Swimming behaviour and ascent paths of brook trout in a corrugated culvert

Elsa Goerig*[1],

Normand E. Bergeron[1]

Theodore Castro-Santos[2]

[1] INRS-Eau, Terre et Environnement, 490 rue de la Couronne, Québec, QC, GlK 9A9, Canada.

[2] USGS-Leetown Science Center

S.O. Conte Anadromous Fish Research Center. 1 Migratory way, Turners Falls, MA, 01376. USA

*Author to whom correspondence must be addressed

Present address:

Harvard University, Department of Organismic and Evolutionary Biology, Cambridge, MA, 02138, USA

Email: goerig.elsa@gmail.com

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ABSTRACT

Culverts may restrict fish movements under some hydraulic conditions such as shallow flow depths or high velocities. Although swimming capacity imposes limits to passage performance, behaviour also plays an important role in the ability of fish to overcome velocity barriers. Corrugated metal culverts are characterized by unsteady flow and existence of low velocity zones, which can improve passage success. Here we describe swimming behaviour and ascent paths of 148 wild brook trout in a 2 m section of a corrugated metal culvert located in Raquette Stream, Québec, Canada. Five passage trials were conducted in mid-August, corresponding to specific mean cross-sectional flow velocities ranging from 0.30 to 0.63 m s^{-1}. Fish were individually introduced to the culvert and their movements recorded with a camera located above the water. Lateral and longitudinal positions were recorded at a rate of 3 Hz in order to identify ascent paths. These positions were related to the distribution of flow depths and velocities in the culvert. Brook trout selected flow velocities from 0.2 to 0.5 m s^{-1} during their ascents, which corresponded to the available flow velocities in the culvert at the low flow conditions. This however resulted in the use of low-velocity zones at higher flows, mainly located along the walls of the culvert. Some fish also used the corrugations for sheltering, although the behaviour was marginal and did not occur at the highest flow condition. This study improves knowledge on fish behaviour during culvert ascents, which is an important aspect for developing reliable and accurate estimates of fish passage ability.

INTRODUCTION

When moving in their natural habitat, fish may encounter challenging hydraulic conditions at waterfalls, riffles, dams or culverts. These elements may act as barriers to fish movements. Thus, culverts are ubiquitous structures that often limit fish upstream movements due to outlet drops, shallow depths or flow velocities that exceed their swimming capacity (Gibson et al. 2005, Goerig et al. 2016). Fish will usually use the sustained swimming powered by their aerobic metabolism to swim against low to moderate flow velocities. However, as velocity increases, they will transition towards prolonged and sprint swimming modes relying on their anaerobic metabolism. These will result in high swimming speeds that could only be maintained for a short period.

Passage success through culverts is a dynamic phenomenon influenced by variables that fluctuate over time, and thus is difficult to predict. Because each culvert is unique, relating the hydraulic conditions within the structure with the fish leaping and swimming capabilities (Castro-Santos 2005, Kondratieff and Myrick 2006, Neary 2012) is essential in order to predict passage.

However, behaviour and motivation can also be key elements in the ability of a species to overcome a barrier. Under challenging conditions, fish may use various strategies to save energy and avoid relying exclusively on their anaerobic metabolism, which will result in rapid fatigue and eventual failure to pass upstream. They can either use roughness elements such as baffles or corrugations to rest or low velocity zones and vortices to achieve greater ascent distances under aerobic processes (Liao 2007, Liao et al. 2003, Stringham 1924). These behaviours may be particularly important with respect to culvert passage as they can increase the fish ability to pass a given structure (Behlke et al. 1988, Goerig et al. 2016, Powers et al. 1997, Richmond et al. 2007).

Models used to predict passage (Furniss et al. 2008, Goerig et al. 2016) are usually based on mean flow velocity, and ignore behavioral aspects of fish passage. If fish select focal velocities lower than the mean cross-sectional velocity, passage success will be underestimated. Accurate and reliable estimates of fish passage at culverts are however of significant importance to the assessment of habitat fragmentation and implementation of cost-effective mitigation measures.

Previous studies have attempted to define a correction factor to apply to the mean velocity for swimming performance assessment and passage predictions through velocity barriers (Behlke 1991, Castro-Santos 2005, Sanz-Ronda et al. 2015). Defining such correction factor requires relating the fish ascent paths to the distribution of flow velocities inside the barrier, in order to compare selected to available velocities and to assess if fish select velocities similar to the mean cross-sectional one. By comparison to studies conducted in experimental flumes, knowledge of actual ascent paths in culverts is surprisingly limited, with only a few studies describing movements of individual fish (Johnson et al. 2012, Peterson et al. 2013, Thurman et al. 2007). Such knowledge is however important as experimental flumes, though convenient for studying fish behaviour, do not truly mimic actual conditions prevailing in culverts.

Here we describe swimming paths of wild brook trout ascending a 2 m section of a corrugated culvert in a field situation. We then model the effects of hydraulic and biological factors (ex: fish length) on the extent to which fish exhibited energy-saving behaviours. We hypothesize that small fish, as well as fish swimming against faster flow, will select paths located within low-velocity zones.

METHODS

Study site

The studied culvert was located on Raquette stream, in the Saint-Louis River watershed, in Québec (48°38’59’’N 70°55’22’’W). It was a 9 m long and 2.7 m diameter steel culvert with a slope of 1.8% and helical corrugations (amplitude of 0.03 m, wavelength of 0.15 m, and right-handed pitch of 5°, Manning’s n = 0.035). The water temperature remained constant around 12 °C during the trials (mean=11.92, SD = 0.22), which corresponds to the average stream temperature for August.

Fish capture

Wild brook trout were caught by electrofishing 0-500 m upstream of the studied culvert (Smith-Root model 15-C, DC varying width pulses, voltage range: 800‑1100 V, frequency: 45/60 Hz, duty cycle range: 0.9%‑72%). Fish were measured (total length, mm) and weighed (wet mass, g) in a graduated container filled with water and previously tared. They were then allowed to rest in an aerated bucket for ~ 5 min. Fish were handled in conformance with the guidelines of the Canadian Council of Animal Care in science (CCPA).

Video recordings

A single video camera (Gopro HD Hero 2011, 30 fps) was mounted 4 m from the downstream extremity of the culvert, at a right angle above the water surface, in order to record individual ascent paths and swimming behaviour. The camera field of view (monitoring zone) was 1.5 m x 2 m, which encompassed the full wetted width of the culvert (Figure 1).

Trout were individually tested in five passage trials conducted in mid-August. Each trial corresponds to a single day when fish were tested under given conditions of flow and water temperature. Trout were introduced 2 m from the downstream extremity by means of a bucket filled with water and gently immersed in the culvert centerline, facing upstream. We observed in preliminary tests that fish introduced in the culvert would either start ascending the structure within one minute or exit downstream. Each fish was thus recorded for a maximum of 3 min, which also allow the testing of 20 to 30 individuals during a given trial. After 3 min, if a fish had not ascended the monitoring zone or returned downstream, it was removed from the trial to allow the testing of a new individual.

Hydraulic data

Variability in hydraulic conditions during the trials was mostly due to natural variation in discharge. However, a gate system was used upstream of the culvert, in order to gain some control over the amount of flow entering the culvert.

Flow velocities were measured with a propeller-type velocimeter (Swoffer, model 3000) for each trial at three transects inside the culvert: one meter downstream and upstream of the camera location and under the camera (Figure 1). At each transect, flow depth and mean flow velocity were measured at 15%, 30%, 45%, 60%, and 75% of the flow cross-section width. Depth was measured from the surface to the crest of the corrugations, and the corrugation amplitude was considered as the boundary roughness height. Velocity at each location was calculated by averaging instantaneous velocities over a 30 s time interval, at two locations corresponding to 20% and 40% of flow depth from the bottom of the culvert. The latter corresponds to the approximate mean flow velocity on the vertical profile, according to the logarithmic distribution of velocities in turbulent flows for open channels (Chow 1959, Von Karman 1931).

Additional points were also interpolated laterally using linear regression in order to obtain a more complete distribution of flow depth and mean velocity in the transects. Mean flow depth and velocity for the culvert were computed by averaging the mean values for each transect. Flow depth and flow velocity distributions in the 2 m monitoring zone were integrated from the measured and interpolated points on a 1 cm grid using kriging interpolation with the octant method (Tecplot 360 2015 R1). For each location on this grid, we obtained a value of flow depth and three values of flow velocity on the vertical profile: surface, mid-depth and bottom (above the corrugations).

Video analysis

Ascent paths of fish were assessed by using a custom semi-automated digitizing program written in Matlab (R2014a). As the fish was ascending the culvert, a point corresponding to its center of mass was digitized at every 10 frames, corresponding to a rate of 3 Hz. The center of mass of fish varies by species and is located at a rostral distance of 25 % to 45 % of total body length (Xiong and Lauder 2014). For brook trout, it corresponds to 37 ± 1.5 % of total body length (Goerig et al, unpublished data). Pixel values were extracted, corresponding respectively to the longitudinal (x) and lateral (y) position of the fish in the culvert. Due to deformation at the edges of the field of view, ascent path were digitized for a zone of 1.2 m, instead of 1.5. For each trial, the extremities and center of the wetted width at each corrugation crest (spaced 15 cm apart) were used as landmarks to calibrate the field of view of the camera. The fish positions in pixels were then translated to x-y spatial coordinates in cm by using a spatial transformation (Matlab R2014a, image processing toolbox, cpt2form function). By applying an inverse spatial transformation, we were able to infer pixel values for the landmarks and estimate the positioning error inherent to the calibration method.

Individual ascent paths were superimposed on the distribution of depths and velocities in the culvert. For each fish x-y position, we associated a value of flow depth and mean flow velocity on the vertical profile. Distribution of available and selected flow velocities were described by boxplots and probability density functions (PDFs). To look for evidence of selection or avoidance of specific flow conditions, we computed the difference between the PDFs of selected and available velocities. Positive values indicated selection while negative values indicated avoidance. The ratios between the flow velocities selected and the actual mean flow velocity in the culvert (‘velocity preference ratio’) were computed and averaged for the ascent path of each fish. Transit time was calculated as the time required to traverse the entire 200 cm-long field of view of the camera. Fish swimming behaviour was also characterized into two gaits 1) continuous swimming or 2) alternating continuous swimming with rest periods.

Statistical analysis

Ascent paths were analyzed to determine the extent to which fish selected reduced flow velocities while ascending the culvert. A linear mixed model approach (R 3.2.0, lme4 package, lmer function) was used to assess how the velocity preference ratio was affected by the fixed effects mean flow depth, mean flow velocity, and fish length. This modelling approach also included a random effect on trial in order to account for any statistical dependence between the fish tested in the same trial (Quinn and Keough 2002). Flow depth and flow velocity were correlated (R = -0.32), so an interaction term was added when they were used together in the same model. The best-fitting model was chosen among candidate models by minimization of the Akaike Information Criterion (AIC).

RESULTS

A total of 148 brook trout of total length 70-190 mm (mean = 114, SD = 27) and weight 2-72 g (mean = 17, SD= 13) were tested in the five trials (Figure 2). They had a mean condition factor ($k = 10^5 \times \text{mass/length}^3$) of 0.99 (SD =0.13). Among all fish tested, 86 trout ascended the monitored section of the culvert. Of these 86, 71 were characterized as swimming continuously and 15 as alternating steady swimming with rest periods involving minimal body motions and no forward progression.

The mean velocity conditions in the five trials ranged from 0.30 to 0.63 m s^{-1} and the mean depth from 0.13 to 0.22 m (Table 1). Flow was always faster in the center of the culvert and slower close to the side walls (Figure 3, upper panel). Due to the angle of the corrugations, the reduced velocity zone was more pronounced along the right wall when looking upstream. This is similar with observations from previous hydraulic studies in corrugated culverts (Barber and Downs 1996, Richmond et al. 2007). However, this also depends of the channel configuration at the inlet. Thus, in the first trial, the reduced velocity zone was located more often along the left side wall.

The average positioning error of the fish in the culvert varied among trials, but was < 1 cm on both the x and y axis in all trials. Given the fact that flow depths and velocities were integrated on a 1 cm grid, the risk of assigning a wrong depth or velocity to a fish was therefore negligible. The ascent path pattern differed among individuals, but also among trials (Figure 3, lower panels). In trials with the slowest mean velocities (trials A & B; 0.30 and 0.33 m $s^{-}1$), fish tended to occupy the center and right side of the culvert, while at higher mean velocities (trials C & D; 0.38 and 0.45 m s^{-1}) trout ascent paths were more distributed in the cross-section, with a few fish also occupying the left side of the culvert. In the trial with the highest mean flow velocity (trial E; 0.63 m s^{-1}), trout were ascending the culvert by swimming close to the side walls. In all trials except the latter, some individuals stopped making forward progress and spent time in the lee of the corrugations, as illustrated by aggregations of point perpendicular to the flow (Figure 3, lower panel). The proportion of fish exhibiting this behaviour varied from 0 to 40% of the ascending fish, depending of the trial. They had a significantly lower average body length than fish making steady forward progress (97 mm ± 14 SD *vs* 117 mm ± 28 SD; t-test: t = 3, DF = 40 and $p < 0.001$).

During their ascents, trout selected a median flow velocity of 0.40 m s^{-1}, regardless of the trial, with an interquartile range from 0.38 to 0.48 m s^{-1}. For trials A, C and D, this closely matched the distribution of available flow velocities (Figure 4, left panels). During the 0.33 m s^{-1} trial (B) about half the fish preferred a reduced velocity zone. During the 0.63 m s^{-1} trial (E) nearly all the fish selected lower velocities located near the side walls of the culvert.

Comparing the probability density functions of selected and available velocities allows identifying preference or avoidance of specific flow velocities (Figure 4, right panels). Brook trout flow preference varied between the trials, with some of them showing a multimodal distribution with more than one preferred flow velocity. Overall, ascending fish selected flow velocities located between 0.2 and- 0.55 m s^{-1} and avoided slower or faster velocities (Figure 5).

Fish selected flow velocities equal to or higher than the mean cross-sectional flow velocity in the culvert for all trials, except the 0.63 m s^{-1} trial (Figure 5). In this trial, they selected velocities ~ 40% lower than the mean cross-sectional velocity.

Among the nine models tested for the velocity preference ratio, only one emerged as providing a good fit to the data (Table 2). This best-fitting model included only mean flow velocity as a predictor, the velocity preference ratio decreasing when the mean water velocity increased (Table 3). Fish were more inclined to select below-average velocities when the mean cross-sectional velocity in the culvert was faster, especially above 0.5 m s^{-1} (Figure 5). The variance of the random effect on trial was very small (0.004), indicating little unobserved variability between trials.

Transit time, or the amount of time spent in the zone covered by the camera was similar among trials and corresponded to a median value of ~ 12 seconds. The distribution was positively skewed, with most individuals having short transit times and a few ones having long transit times, up to 150 s. These individuals were present in every trial, except the 0.63 m s^{-1} trial (E), and they correspond to trout alternating continuous swimming with rest periods.

DISCUSSION

This study describes wild fish ascent paths in a corrugated metal culvert located in their natural environment. Other studies have made visual observations of juvenile fish swimming in culverts (Behlke et al. 1988, Blank 2008, Kane et al. 2000), although without detailed descriptions of their ascent paths. This is however necessary to understand fish hydraulic preferences and how these relate to hydraulic metrics commonly used in fish passage models. Thus, despite the limited range of tested flow velocities, we believe the present results bring an interesting insight on fish ascent behaviour in culverts.

In the current study, trout exhibited preference for flow velocities located between 0.2 and 0.5 m s^{-1}. Locations with flow velocities slower than 0.2 and higher than 0.5 m s^{-1} were rarely selected during the ascents. This may be due to distinct causes. At low flow conditions, velocities > 0.2 m s^{-1} may be more attractive to trout and increase their motivation to swim upstream. During the trials with mean flow velocities < 0.5 m s^{-1}, fish occupied a larger area of the flow cross-sectional area. At the highest flow, fish selected locations with velocities below the mean cross-sectional velocity in the culvert, which could indicate that the level of challenge was increasing. Movement was also more directed, with no period of reduced activity in the corrugations. This may be a behavioural response to a challenging environment, with fish altering their usual behavior to expedite passage at fast flows. Paths were located close to the walls, in shallow depths. For brook trout, the transition from sustained to prolonged swimming mode, and thus from the aerobic to the anaerobic metabolism, occurs when the flow velocity is between 2.5 to 4 body lengths (Peake 2008). The mean fish length being 115 mm in the current study, this transition should have occurred at ~ 0.45 m s^{-1}. The behaviour observed in the trial with the mean velocity of 0.63 m s^{-1} (E) may correspond to fish selecting locations with slower velocities to avoid the transition to the anaerobic metabolism. Similar behaviour was also observed in studies performed in an experimental culvert, where most fish ascended the culvert by swimming close to the walls at higher discharge (Powers et al. 1997, Thurman et al. 2007) or exit the culvert on the right side of inlet (Behlke et al. 1988, Kane et al. 2000), where the reduced velocities are usually located. The current results however differed from Castro-Santos et al. (2013), where trout swam mostly halfway between the center and the walls of a smooth open flume, at velocities close to the mean cross-sectional channel velocity. That study was performed under high flow velocities (1.6 to 2.5 m s^{-1}), where fish used the prolonged or sprint mode, and results are therefore hard to compare with those of the current study.

Mean transit time was consistent among trials, despite a twofold range of mean flow velocity. Some individuals however used the lee of the corrugations, either to swim in parallel with the small trough they created, or to hold position, with their body oriented perpendicular to the flow. Similar behaviour was also observed in the study from Kane et al. (2000). In the current study, all fish exhibiting periods with minimal body motions had a total body length < 150 mm, and the spacing between the corrugations was also 150 mm, which may suggest a mechanistic influence on behaviour. Diameter of turbulent eddies has been shown to scale with fish body size with regards to its effect on swimming ability (Cotel et al. 2006, Tritico and Cotel 2010). Trout < 150 mm may be displaced by large eddies while ascending the culvert, and thus more likely to seek shelter in the corrugations.

A previous study (Goerig et al. 2016) indicated that passage success of brook trout was higher in corrugated culverts (~ 75-90%) than in smooth ones (~30-50%) at flow velocity of 1 m s^{-1}. This could be explained by the higher hydraulic complexity in corrugated culverts and the existence of reduced velocity zones which fish could use during their ascents. The level and structure of turbulence may also be higher in corrugated culverts (Richmond et al. 2007). Future studies on the structure of eddies within and above corrugations would help to understand the biomechanical aspects driving swimming and sheltering behaviours.

When modelling the effect of hydraulic or biological factors on the velocity preference ratio, only the mean flow velocity in the culvert was retained as an explanatory variable. Surprisingly, the fish body length was not retained as a predictor, large trout being as likely to select reduced flow velocities as small ones. In the current study, smaller trout were however more likely to use the corrugations as rest areas than large ones. Velocity selection and sheltering are thus two discrete behaviours that may or may not occur concurrently.

The current study shows that trout had a preference for velocities between 0.2 and 0.5 m s^{-1} and that they used velocities ~ 40% slower than the mean cross-sectional velocity in the culvert when flow increased. This is similar to the 0.4 to 0.6 correction factor for the mean velocity developed by Behlke (1991) for design and retrofit of culverts for Arctic grayling. However, based on the results from the current study, this factor seems relevant only when flow exceeds the sustained swimming ability of the fish.

The study has limitations because it monitored only a small area in the culvert over a limited range of hydraulic conditions. However, the methods used can be applied easily to a larger study, with an emphasis on testing a wider range of velocities, characterizing flow turbulence and fish ascent paths along the entire culvert. The use of more advanced videography methods (Hughes and Kelly 1996, Neuswanger et al. 2016) would also allow describing the position occupied within the water column. Other factors that may have effects on motivation, swimming ability or dispersal patterns, were not included in this study. Recent studies on brook trout passage performance in culverts indicated that spawning time and diel period both influence motivation to ascend culverts, while water temperature has a non-linear effect on passage success, with an optimum in performance around 14°C (Goerig et al. 2016, Goerig and Castro-Santos 2017). This temperature also corresponds to the maximal aerobic capacity for brook trout (Tudorache et al. 2010). Thus, it is possible that more fish would have ascended the culvert if the current study was performed near spawning time, at dusk or during night. Conversely, fish would have been less active or more susceptible to choose low velocity zones in the culvert at temperatures < 14 °C.

CONCLUSION

Results from the current study apply to brook trout of 70 to 190 mm swimming in corrugated culverts against mean flow velocities ranging from 0.30 to of to 0.65 m s^{-1}. They show that individual fish vary in their ascending behaviours, although they select paths comprising low-velocity zones when the mean cross-sectional velocity in the culvert increases above 0.5 m s-^{1}. This is an important finding as it can help improving accuracy of preference estimates and correction factors for use in predictive fish passage models. Culverts with roughness elements such as corrugations may be favorable to fish passage as they provide both low velocities pathways and sheltering options.

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TABLES

Table 1: Hydraulic conditions during trials

ID	Date	Velocity (m s^{-1})	Depth (m)	n
A	8/17	0.30	0.19	22
B	8/18	0.33	0.17	36
C	8/25	0.38	0.19	35
D	8/24	0.45	0.22	32
E	8/23	0.63	0.13	23

Note: Hydraulic conditions prevailing during the five trials. Velocity refers to the mean cross-sectional flow velocity in the culvert, depth to the mean depth and n to the number of fish individually tested during the trial.

Table 2: Model selection based on the Akaike information criterion (AIC)

Model $_i$	RE	-2 log (L)	K	AIC $_i$	Δ_i AIC	w $_i$
Flow velocity	**(1 |Trial)**	**-1.643**	**4**	**11.29**	**0.00**	**1.00**
Flow depth	(1 |Trial)	-6.862	4	21.71	10.43	0.00
Flow velocity + body length	(1 |Trial)	-7.565	5	25.13	13.85	0.00
Fish length	(1 |Trial)	-11.146	4	30.29	19.01	0.00
Null	(1 |Trial)	-12.528	2	29.06	17.77	0.00

Note: Subset of tested models (n = 9) showing the four models with the lowest−2 log likelihood (penalized) and AIC values, as well as the null model. Explanatory variables are mean flow velocity (m s-^{1}), mean flow depth (cm) and fish body length (mm). RE represents the random effects structure, K (df) the number of degrees of freedom in the model, Δ_i AIC is the difference between AIC of model$_i$ and AIC of the best model. Akaike weight of model$_i$ (w_i) is interpreted as the probability that model$_i$ is the best model given the data. One model (in bold) emerged as providing the best fit to the data.

Table 3: Parameter estimates for the best-fitting model

Parameter	**β**	**± SE**
Intercept	1.562	0.153
Mean velocity (m s^{-1})	-1.332	0.361
Random effect	**Variance**	**SD**
Trial	0.004	0.064

Note: Estimates (β) and standard errors (± SE) of parameters for the best-fitting model for the mean velocity preference ratio s estimated for all fish tested in the five trials (n = 87). The velocity preference ratio is the ratio between the mean flow velocity selected by the fish during its ascent and the mean cross-sectional flow velocity in the culvert.

FIGURES

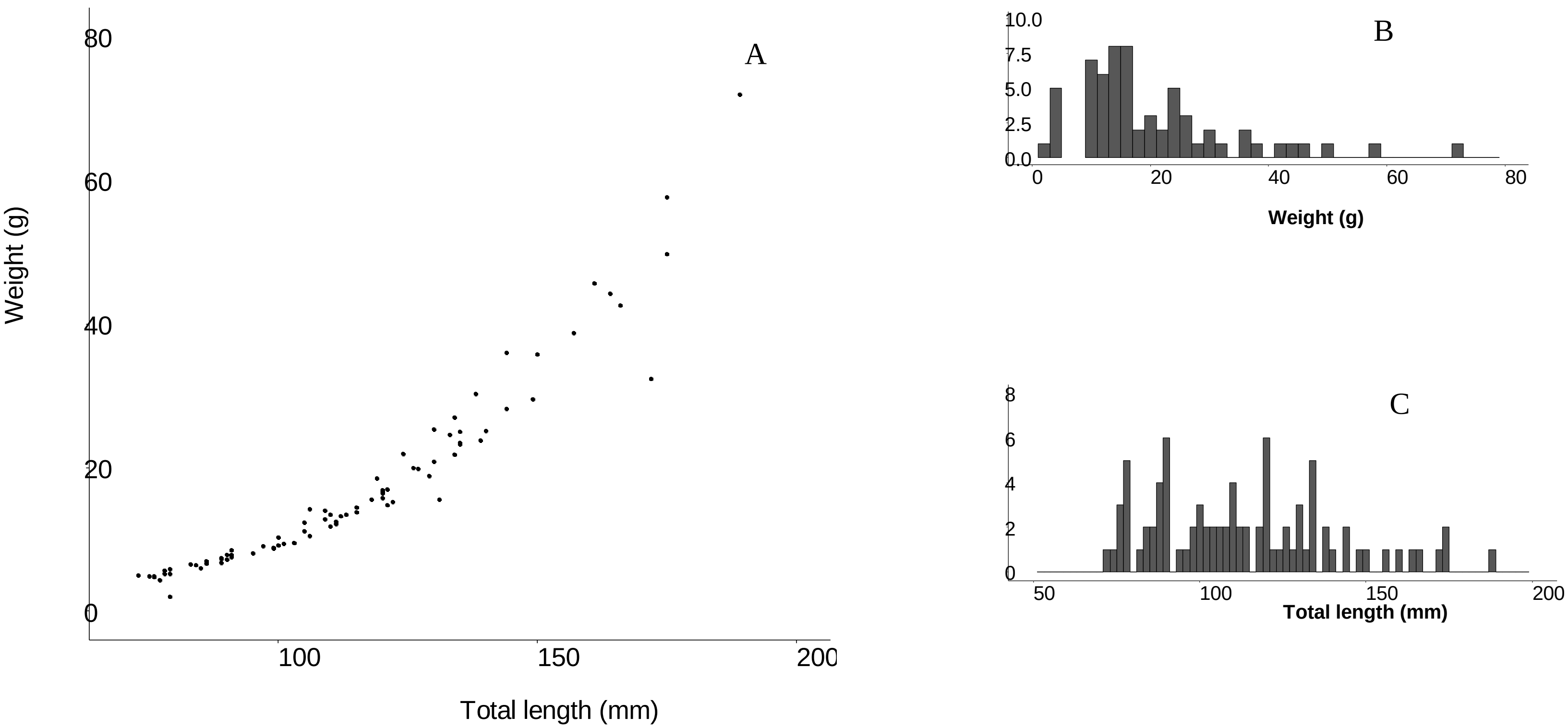


Figure 2: Relationship between weight and total length (A), as well as distribution of weight (B) and total length (C) for the 86 tested fish.

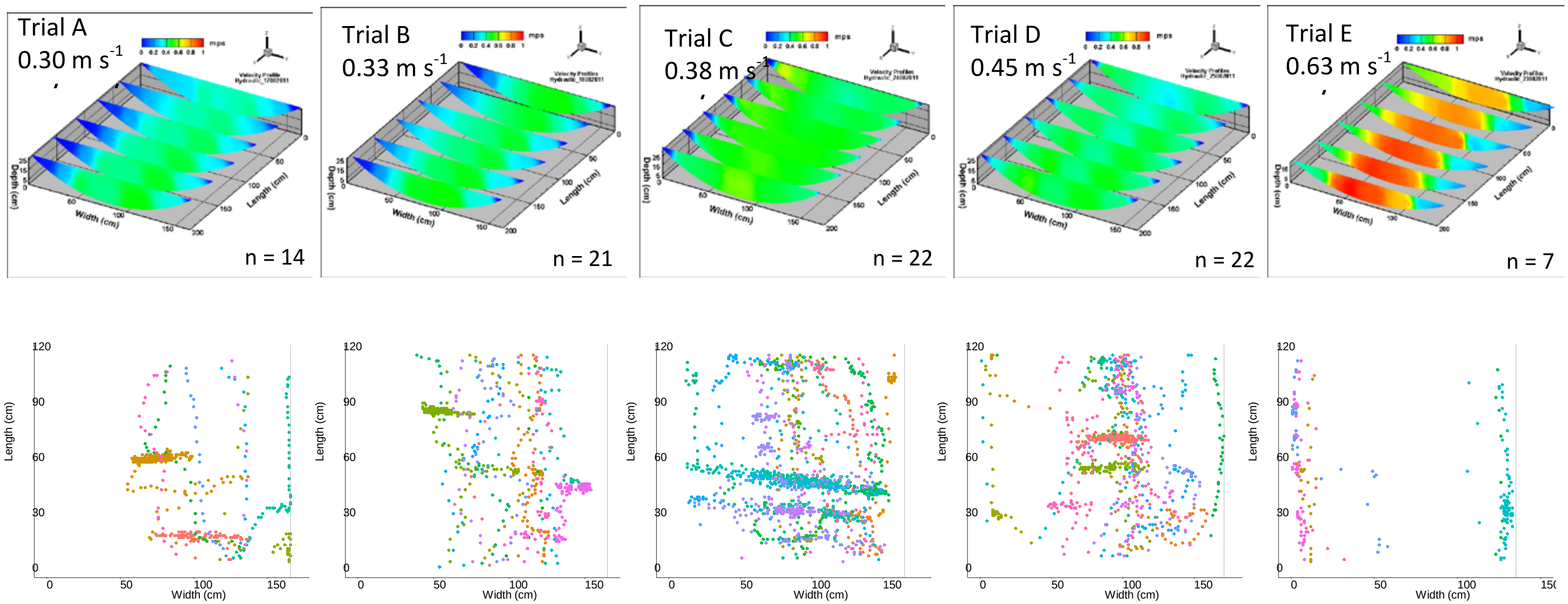
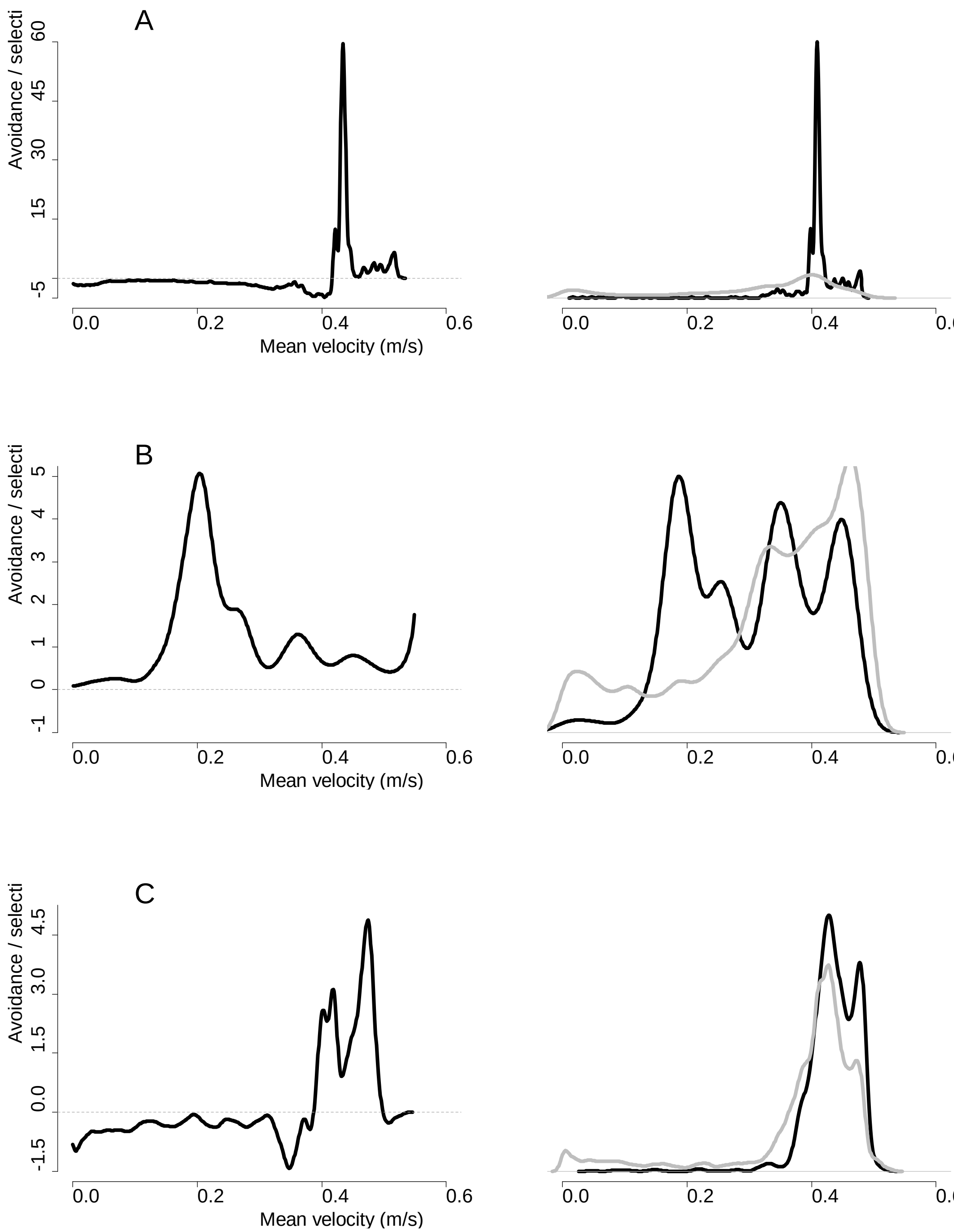


Figure 3: Distribution of flow velocities and depths (upper panels) and individual fish ascent paths (lower panels) in the zone covered by the camera, for the five trials ordered by increasing mean flow velocity. The boundary of the wetted width is indicated by 0 on the left side and by a grey vertical line on the right side. The number of ascending fish is indicated in the upper panels. Colors in the upper panels go from blue (0-0.4 m s^{-1}) to red (0.8-1.0 m s^{-1}). Colors in the lower panels identify ascent paths of individual fish. Lateral aggregations of points correspond to fish swimming or holding position in the lee of the corrugations, as it was the case for 40% (trial A), 31% (trial B), 16% (trials C & D) and 0% (trial E) of ascending fish.


A
Avoidance / selecti
60
45
30
15
-5
0.0
0.2
0.4
0.6
Mean velocity (m/s)
B
Avoidance / selecti
5
4
3
2
1
0
-1
0.0
0.2
0.4
0.6
Mean velocity (m/s)
C
Avoidance / selecti
4.5
3.0
1.5
0.0
-1.5
0.0
0.2
0.4
0.6
Mean velocity (m/s)

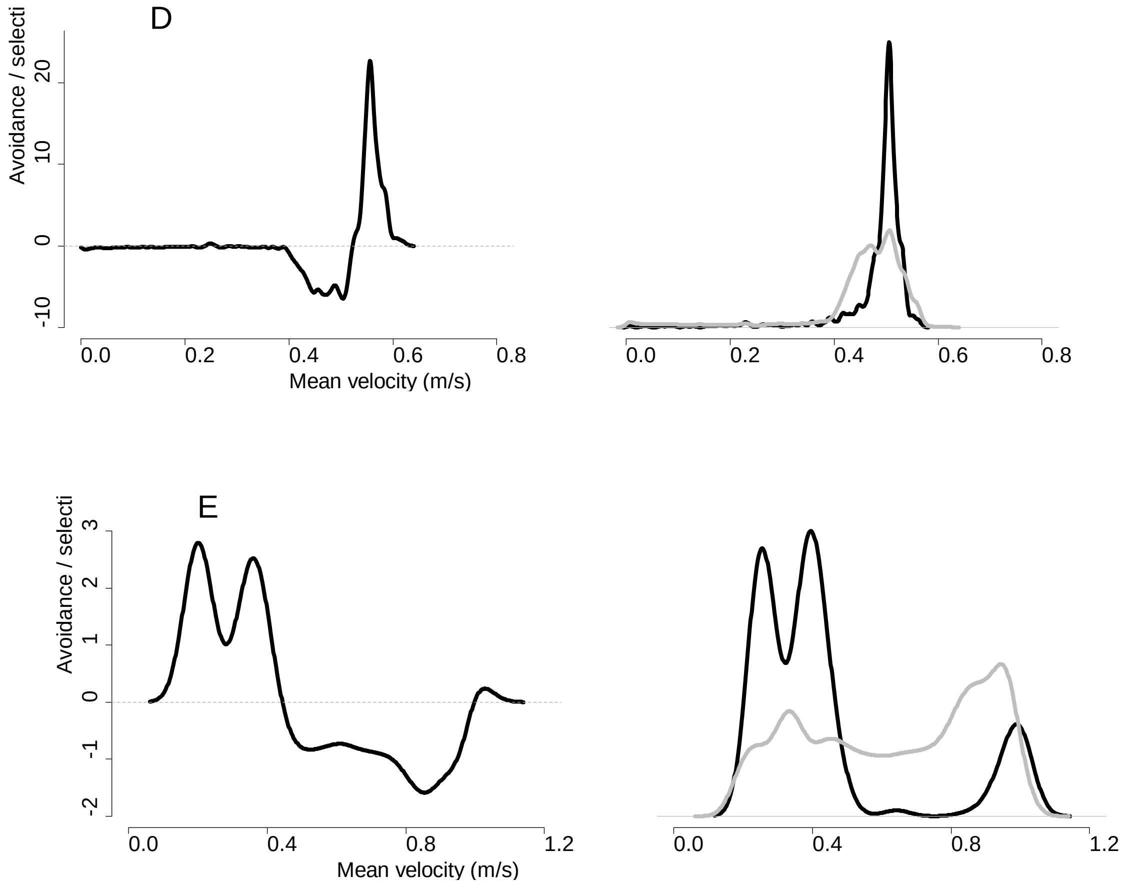


Figure 4: Left panels show the difference between the probability density functions (PDFs) of selected velocities and available velocities for the 0.30 m s^{-1} (A), the 0.33 m s^{-1} (B), the 0.38 m s^{-1} (C), the 0.45 m s^{-1} (D) and the 0.63 m s^{-1} trial (E). The PDFs of selected velocities are calculated based on velocities selected by ascending fish in each trial while the PDFs of available velocities included all velocities present in the culvert monitoring zone. Positive or negative values indicate selection or avoidance for specific flow conditions, respectively. For reference, right panels show the actual probability density functions of available (in grey) and selected (in black) flow velocities, for the trials A, B, C, D & E. Relative densities on the y-axis are not shown. The probability density function integrates to 1.

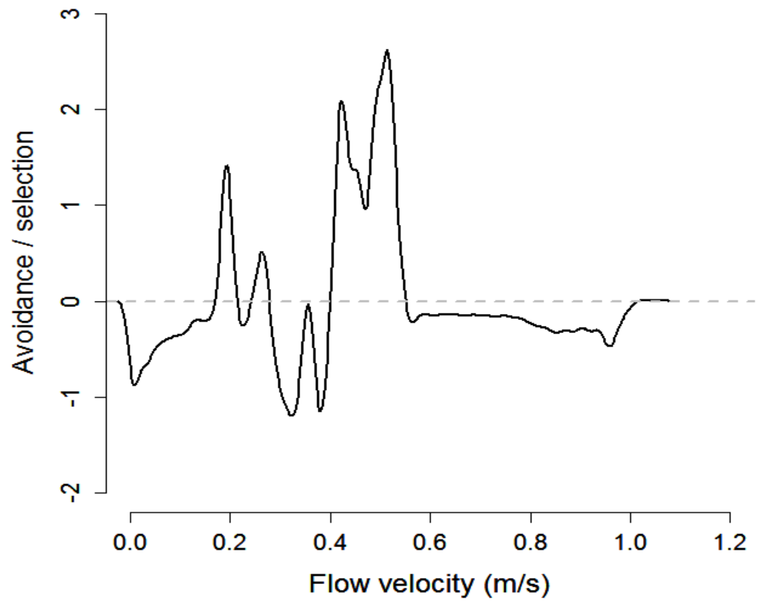


Figure 5: Difference between the probability density functions of selected velocities and available velocities, summarized for all trials. Positive or negative values indicate selection or avoidance for specific flow conditions, respectively.

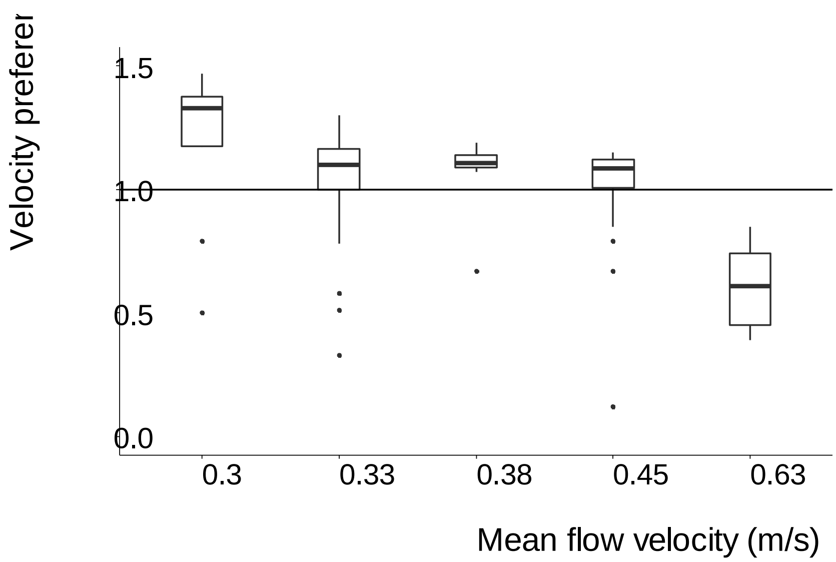


Figure 6: Distribution of velocity preference ratios as a function of mean flow velocity in the culvert during the five trials. Box show the median and interquartile range while the whiskers show the 10th and 90th percentiles and points refers to outliers. The velocity preference ratio is the ratio between the mean flow velocity selected by the fish during its ascent and the mean cross-sectional flow velocity in the culvert.