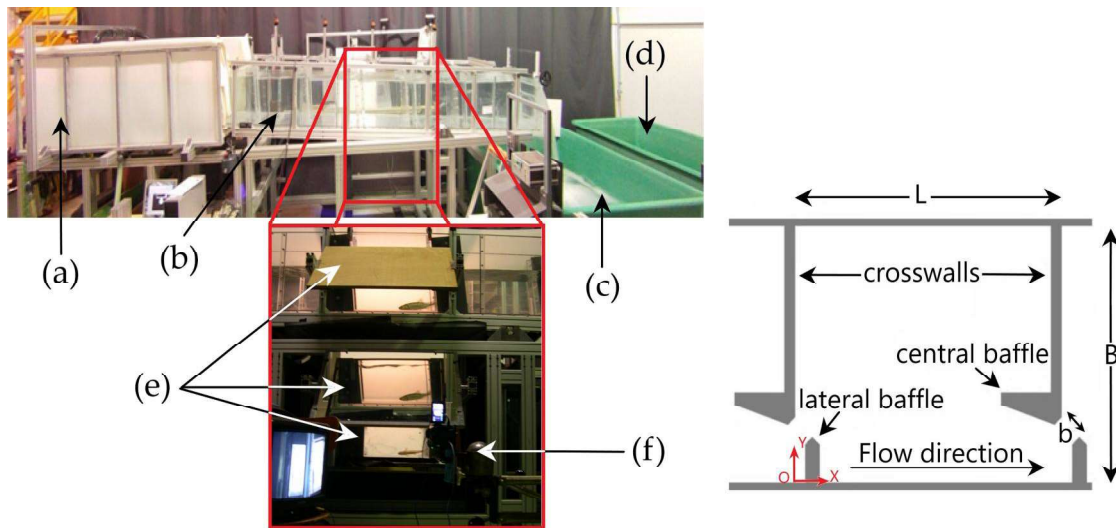
Based on the definition of possible resting zones (Calluau et al. 2014), movement patterns and trajectories inside the pool were identified as well as preferential and favourable zones from which fish can pass upstream successfully. A focus was made on the last position and orientation of fish just before leaving a zone for another.

## Methods

### Experimental device

The used VSF model has previously been described in detail (Tarrade et al. 2011). It consisted of five similar pools of length  $L=0.75$  m, height  $H=0.55$  m, and width  $B=0.50$  m (Figure 1). The width of the slot was  $b=0.075$  m. The slope was set to 7.5% and the discharge to  $23 \text{ L}\cdot\text{s}^{-1}$ . The VSF model was designed to reproduce flow conditions observed in a real scale VSF (Cornu, David, et al. 2012) situated at Vichy in central France, where fish behaviour was also investigated by both analyzing video recordings of fish inside a pool and by counting fish passage using telemetry. Each pool was made of plexiglass covered with black paper to ensure environmental conditions as close as possible to real ones from the fish point of view. Only the third pool (P3) was not covered to observe fish movements. A mirror was positioned at a  $45^\circ$  angle under this pool, to allow fish visualization and image acquisition from above.

Fish behaviour and positioning were continuously recorded, over a period of 90 min, by a video camera (SONY, HDR-HC9E model). This limit of 90 min was chosen after some preliminary tests that showed no significant evolution of the observed results after this period of time, according to other studies (Cornu, Baran, et al. 2012; Romão et al. 2018). The acquisition frequency was 25 fps. Frosted plexiglass plates were positioned above the pools to obtain video images without reflected light. The video recording device was blacked off with a tarp



**Figure 1.** Experimental device: (a)-upper water filling tank, (b)-vertical slot fishway model [geometry of a pool detailed on the right part of the figure, and see (Tarrade et al. 2011)], (c)-pump tank, (d)-stall tank with four compartments, (e)-mirrors for fish observation and image acquisition for lateral view and lower view of the pool, and (f)-camera.

to avoid light reaching the monitored pool from below.

Water for the experiments was drawn from the domestic water supply and pumped through the system at least one week before experiments to ensure dechlorination. A temperature regulation system was installed in the lower tank. It consisted of a copper coil supplied with chilled water flow controlled by a valve to maintain the desired temperature in the installation. The water was checked for temperature daily. A filter pump was set up in the stall tank and recirculation pump was set up between the lower and the stall tanks to ensure good oxygenation of the water and homogenization of the temperature between the VSF model and the stall tanks.

Four stall tanks provided the fish with resting conditions similar to experimental conditions. Differences in water temperature between experiments were limited (mean  $\pm$  SD temperature =  $16 \pm 0.3$  °C). The room was illuminated with projectors at constant brightness between 8:00 am and 6:00 pm.

### Flow conditions

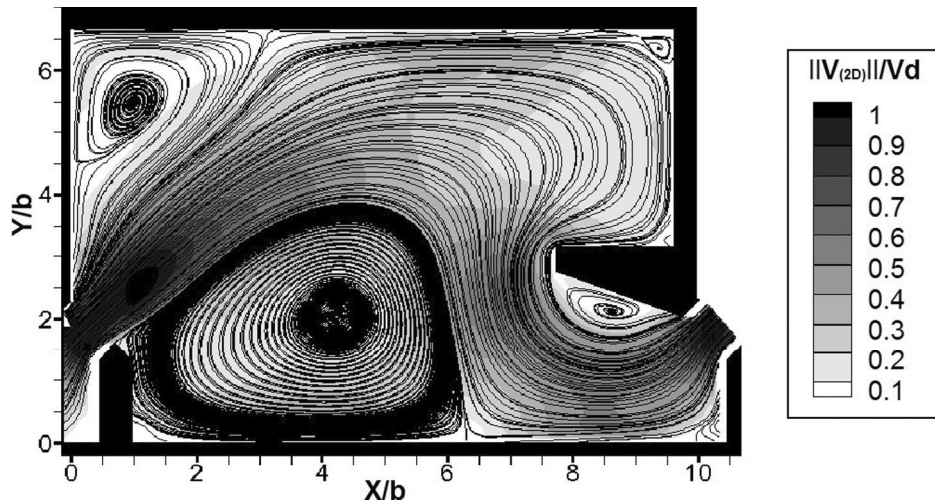
Hydrodynamic conditions inside the pool have been previously described (Tarrade et al. 2011; Callaud et al. 2014). Flow visualizations and two velocity components measurements by Particle Image Velocimetry (2C-2D PIV) were performed (Tarrade et al. 2011) to obtain the flow topology in pool P3. Under the experimental conditions, the jet from the slot had a significantly curved shape. It impacted the opposite side wall and generated two contra-rotating large swirls in the upstream corner of the pool and in the convex part of the jet (Figure

2). This flow topology corresponded to the FP2 topology previously described by Wang et al. (2010) and Tarrade et al. (2011). The maximum velocity value was reached in the jet and was  $1.1 \text{ m}\cdot\text{s}^{-1}$  based on the water depth, and the volumetric dissipated power in the pool was  $110 \text{ W}\cdot\text{m}^{-3}$ .

### Fish capture

Two common fish species known to be good swimmers in France rivers were used in this work: chub (*Squalius cephalus* L.) and brown trout (*Salmo trutta* L.). Chubs were collected from the “Petite Blourde” stream, a tributary of the Vienne River, in central France. Sampling was conducted using an electrofishing technique (DREAM Electronique company, HERON<sup>®</sup> model). Ninety chubs, divided into 3 batches of 30 individuals, were placed into three stall tanks (Figure 1). The size and weight of fish were measured: mean total length (TL)  $\pm$  SD =  $12.1 \pm 2.0$  cm and mean weight (W)  $\pm$  SD =  $17.2 \pm 8.6$  g on the sample population of 90 chubs (the values for each batch are given in Table 1). Trouts were obtained from the Cauterets hatchery in southern France. The 120 trouts, divided into 4 batches of 30 individuals, were also introduced into the 4 stall tanks. Their size and weight were measured: mean total length TL  $\pm$  SD =  $10.2 \pm 0.6$  cm and mean weight W  $\pm$  SD =  $10.1 \pm 1.9$  g on the sample population of 120 trouts (the values for each batch are given in Table 1). Fish were kept in the stall tanks one day before the beginning of experiments to reduce the stress caused by their caught and the transfer from their initial environment to the laboratory. They were left without food. Experiments were conducted in autumn for practical reasons (e.g. to limit water temperature in the laboratory): in October for chubs and





**Figure 2.** Flow streamlines and mean velocity-norm isocontours (dimensionless values where  $b$  is the width of the slot and  $V_d$  is the velocity in the slot) obtained by PIV measurements in pool P3 (Tarrade et al. 2011).

**Table 1.** Mean values and standard deviation ( $SD$ ) of the total length (TL) and weight (W) for the three batches of 30 chub individuals each and for the four batches of 30 trout individuals each.

Batch number	Chub		Batch number	Trout	
	TL $\pm$ SD (cm)	W $\pm$ SD (g)		TL $\pm$ SD (cm)	W $\pm$ SD (g)
1	12.5 $\pm$ 1.9	17.7 $\pm$ 8.7	1	10.2 $\pm$ 0.7	10.6 $\pm$ 2.5
2	10.3 $\pm$ 1.4	10.0 $\pm$ 3.9	2	10.1 $\pm$ 0.5	9.6 $\pm$ 1.7
3	13.6 $\pm$ 1.1	23.9 $\pm$ 5.9	3	10.2 $\pm$ 0.6	10.0 $\pm$ 1.8
			4	10.2 $\pm$ 0.5	9.9 $\pm$ 1.4

November for trouts. Once the experiments were completed, the fish were released into their original environment.

One can find in the literature (Peake, McKinley, et al. 1997; Garner 2006; McKenzie et al. 2007) some data about the critical swimming speed ( $U_{crit}$ ) of fish as a function of their size and water temperature. On the other hand, Videler (1993) defined the maximum swimming speed of fish from their body size. This maximum swimming speed can be considered as the burst speed (Baudoin et al. 2014; Kreutzenberger et al. 2020). Considering the body size of our experimental target species, chubs and trouts were supposed to present maximum swimming speeds of about 0.90 and 0.76  $\text{m}\cdot\text{s}^{-1}$ , respectively. Thus, with respect to their theoretical swimming abilities, the tested individuals were placed in challenging velocity conditions in our VSF model (the mean velocity in the jet being about 1.1  $\text{m}\cdot\text{s}^{-1}$ ). A priori, the dissipated power was not restrictive in this case.

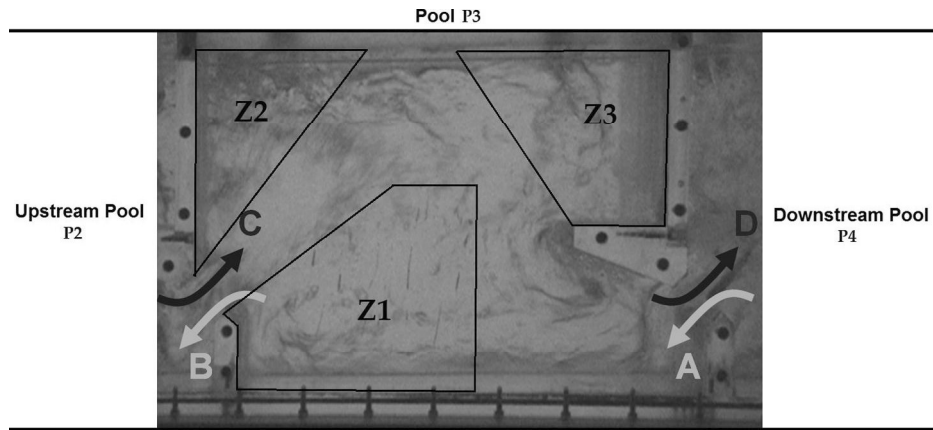
### Experimental procedure

After starting the water feeding of the model and waiting for the water level in the pools to balance, a group of 20–25 individuals (of a single species), randomly selected from a batch in a fish tank compartment, were transferred to the downstream pool (P5) that was separated from the upstream pools by a

screen. The fish were held in pool P5 for 15 min before each test to allow them to adapt to the new flow conditions (Tan et al. 2019). The screen was then removed and the experiment began for a duration of 90 min, after which the trial was stopped and the fish were transferred to another fish tank compartment. A total of 18 trials were conducted: 11 for chubs and seven for trouts. Each batch of fish was used at least two times for the experiments (maximum four times for chubs and two times for trouts). This implies that the total number of fish used during the experimentations was higher than the number of caught individuals (263 chubs and 144 trouts were effectively used during the experiment). Consequently, fish learning could not be completely avoided but a minimum of one day of rest (sometimes more than one day taking into account the alternance of used batches) assured to avoid a bias due to fish fatigue.

### Video analysis and fish-behaviour descriptors

The tested individuals were not individually marked, but as a maximum of 5 individuals swam at the same time in P3, it was possible to collect different observations about individuals' behaviour with a two steps video analysis (see below). The software used for the sequence analysis was Virtual Dub 1.9.10 which allowed visualizing the video frame by



**Figure 3.** Basic movements of fish between pools (A, B, C, D) and potential resting zones (Z1, Z2, Z3) in pool P3 identified based on a combination of three hydrodynamic quantities (velocity, turbulent kinetic energy and vorticity) determined in Calluaud et al. (2014).

frame. Then, the image analysis was made with Gimp 2.6.11 software.

The first step of video analysis was to determine the global fish movements in the VSF. The number of entries in pool P3 was counted as well as the number of exits. A differentiation was made between upstream movements and downstream movements. Consequently, four basic movements between pools were defined (Figure 3):

- A: a fish entered the pool through the downstream slot,
- B: a fish exited the pool through the upstream slot,
- C: a fish entered the pool through the upstream slot,
- D: a fish exited the pool through the downstream slot.

Then, these basic movements were combined to create four crossing events which represented the different possible movements between successive pools:

- AB: a fish passed through the pool, heading upstream, which corresponded to a Successful Upstream Move (SUM),
- AD: a fish entered the pool, but washed back later to the downstream pool, which corresponded to a Failed Upstream Move (FUM),
- CB: a fish washed back from the upstream pool, then exited upstream again, which corresponded to a Failed Downstream Move (FDM),
- CD: a fish washed back from the upstream pool and exited downstream, which corresponded to a Successful Downstream Move (SDM).

The second step of the analysis was meant to investigate in details the fish behaviour inside pool P3. A particular attention was paid to three zones in the pool (Z1, Z2, and Z3), previously identified as potential resting zones (Bermúdez et al. 2012; Calluaud

et al. 2014). Those zones were defined based on a combination of the lowest velocity (lower than  $0.47 \text{ m}\cdot\text{s}^{-1}$ ), the lowest turbulent kinetic energy (lower than  $0.066 \text{ m}^2\cdot\text{s}^{-2}$ ), and the lowest vorticity (lower than  $10.41 \text{ s}^{-1}$ ) zones, determined from previous experiments in same flow conditions (Calluaud et al. 2014; Ballu 2017). Firstly, the fish behaviour was decomposed into two distinct attitudes: a movement characterized by a significant displacement either between pools (i.e. crossing a slot) or inside the pool, or a resting period corresponding to a fish holding its position for at least 5 s. Secondly, fish trajectories as they entered in the pool P3 and the proportion of access to the different zones or to another pool from a given zone were analyzed. The chronologically tracking of the crossed zones enabled to identify the 4 first moves of fish after entering the pool. These moves were used to construct movement patterns for individuals finally crossing the upstream slot. A differentiation between a direct passage in the pool and a passage with resting times was made; each time a fish rested in a given zone, the resting time and the corresponding zone were noted. Thirdly, an appreciation of the fish movement was made to determine if a change of zone was due to an actively swimming movement of the fish recognized as a voluntary motion or if the fish was subjected to the surrounding flow (mainly the jet) and could not control its displacement. Video analysis enabled to consider an active swimming movement based on the movement of the fish tail and paired fins. Finally, the position and orientation of the fish in the zone before its leaving were particularly considered.

### Indicators considered

Two different durations were measured during the experiments: the transit time and the holding time. The transit time corresponded to the time for a fish to pass through the pool. The timing began when a

part of the fish entered the pool and ended when its entire body left it. The holding time corresponded to the time a fish stayed in a given zone with a stationary movement. In cases of passage with resting periods, the transit time corresponded to the sum of the holding times and the times between each resting period.

Two types of efficiencies were also defined: the total efficiency ( $Eff_{total}$ ) and the local efficiency ( $Eff_{local}$ ). The total efficiency of the VSF model compared the number of fish that managed to pass and stayed upstream ( $N_{fishup}$ ) to the number of fish used in the trial and that were put in pool P5 ( $N_{trial}$ ):  $Eff_{total} = N_{fishup}/N_{trial}$ . The local efficiency compared to the total number of successful upstream movements ( $N_{SUM}$ ) to the number of entries in the pool by the downstream slot ( $N_A$ ):  $Eff_{local} = N_{SUM}/N_A$ .

Finally, two indices were defined: the attractive index ( $AI$ ) and the downstream index ( $DI$ ). The attractive index was used to determine if the fishway was attractive so it compared the total number of entries in the pool P3 by the downstream slot ( $N_A$ ) to the number of fish in the trial considered ( $N_{trial}$ ):  $AI = N_A/N_{trial}$ . This index could be  $>1$  if one or more fish entered many times in the pool because of one or more successful downstream movements. The downstream index was used to compare the number of observed downstream movements ( $N_C$  and  $N_D$  from the upstream and downstream slots, respectively) to the number of observed upstream movements ( $N_A$  and  $N_B$  from the downstream and upstream slot, respectively):  $DI = (N_C + N_D)/(N_A + N_B)$ .

## Statistical analysis

Statistical analysis was conducted with the SciPy library in Python environment and validated with R software v2.13.1. Non-parametric statistical analysis (Kruskal–Wallis and Mann–Whitney tests) was used to compare (i) fish transit time through the pool for the crossing events between the species and (ii) fish holding time in the three different zones between the species. We also used homogeneity  $X^2$  test with Yates continuity correction to compare the distribution of fish associated with different patterns of using the resting zones in pool P3.

## Results

Whatever the species, upstream (A) and downstream (C) movements occurred. They were accomplished with or without rest in the different zones identified earlier (Figure 3).

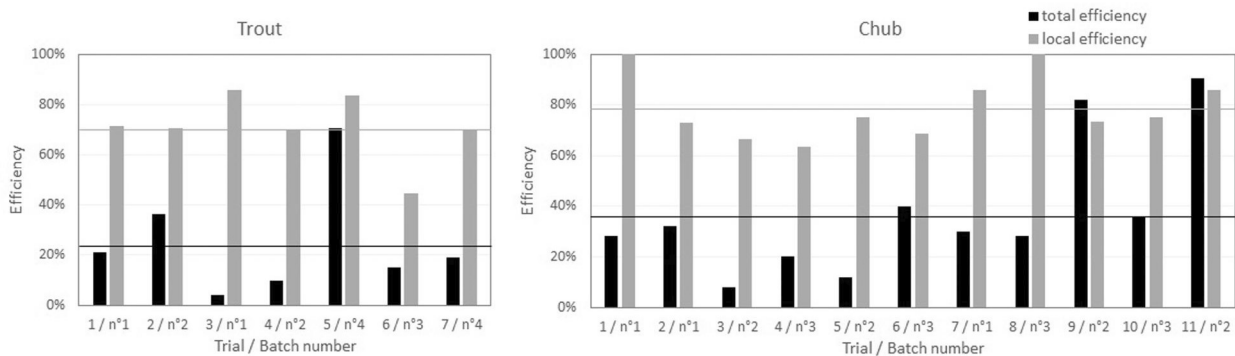
### VSF efficiency

A total of 396 movements were observed for the 407 fish used in the experiment (Table 2). The successful rate is based on the successful upstream movement and was about 10.6 and 11.5 slot crossing per hour for trout and chub, respectively.

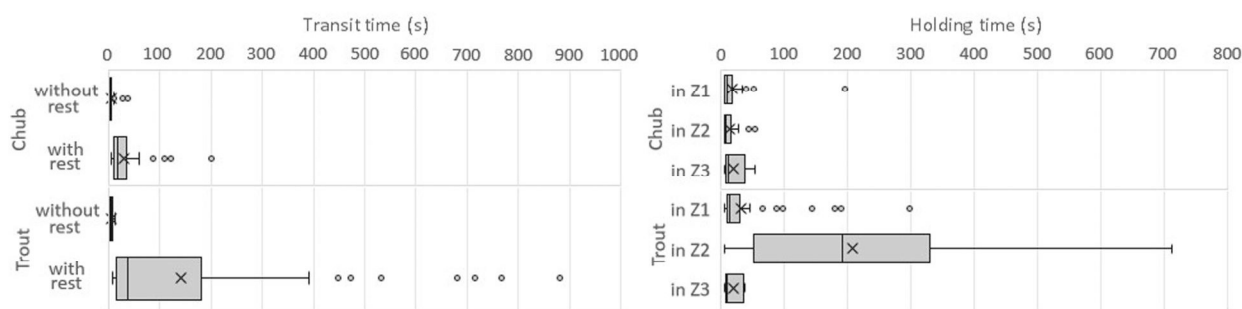
The mean total efficiency of our VSF model was 23.6% for trout and 35.7% for chub. However, this value is only a mere indicator since this parameter depends greatly on the trial (Figure 4). This variability can be explained by an important number of downstream movements (CD) and also by a

**Table 2.** Count of basic upstream movement (A), downstream movement (C), and crossing events for trout and chub as well as the number of observations of resting periods in a given pool.

Species	Total number of fish	Movement	Number of observations	Crossing event	Number of observations	Resting	Number of observations
Trout	144	A	110	AB	77	yes	49
						no	28
				AD	33	yes	26
		C	44			no	7
				CB	1	yes	1
						no	0
Chub	263	A	186	AB	146	yes	28
						no	118
				AD	40	yes	24
		C	56			no	16
				CB	4	yes	4
						no	0
		CD	52	yes	10		
				no	42		



**Figure 4.** Total efficiency (black) and local efficiency (grey) for trout (left) and chub (right). Values are reported for each trial and batch number. The mean values are represented by the horizontal lines of corresponding colours.



**Figure 5.** Left: Transit time of chub and trout with or without staying in the resting zones. Right: Holding time of chub and trout in the different zones in pool P3 in the case of fish resting at least 5 s in a given position during their passage in the pool. The cross corresponds to the average value, the box is delimited by the first and third quartile and the line in the boxes corresponds to the median value.

potential of fish learning (especially for chubs that managed to pass through the fishway more times than trouts). On the contrary, mean values of local efficiency, which takes into account only the number of movements and not the number of fish, were quasi constant over trials and of higher values than the mean total efficiency, with 70.0 and 78.5% mean values obtained for trout and chub, respectively. This difference can be explained by considering the attractive index and the downstream index. Here, *AI* values were about 76.4 and 70.7% for trout and chub, respectively while *DI* values were about 63.8% for trout and 44.0% for chub.

### Transit and holding times

Two different behaviours were observed: a direct passage without resting in the pool and a passage with stops in one or more resting zones, previously defined from hydraulic descriptors (Calluaud et al. 2014). The transit times including resting behaviours were significantly greater, for both species than those of direct passages (Mann-Whitney  $p < 0.05$ , left part of Figure 5). For direct passages, the median transit times of trout (4.44 s) and chub (4.02 s) were the same (Mann-Whitney  $p > 0.05$ ). When a resting behaviour was observed, the transit times were significantly greater for trout than for

chub, respective median time: 38.4 and 18.0 s (Mann-Whitney  $p < 0.05$ ).

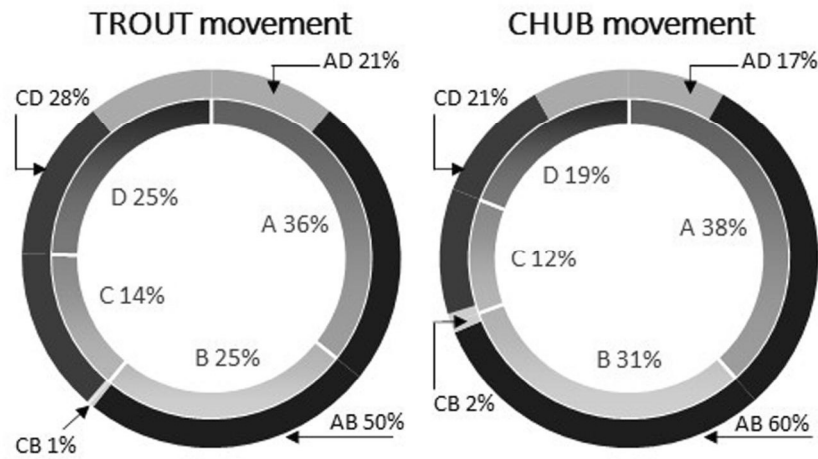
There were no significant differences in chub holding times between the three resting zones of the pool (median holding time: 10.0 s in Z1, 8.0 s in Z2, and 11.3 s in Z3, Kruskal-Wallis  $p > 0.05$ ). On the other hand, trout spent more time in Z2 (median time = 191.0 s) than in the other zones (13.0 and 10.0 s in Z1 and Z3, respectively) (Mann-Whitney  $p < 0.05$ ). Trout spent more time than chub in Z1 and Z2 (Mann-Whitney  $p < 0.05$ ), while both species spent the same amount of time in Z3 (Mann-Whitney  $p > 0.05$ ).

### Fish movements in a given pool

Within SUM, movements with a resting behaviour represented 64 and 19% for trout and chub, respectively (Table 2). Within SDM, these proportions were 28% for trout and 19% for chub. All fish that washed back from the upstream pool and exited upstream again took a rest during their passage in the pool. Finally, the percentage of resting behaviour for fish entering the pool through the downstream slot and washing back by the same way was 79 and 60% for trout and chub, respectively.

The repartition of basic movements and corresponding crossing events for trout and chub are





**Figure 6.** Inner circle: Proportions of movements (A, B, C, D). Outer circle: Crossing events (AD = FUM, AB = SUM, CB = FDM, CD = SDM) observed in the VSF model for trout (left) and chub (right).

given in Figure 6. SUM represented the major part of events (50 and 60% for trout and chub, respectively). Almost all fish that crossed the upstream slot on an upstream movement (i.e. crossing events AB and CB) came from the downstream pool, with the percentage of scenario CB being very low in comparison to SUM (scenario AB). This also implies that most of the fish coming from the upstream pool (CB and CD scenarios) slide down to the downstream pool (28 and 21% for CD vs. 1 and 2% for CB of the total movements for trout and chub, respectively).

### Upstream movement patterns

In the case of an SUM, the upstream movement patterns were defined from the four first moves of fish entering the pool by the downstream slot (Figure 7). The movement pattern of fish during their passage in the pool depended greatly on the species and on the direct/resting passage.

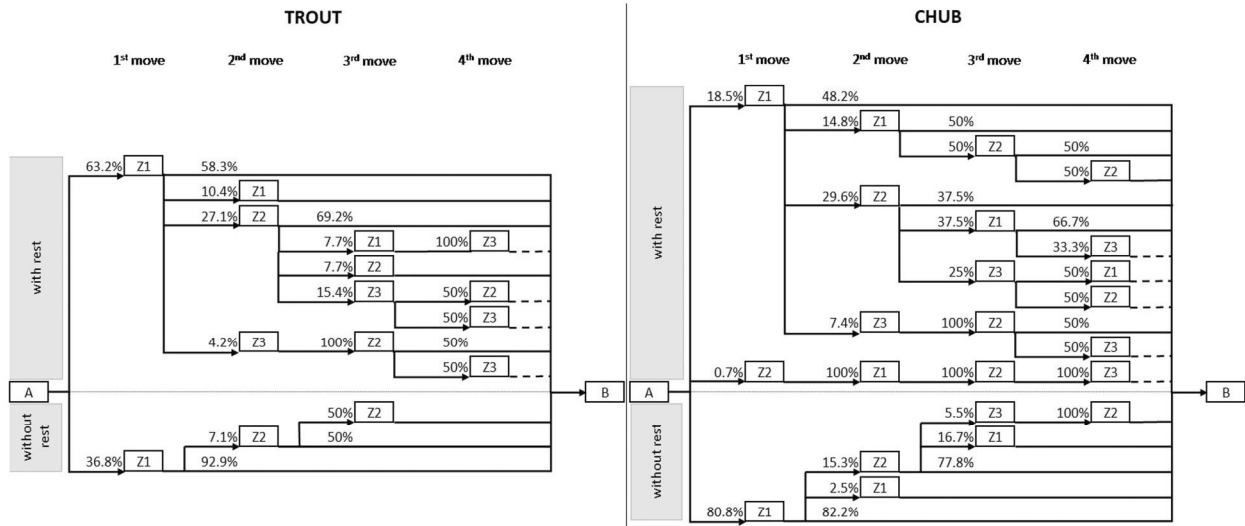
Whatever the species, the movement pattern was simpler and shorter if fish directly went from the downstream slot to the upstream pool. A maximum of 4 and 5 moves were observed for trout and chub, respectively. A major part of chub (80.8%) chose a direct passage in the pool while a lower percentage of trout (36.8%) chose this option ( $X^2 = 45.3$ ,  $df = 1$ ,  $p < 0.05$ ). Moreover, the individuals of both species started by a passage in the zone Z1. After entering Z1, 92.9 and 82.2% (trout and chub, respectively) of fish directly accessed to the upstream pool from this zone. After a brief exit of Z1, some of the fish still present in the pool returned to Z1 while some went to Z2 to access the upstream pool after some change of zone. None of the trout used the zone Z3, and only a few percentages of chub used this zone. Finally, none of the fish exited the pool by the upstream slot from the zone Z3.

The movement pattern for a passage with resting periods is more complex, whatever the species. However, while all the trout that chose to rest during their passage in the pool first went to the zone Z1, a few percentages of chub (0.7%) chose to go to the zone Z2 after entering the pool from downstream, which complexifies the pattern even more. It is however noted that this behaviour could be considered as insignificant since it concerned only 2 chubs over a population of 263 fish. In the latter case, more than 5 moves were needed to achieve the passage of the pool as indicated by the dotted line in Figure 7.

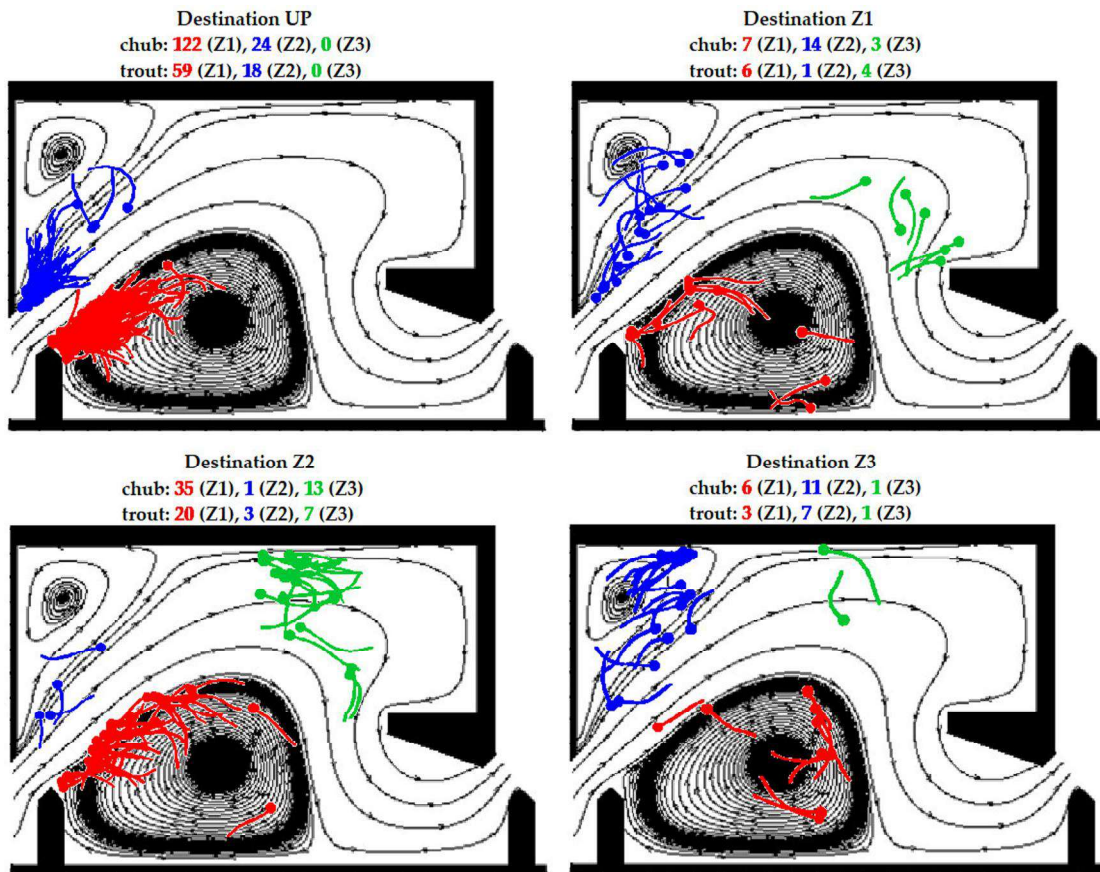
While the zone Z3 was used only by a few chubs when directly passing through the pool, this zone was used by some trouts and chubs as a resting zone. The zones Z1 and Z2 were always the preferred zones before the exit of the pool by the upstream slot. Even with a denser attendance, none of the fish, trout, and chub together, exited the pool from the zone Z3. The maximum number of moves between zones was also higher for chub (16 moves) than for trout (11 moves). The chub appeared to be more mobile in the pool even if their transit time was lower (Figure 5).

### Fish position and orientation inside a pool

The position of each fish in the pool before crossing the upstream slot or changing of the zone was recorded. The video analysis enabled to collect the position of fish head and the orientation of its body, just before a change of zone in the pool or a passage to the upstream pool. The fish position and the flow inside the pool (mean streamlines known from (Tarrade et al. 2011), shown in Figure 2) were gathered for a better visualization of possible relationships (Figure 8).



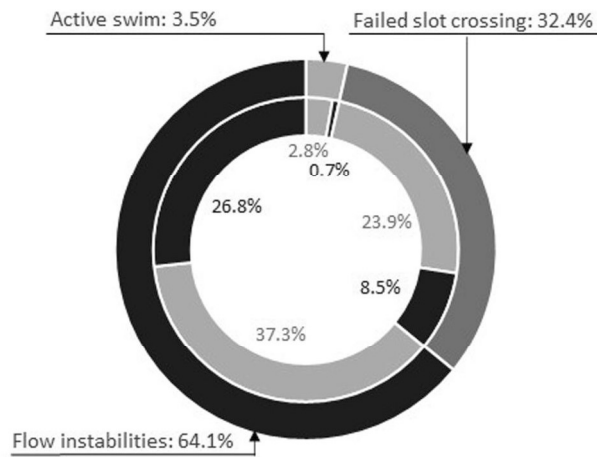
**Figure 7.** Movement patterns of trout (left) and chub (right) determined from the 4 first moves of fish in the pool, in the case of a SUM. The upper part of the diagrams considers fish using resting zones and their lower part considers a direct passage to the upstream pool (without resting). Dotted lines indicate that there are still some moves before reaching the upstream pool.



**Figure 8.** Last position and orientation of fish before leaving an origin zone (Z1: red, Z2: blue, Z3: green) towards the upstream pool (destination up, top left graph) or another zone (Z1: top right graph, Z2: down left graph, Z3: down right graph). The fish position and orientation are superimposed to the mean streamlines in the pool obtained from a previous study (Tarrade et al. 2011). No difference is made between trout and chub, but the number of individuals of each species is indicated on top of each graph.

This representation clearly showed that, as mentioned before, no fish coming from the zone Z3 succeeded to cross the upstream slot. 81.2% of fish came from the zone Z1 (76.6% of trout individuals

and 83.6% of chub individuals). Moreover, for a SUM, the head of fish was oriented towards the upstream slot, and its body was aligned with the streamlines in the jet.



**Figure 9.** Outer circle: Proportion of the different reasons (active swim—light grey, slot crossing attempt failure—dark grey and flow instabilities—black) for fish to make a change of zone in the pool during a SUM pattern. Inner circle: Proportion of chub (light grey) and trout (black) concerned by each reason for a zone changing.

As mentioned before with movement patterns, the probability to return in the same zone after quitting it is non-null. In fact, 5.8% of fish leaving the zone Z1 returned to Z1 and this behaviour was also observed for Z2 (1.8%) and Z3 (0.9%). In order to quit a zone, the head of the fish must be oriented towards the outside of the zone. The combination of the orientation of the fish's body and its location inside the pool at this time allowed to predict where it will be next. For example, if a fish located in Z3 was near the central baffle, then it went to Z1. On the contrary, if it was close to the wall, it went to Z2.

A third of fish (38.6%) move to another zone during their passage in the pool before accessing the upstream pool. Three reasons were identified (Figure 9): (i) a voluntary motion (active swim) to another zone in the pool, (ii) a slot crossing attempt failure leading to a passage in the jet and a release in one of the zones in the pool, and (iii) flow instabilities inside the zone leading to an ejection of the fish from the zone. For the two last cases, the fish was exposed and subjected to the flow without apparent control of its movement.

Whatever the species, a voluntary motion between zones in the pool was circumstantial (0.7 and 2.8% for trout and chub, respectively for a total of only 3.5%). On the contrary, flow instabilities were the main cause of motion between zones up to a total of 64.1% corresponding to trout for 26.8% and chub for 37.3%. The rest was due to a failed attempt at the slot crossing. In this latter case, the proportion of chub was significantly higher (23.9%) than trout (8.5%). Moreover, the passage from Z1 to Z2 was mainly due to a slot crossing attempt failure, up to a proportion of 69.1%. These failed tentative may be due to a too intense flow conditions for fish to handle or to a too long distance from the slot since the beginning of the attempt. In fact, the percentage of

access to the upstream pool was the highest when the fish was coming from a distance equivalent to the width of the slot and decreased to become null for distances higher than 4 times the width of the slot (Figure 10 left).

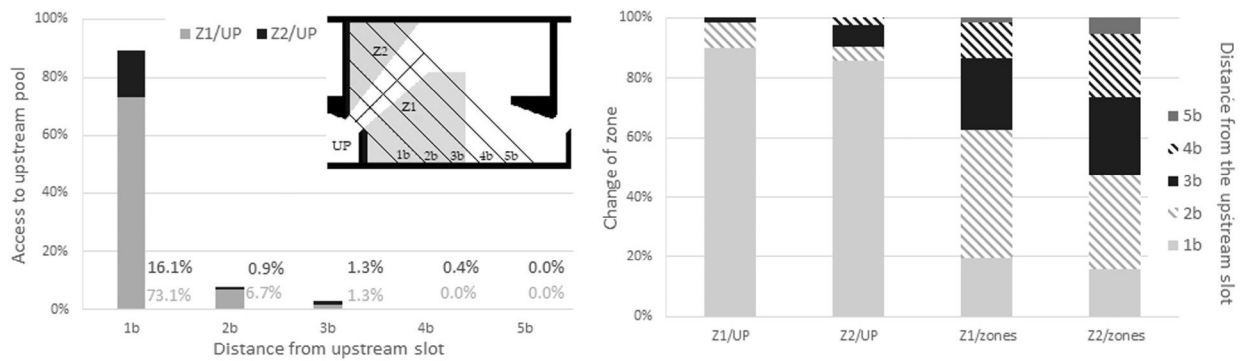
The closer the slot, the higher the chance to cross the upstream slot. 90.1% of fish in Z1 and 85.7% in Z2 accessed to the upstream pool from a distance lower than the width of the slot (Figure 10 right). This represents 89.2% of the 223 fish observed crossing the upstream slot (73.1% from Z1 and 16.1% from Z2). Then, the chance to access to the upstream pool decreases drastically with the distance from the slot, but the probability for a fish to go to another zone increased with this distance.

## Discussion

### VSF efficiency

VSF efficiency values often reported in the literature (Bermúdez et al. 2012; Rodríguez et al. 2015; Bao et al. 2019; Tan et al. 2019; Dębowski et al. 2022) are generally around 70% but they depend greatly on flow conditions and on the species and their body size. In fact, bighead carps (*Hipophthalmichthys nobilis*) of mean total length  $\approx 11$  cm exhibited an efficiency of about 69.7% in a VSF model in laboratory (Tan et al. 2019). However, this value needs to be put in perspective with the flow velocity within the slot which was lower (about  $0.3 \text{ m}\cdot\text{s}^{-1}$ ) than the maximum swimming speed of fishes (around  $0.7 \text{ m}\cdot\text{s}^{-1}$ ). On the contrary, high values of mean total efficiency could also be obtained with higher flow velocity conditions if the fish length was in accordance. A study by Dębowski et al. (2022) reported a 70% mean efficiency value for 8 species encountered during a 4 years period of observation of a VSF on the longest Baltic River (mean flow velocity of  $1.7 \text{ m}\cdot\text{s}^{-1}$ ). In this





**Figure 10.** Left: Percentage of access to the upstream pool from Z1 (grey) and Z2 (black) as a function of the distance from the upstream pool, expressed as a function of the slot width  $b$  (1–5 times the width  $b$  of the slot). The insert represents the zones Z1 and Z2 in the pool and the distance from the slot (from 1b to 5b). Right: Proportion of access to the upstream pool or zone changing from Z1 and Z2, conditioned by the distance from the upstream slot.

study, only 2 over 115 tagged fish were of small size (mean total length = 14 cm) while all others were larger (length comprised between 25 and 92 cm). Other studies with intermediate flow velocity conditions [between  $0.7$  and  $1.1 \text{ m.s}^{-1}$  (Bao et al. 2019) and  $1.2$  and  $1.4 \text{ m.s}^{-1}$  (Bermúdez et al. 2012; Rodríguez et al. 2015)] reported variable values of efficiency for different species of different lengths (from 9 to 43 cm). They observed that the efficiency increased with the fish length. From this point of view, our value of mean total efficiency of about 30% is in accordance with the literature for VSF model in laboratory as well as in-situ VSF.

Our results also showed that the efficiency could depend on the trial (Figure 4). Variations of total efficiency were observed not only between trials of different batches but even between trials of the same batch. As experiments were conducted over a short period, we can impute this observation to some fish learning bias, at least for the second batch of chubs. A way to limit this bias in our observations is to consider the local efficiency. In fact, it has been shown (Figure 4) that the local efficiency was mostly constant over all the trials for both trouts and chubs. This can be explained by the difference in definition of both efficiencies: one is based on the number of fish that managed to pass through the fishway (total efficiency) while the other is based on the number of successful upstream movements (local efficiency). Moreover, the dependency of the efficiency on the trial was also observed in other studies from the literature. In fact, studies conducted at different times in the same VSF model with the same experimental conditions (Bermúdez et al. 2012; Rodríguez et al. 2015) led to different efficiencies for brown trout: mean efficiency of 36% for fish length comprised between 15 and 20 cm, and 63% for length comprised between 20 and 25 cm during the first period and 14 and 43% for similar length ranges during the second period.

Finally, note that the final efficiency values greatly depend on fish motivation to move upstream, which can be very different between different studies (season, water temperature, level of fish stress ...) and especially between laboratory and field studies (but see below the discussion part about scale effects).

### Transit times

The transit time of fish has been evaluated in our VSF model. Only a few seconds (about 4 s) were necessary to pass through the pool for trouts and chubs when passing without resting in the pool. Another study (Tan et al. 2019) reported short transit times of the same order (considering the size of the VSF), between 18 and 26 s depending on the discharge: the higher the discharge, the longer the transit time. They did not mention differences between a direct passage and a passage with resting periods but in our case, the transit time was significantly impacted by resting periods, especially for trouts for which it could take a few minutes to pass through the pool. For slightly higher flow velocity (about  $1.2$ – $1.4 \text{ m.s}^{-1}$ ), a study by Bermúdez et al. (2012) reported averaged resting times of 412 s for brown trout in different zones of the pool. These values are slightly higher than ours (median value of 191 s when resting periods were observed) and no difference in resting time was mentioned between the zones Z1 and Z2, the zone Z3 being less occupied by all fish. In the present case, the resting time in Z2 for trout was the longest while they stayed for a shorter time both in Z1 and Z3. Even higher transit times can be registered for the passage of in-situ VSF. For example, it has been highlighted (Dębowski et al. 2022) that a transit time of several hours to days can be registered for different species to pass the entire in-situ fishway. This difference in transit time is mainly explained by the size and the number of pools to pass as well as harder flow



conditions (higher flow velocity) but it must not be neglected because of the fish fatigue that results from a long-time passage. These results underline the importance of better understanding the behaviour of different species in VSF, to provide hydraulic conditions in the pools that minimize both times of passage and fatigue for fish. The design of VSF must lead to the creation of resting zones, well placed in the pool (such as the zone Z1), to favour the success of crossing attempts.

### **Zone occupation inside a pool**

Our study has shown that fish can adopt different behaviours when crossing a vertical slot fishway pool, either for individuals of the same species or globally for the different species. Some fish swim straight through the pool without stopping, while others make one or more stops in different resting zones of the pool as also observed in Bermúdez et al. (2012) and Rodríguez et al. (2015). By defining movement patterns for both species (brown trout and chub) in both cases, a preferential zone (Z1) was identified after entering the pool by the downstream slot. To exit the pool, this zone was also preferentially used. This behaviour was also observed in other studies (Bermúdez et al. 2012; Rodríguez et al. 2015). However, one zone was avoided to access to the upstream pool: the zone Z3 which is the furthest from the slot. If a fish enters this zone, it can only rest there and then go to another zone (Z1 or Z2), depending on its position in the zone and its orientation. Finally, the choice or the need to rest during the passage of a pool of a VSF complexifies the movement pattern, as we observed for trouts and chubs. However, the number of resting periods and the number of moves during the passage were not directly linked to the transit time. In fact, chubs made more moves than trouts when passing through the pool with some resting periods but it took them less time to achieve the passage to the upstream pool. Considering that the critical swimming speed of chubs was lower than that of trouts, chubs were submitted to more restrictive conditions inside the VSF. It clearly highlights differences in fish behaviour between species. All the observations of fish behaviour and zone occupation were made here under uniform flow conditions. Fuentes-Pérez et al. (2018) modified the hydrodynamic conditions inside their 1:1 scale VSF model to be non-uniform and they obtained identical zones location, based on the lowest velocity, the lowest turbulent kinetic energy, and the lowest vorticity zones. Consequently, we can argue that the fish behaviour observations made here may not change significantly under different flow conditions.

### **Fish behaviour and hydrodynamic conditions inside a pool**

Many studies (Bermúdez et al. 2012; Rodríguez et al. 2015; Li et al. 2019; Tan et al. 2019) have mentioned the link between the flow hydrodynamics and the fish behaviour inside a VSF pool. A recent paper (Li et al. 2019) mentioned that a flow topology FP2 tends to be the most suitable for fish passage. In fact, this topology implies the presence of the zones Z1 and Z2 of low velocity, low turbulence kinetic energy, and low Reynolds shear stress which are preferred by fish after their entry into the pool as well as before their exit by the upstream slot. In the present study, the analysis of the last fish position and orientation before leaving the pool exhibited a preferential behaviour: the need for a low velocity zone near the jet boundary to be able to go upstream. All the studies on the hydrodynamics in our VSF model (Tarrade et al. 2011; Callaud et al. 2014) have shown the presence of the low velocity zone Z1 and its use by fish. During our experiments, it was noted that if the fish was not in a low velocity zone, it exposed itself to a failed attempt of crossing the upstream slot. We can hypothesize that if hydrodynamic conditions are too high for the fish to handle, they act like walls and can guide the fish through the different zones of the pool. In that case, the fish is not free of his movement and is submitted to the flow conditions, that conduct it into another zone or keep it into its initial zone, which can lead to a delay in passing upstream, a stress charge for the fish and/or to an additive fatigue. Moreover, in this particular case, another condition to expect crossing the upstream slot emerged from our experiments: the fish must not be further away from the slot than a distance corresponding to the width of the slot. Otherwise, they failed to pass through the pool and stay for a longer time inside it. This observation still needs to be further analyzed to check, under different conditions, the potential relationships between slot width and fish positioning before a successful passage.

### **Scale effect**

The biological scale was chosen according to the hydraulic scale in our VSF: small individuals of each species were used during experiments. As mentioned before, for fish that managed to pass upstream in our VSF, the expected maximum swimming speed was about  $0.76 \text{ m.s}^{-1}$  for trout and  $0.90 \text{ m.s}^{-1}$  for chub (Videler 1993). We observed similar fish behaviours in other studies (Bermúdez et al. 2012; Rodríguez et al. 2015). The values of efficiency that we obtained, in the lower range of efficiencies compared to those other studies, can be

easily explained by the more restrictive conditions imposed on the fish inside our VSF model. While in other studies the velocity ratio ( $V_R$  = maximum swimming speed/velocity in the slot) is generally  $>1$  (e.g. mean value of  $1.17 \pm 0.43$  in Bermúdez et al. (2012),  $1.02 \pm 0.42$  in Rodríguez et al. (2015), and values up to 3.42 in Dębowski et al. (2022) for in-situ VSF), in the present study this ratio was about 0.69 and 0.82 for trout and chub, respectively.

To assess potential scale effects due to observations in laboratory conditions, real scale observations of fish behaviour were made in a VSF situated at Vichy (Cornu, David, et al. 2012), in central France. Similar flow conditions (considering the scale effect) were reproduced in our laboratory VSF model, which means that the identified hydraulic zones remained at the same location within the pools. Different species (salmon, shad, bream, barbel, chub...) used the in-situ VSF in Vichy, and similar behaviours (zone occupation, trajectories, resting behaviour) were observed. Small individuals of different species, such as bream, barbel, and chub used the resting zones previously to their upstream passage. In contrast, species with higher swimming capacity (salmon, shad) generally passed directly through the pools of the fishway, without using the resting zones. However, it is interesting to note that, even if these resting zones could be unused by larger specimens, they did not interfere with their progression through the fishway. Consequently, the presence of resting areas in the pools of fishways and their hydraulic optimization should not reduce the passage success of larger fish.

## Conclusion

As many works are still ongoing to enhance the VSF efficiency, the relationship between the fish behaviour and the hydrodynamic conditions inside a VSF is still to be highlighted. In this work, the local and total efficiencies of our VSF model were analyzed and compared to other studies with laboratory VSF model as well as in-situ VSF. Variations upon different trials were obtained for the total efficiency of both species (brown trout and chub) but the local efficiency was quasi constant. Reasonable values were obtained considering the harshness of the flow conditions with respect to the fish size and swimming capabilities. Taking this difficulty into account, resting periods were needed. The measurement of the holding time showed that a particular zone (Z3) was used as a resting zone. On the other hand, the importance of the zone Z1 of low velocity has been evidenced here as fish seemed to privilege this zone either after their entry into the pool or before their exit towards the upstream pool. The

proximity between this resting zone and the slot could explain the use of this zone before a successful upstream passage.

Field studies are difficult to conduct for many reasons: uncontrolled flow conditions (velocity, temperature), difficulties to visualize a pool (because of debris, suspended sediment, no direct access to the pool). Hence, laboratory studies are useful to avoid those difficulties and observe the behaviour of fish subjected to the flow conditions encountered in VSF. A basic comparison of fish behaviour in an in-situ VSF and during the present laboratory experiment enabled to conclude that observed behaviours in a scaled VSF model could be representative of fish behaviour at 1:1 scale. Consequently, it confirms that laboratory experiments can represent an opportunity to test the effect of some structure arrangements and modification on VSF efficiency if the experiment is correctly scaled.

## Disclosure statement

No potential conflict of interest was reported by the authors.

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