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Running title

Brook trout body shape and culvert passage

Title

Body shape is related to the attempt rate and passage success of brook trout at in-stream barriers

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Abstract

1. The ability to move between habitats has important implications for fitness in many species. In-stream barriers such as culverts can impede movements of riverine fishes and thus reduce connectivity between habitats. The ability of fish to overcome barriers is related to the features of the environment and the barrier itself, but also to physiological, morphological, and behavioural traits of the fish. Among these, body shape varies among and within species, and influences swimming ability, a key component of passage performance through culverts.
2. We conducted an experimental study on wild brook trout (*Salvelinus fontinalis*) to assess the effects of individual body shape on attempt rate and passage success through culverts on six streams.
3. A more streamlined body shape was associated with an increased motivation to enter and ascend the culverts, and, to a lesser extent, with probability of successful passage once an attempt was staged. Motivation and successful passage were also influenced by the density of conspecifics below the culvert, time of day, fish body size, and water velocity.
4. *Policy implications.* While fish body shape is expected to influence swimming performance, our research shows the most important effect of body shape to be on an individual's motivation to stage passage attempts at culverts. This study points to an important connection between behaviour and morphological traits that influence passage success and suggests that in-stream barriers may be an important agent of selection on behavior and morphology in wild fish populations.

Introduction

In riverine habitats, fish movements are often impeded by physical barriers or challenging hydraulic conditions (Goerig et al., 2016, Gibson et al., 2005, Gallagher, 1999). These barriers can occur naturally and may be persistent (such as those caused by geologic features such as waterfalls) or ephemeral (as may be caused by beaver dams). Both persistent and ephemeral barriers hold the potential to fragment habitat, and can lead to evolution of body shapes and behaviours for overcoming them (Castro-Santos and Haro, 2006). Human development in many watersheds has led to the creation of large numbers of persistent barriers across the landscape in the form of culverts and other road crossings. These barriers reduce ecological connectivity and may impose selection on fish populations (Morita 2000, 2002).

Fish passage at culverts and fishways is a multi-step process, with fish sequentially approaching, entering, and eventually passing the barrier (Castro-Santos and Perry, 2012, Castro-Santos, 2012). Failure at each of these steps may impede or delay fish movement. Culverts at road crossings are highly unnatural structures that fish must be willing to approach and enter, thee willingness to do so beingrelated to behavioural traits. Once the fish has entered the culvert, morphological and behavioural traits that influence swimming and leaping ability become important determinants of successful passage (Haro et al., 2004, Gallagher, 1999). Fish that attempt but fail to pass a culvert may re-enter repeatedly to make additional attempts. We refer to the attempt rate as an index of motivation (Castro-Santos, 2004, Goerig and Castro-Santos, 2017). Indeed, the behavioural and morphological traits that may facilitate high passage performance may not be independent, but rather bundled together into what have been termed dispersal syndromes (Comte and Olden, 2018). Variation in dispersal syndromes may lead to different rates of passage success among populations and individuals, with important ecological and evolutionary implications. Here we present results from a field experiment testing whether culverts act as selective filters on the traits of wild brook trout, a widespread species in North America. We evaluate the degree to which trait variation determines entry and successful passage through the culverts. Our hypothesis is that successful passage is influenced by motivation and body shape, and that these traits, along with culvert and environmental characteristics, explain variability in passage success. Consistent with the idea of dispersal syndromes, we predict that trait variation in motivation and morphology will be related such that fish with streamlined bodies, a trait often associated with higher swimming ability, will show higher motivation and therefore higher rates of passage success. If so, then culverts – which have become ubiquitous features of modern river networks – may be imposing large-scale selection on wild fish populations.

Materials and Methods

Study sites

Brook trout passage attempts were recorded during field experiments at six circular culverts located in the Saint-Louis and Bécancour River watersheds (Québec, Canada), two systems separated by ~ 300 km. The Bécancour watershed is characterized by low gradient streams with silty bottom, and occasional riffles flowing on sedimentary rocks. The two studied streams in this watershed are located far from each other and fish are not able to move between them. The Saint-Louis watershed is located in the Canadian Shield and houses high-gradient gravel-bed streams, with presence of boulders and 'step-pools' reaches. It was possible for fish to access the different studied streams via the main river, but this is unlikely because the streams are separated by long distances and zones of high-velocity water.

Culverts were 8 to 20 m in length and 1.5 to 2.7 m in diameter. Their slopes varied from 1.15 to 4.5 %, and their outlet drop was < 5 cm above the water level of the stream. They were made of either corrugated metal or smooth concrete (Table S1). All culverts had quality feeding and spawning habitat located upstream, although no previous knowledge of fish movement patterns existed for these streams.

Fish sampling

Fish were caught by electrofishing (Smith-Root backpack electrofisher, model 15-C, USA) 0 to500 m upstream of the culvert in which they will be tested. All individuals were from resident freshwater populations, as the studied streams have no direct access to the ocean. Voltage and waveforms were adjusted to account for water conductivity and to minimize risks of injury to the fish (DC, varying width pulses: frequency: 45 – 60 Hz; duty cycle: 0.9% - 72%; voltage range: 800-

1100 V). They were anesthetized by immersion in a 1:9 solution of clove oil and 95% ethanol diluted in water (0.8 to 1.2 ml of solution for 1400 ml of water), measured (fork length, mm), weighed (wet mass, gr) and surgically tagged with half-duplex passive integrated transponders (PIT) tags (Texas Instruments, 23 or 12 mm in length). A standardized lateral body photograph was taken of each fish. Fish were then allowed to recover in holding pens in their river of origin, for an average of 22 h (SD = 7 h).

Study design and instrumentation

Groups of fish were transferred from the holding pens to a large cage (2 x 2 x 1 m) secured to the downstream end of each culvert and allowed to volitionally stage passage attempts in trials of 48 h. Each cage was fitted with a top net to prevent avian predation and contained rocks to provide cover and low-velocity resting areas. Water temperature was recorded hourly by a data logger (Onset, HOBO 020-001-04) located 20 m upstream of the culvert and averaged for the duration of each trial. Distributions of water velocity and depth in the culverts were quantified before each trial using a propeller-type velocimeter (Swoffer, model 3000) at lateral transects spaced 2 m along the culvert. Mean water velocity for the culvert during each trial was computed by averaging the mean values for each transect.

The six tested culverts were instrumented with a telemetry system consisting of four passive integrated transponder (PIT) antennas evenly spaced along the pipe and located above the water surface, as described in Goerig et al. (2016). The first antenna was located at 0.5 m inside the culvert while antenna 4 was located at the upstream end. The antennas interfaced with a half-duplex PIT reader (Technologie Aquartis, control module Quatro) recording tag number, antenna number, and time to the nearest 1 s. This allowed the observation of passage attempts and successes in the culverts.

Analysis of body shape

We used geometric morphometric methods to quantify the lateral two-dimensional body shape of the fish used in this study (Rohlf and Marcus, 1993, Adams et al., 2004). Separate analyses were performed on two nested datasets. In the first, we used all fish to compare body shape amongst fish that entered the culvert (attempters) and those that did not (non-attempters). In the second, we included only attempters and compared body shape of attempters that successfully passed through the culvert with those that did not. From photographs of each fish, the locations of 15 homologous landmarks were digitized (Figure 1), using tpsDig2 version 2.18 (Rohlf, 2015).

A generalized Procrustes Analysis (GPA) removed the effects of translation, rotation, and the isometric effects of size on body shape as well as described this body shape variation as a set of residual landmark coordinates, or Procrustes residuals (Rohlf and Slice, 1990). A principle components analysis of these residuals indicated that significant variation in body shape was associated with some arching of the fish body while being photographed. To 'unbend' the specimens, we fit a quadratic curve through the raw (pre-GPA) landmarks 1, 13, 14, 15, and 6, and transformed the whole set of landmarks such that these were fit along a straight line for each fish using tpsUtil version 1.76 (Rohlf, 2015). All further analyses were carried out on unbent landmarks 1-12 only. For each fish, we calculated centroid size, which is the sum of the squared distances from the landmarks to their centroid and is used as a measure of overall body size that is approximately independent from the shape variables (Rohlf and Slice, 1990).

In each analysis, we performed a GPA on the unbent specimens which produced 24 procrustes residuals that describe shape. In order to account for the allometric effects of body size and any differences in shape amongst the different stream populations, we performed nonparametric Procrustes MANOVAs (np-MANOVAs) with shape as the dependent variable and log centroid size, stream, and their interaction as predictors (Collyer et al. 2015). The residuals of these regressions represent variation in shape that is independent of body size and population of origin (Mitteroecker and Bookstein 2011) .

We focused on two binary performance metrics: attempters vs. non-attempters, and passage vs. failure to pass. In order to evaluate how body shapes differed between each of these two metrics, we performed two-block partial-least-squares regression (PLS) with shape as one block and a single variable (attempt/non-attempt or pass/fail) as the alternate block (Rohlf and Corti 2000; Mitteroecker and Bookstein 2011). PLS describes the axis of shape variation that most closely covaries with each performance metric (Rohlf and Corti 2000; Mitteroecker and Bookstein 2011). Each individual is assigned a PLS score. Since our second block of data is a binary group, the PLS score represents that individual's position along the vector that best discriminates between the mean of the two groups and can be used to reliably reconstruct predicted body shapes (Mitteroecker and Bookstein 2011). We resampled the data 10,000 times to determine how shape was associated with attempt and passage (Adams and Collyer 2016). These analyses were performed in R version 3.5.1 and package geomorph version 3.0.5 (Adams and Otárola-Castillo, 2013, Adams et al., 2017). The PLS scores were then used as continuous shape variables in the analysis of passage performance through culverts.

Analysis of passage performance in culverts

We quantified brook trout passage performance through culverts using two metrics: attempt rate and probability of successful passage. Attempt rate refers to the proportion of available fish staging an attempt per unit of time and can be used as an index of the fish's motivation to enter and ascend culverts in this study (Goerig and Castro-Santos, 2017). Once a fish has entered the culvert, the probability of successful passage ranges from 0 (failure) to 1 (success).

Attempt rate

We used time-to-event analysis (Allison, 2014, Castro-Santos, 2004, Hosmer et al., 1999) to quantify attempt rate of fish present in the cages downstream of culverts. Each attempt constitutes a single event and has an associated instantaneous event rate (or hazard). An attempt was defined as an exposure to antenna 1, meaning that the fish has entered the culvert. Cox regression estimates the relative effect of covariates on the event rate (Castro-Santos and Haro, 2003, Allison, 2014). We used the package Coxme in R 3.2.0 (R Core Team, 2015, Therneau, 2015) to fit Cox mixed models including fixed effects and nested random effects for stream of origin and individual fish. These random effects accounted for unexplained variability in attempt rate related to the stream of origin and statistical dependence among repeated attempts from the same fish (Therneau et al., 2003). Fixed effects included fish log centroid size, body shape (fish scores from the PLS discriminating between attempters and non-attempters), fish condition factor (Fulton's $K_{FL} = 10^5$*weight/length^3), diel period (dawn, day, dusk or night), mean velocity, depth of the pool downstream of the culvert, ratio of openness of the culvert (cross-sectional area / length), water temperature, and number of conspecifics in the cage. The number of fish in the cage was set to a starting value corresponding to the number of fish introduced at the beginning of a trial. It was then allowed to vary according to individuals staging attempts, and then either passing upstream of the culvert or returning downstream after an attempt. We used a correlation matrix (Figure S1) to detect collinearity in the fixed effect variables. Any pair of variables with a correlation coefficient Pearson's $r > 0.35$ or <-0.35 would not be used together in a model.

A set of biologically meaningful candidate models was developed using the following criteria to minimize the number of models : (i) maximum of seven main effects; (ii) depth of downstream pool was not used in a model with water velocity ($r = 0.54$, $p= < 0.0001$) or number of conspecifics in the cage ($r = 0.63$, $p= < 0.0001$) due to their correlation), as well as water temperature and velocity ($r = -0.69$, $p < 0.0001$), and condition factor (K_{FL}) and shape ($r = 0.55$, $p=< 0.0001$); and (iii) no interactions. Selection of the best model was performed by minimizing the Akaike Information Criteria (AIC).

Once a best model was selected, the baseline hazard, as well as the fixed and random effects coefficients, were extracted and used to plot mean response curves adjusted for representative levels of the predictive variables.. Random effect coefficients also served as an index of the individual level of motivation for further analyses, a high coefficient indicating a high level of motivation. In this context, motivated fish were those attempting to pass the culvert at a high rate (early in the trial) or staging repeated attempts.

Passage success

Once an attempt was initiated, a successful passage was defined as a detection at antenna 4, regardless of whether the fish returned downstream or moved upstream. For each attempting fish, the probability of successful passage through the culvert was quantified with a generalized linear model with a logistic link. A set of candidate models was developed by considering independent fixed effects such as culvert length, mean water velocity and depth in the culvert, water temperature, fish log centroid size, and body shape (scores from the PLS discriminating between successful and unsuccessful attempters). The individual level of motivation, previously extracted from the attempt rate analysis, was also included in some candidate models. Culvert material (i.e: smooth concrete or corrugated metal) was not considered as a covariate because mean velocity and depth were not distributed evenly among the two types of culverts. Mean water velocity and depth were not used together in a model since they were correlated ($r = -0.38$, $p < 0.0001$). Model selection was done by minimizing AIC.

Results

A total of 362 brook trout (FL from 58 to 215 mm, mean =133.5 mm) was tested in nineteen trials conducted in six culverts. Sample sizes were not evenly distributed among studied culverts, however (Table S1). Trials were conducted from June to August, at mean water temperatures between 10 and 17.5°C. Mean water velocity within trials ranged from 0.5 to 2.0 m s^{-1}, and mean depth from 0.03 to 0.46 m. Overall detection efficiency by the PIT system was ~ 97% in this study, as reported in Goerig (2016).

Body Shape

Shape varied as a function of size, and across streams (Table S1). The residuals of the np-MANOVA represent shape independent of these predictors. According to the PLS analysis, the residual shapes were significantly correlated with the fact to attempt or not to pass the culvert (Table 1), 23% of the variation in shape being explained by the attempt status (attempter / non-attempter). Attempters were relatively shallower-bodied and had slightly shortened caudal-peduncles when compared to non-attempters (Figure 2). Successful fish were also shallower-bodied, especially in the anterior half of the body, and had slightly shortened caudal-peduncles when compared to unsuccessful fish (Figure 3). Howeverthe difference was not statistically significant (Table 1). The individual scores from the PLS analysis were used as continuous shape variables in the attempt rate and passage success analyses, along with environmental covariates and culvert characteristics.

Passage performance in culverts

Attempt rate

Among the 187 models estimated, two models had a similar AIC and an optimal fit to the data (Δ AIC from null model = 81.5 & 81.2, Δ AIC from closest competing model = 3.4 & 3.7, total Akaike weight = 0.63). These models included diel periods, mean water velocity, centroid size, body shape and number of conspecifics in the cage as predictors of attempt rate, which is used as an index of the fish motivation to pass the culverts (Table 3A), a higher attempt rate implying greater motivation. The second best model included the culvert openness ratio as an additional predictor. We selected the most parsimonious model minimizing AIC.

The number of conspecifics in the cage below the culvert was negatively correlated with the fish motivation, the individual attempt rate being higher when fewer fish were present in the cages. Fish were more motivated to pass the culverts at dawn and under higher water velocity conditions (Table 2): an increase of 1 m s^{-1} in water velocity had the effect of nearly doubling the attempt rate (Table 3 A, HR = 1.870). Attempt rate was reduced during the day, at dusk and during the night, by comparison to dawn (Table 3 A, HR = 0.67, 0.87 and 0.77). Larger trout had a higher attempt rate. Finally, body shape had an influence on motivation; fish with low PLS scores staged attempts at a higher rate (Figure 4, A). This confirmed the differences in body shape observed between attempters and non-attempters and means that fish with shallower bodies and shortened caudal peduncles entered and ascended the culverts at a greater rate.

Random effects account for variability in attempt rate that is associated with stream of origin and the individual fish themselves, but that is not captured by the fixed effects in the models. The variance of both random effects was substantial, suggesting that individuals varied significantly in their motivation, and that fish within a stream were more similar to each other than to the population as a whole. (Table 2, section A). Fish from Grégoire Stream staged attempts to pass the culvert at a much faster rate than average for all streams combined, while fish from Femmes and Saumons Streams had the slowest attempt rates (Figure 4, B). Fish from the Bécancour watershed were overall more motivated to enter the culverts than those from the Saint-Louis watershed.

Passage success

Among the 84 models estimated in the analysis on culvert passage success, the model with the lowest AIC (Δ AIC from null model = 50.8, Δ AIC from closest competing model = 0.85, Akaike weight = 0.22) included mean velocity, motivation and body shape as main predictors of culvert passage success. There were no large differences in AIC values between the selected model and the following competing models, meaning that there was no strong evidence for a single model explaining passage success. However, mean velocity, motivation, and body shape were included in all competing models, along with culvert length and water temperature in some cases. Thus we selected the most parsimonious model minimizing AIC.

Mean velocity had the greatest effect on passage success, followed by motivation and body shape (Table 3B, *β). The probability of successful passage decreased with increasing velocity. Motivated fish were more likely to successfully pass, as were fish with low PLS scores (i.e: shallower bodies and shortened caudal peduncles).

Discussion

The overall goal of our study was to evaluate whether trait variation impacts motivation and successful passage through culverts for wild brook trout. We predicted that passage success would be influenced by both motivation and body shape and we expected to find variation in traits and passage success among populations and among individuals within populations.

Our study reveals the existence of a clear link between body shape and brook trout motivation to pass in-stream barriers. Propensity to move may result from a distinct body shape. Fish with dorso-ventrally streamlined bodies and shortened caudal peduncles were more likely to enter and ascend the culverts. Body shape may correlate with distinct dispersal syndromes, with some fish being more sedentary while others are active movers. Evidence for dispersal syndromes have been observed for several freshwater fish species (Comte and Olden, 2018, Rodriguez, 2002), including brook trout (Rodriguez, 2002). Fish with streamlined bodies and a short caudal peduncle may also exhibit higher swimming ability and a propensity to move over long distances and diverse physical habitats. Thus, these fish may encounter in-stream barriers and be more motivated to overcome them.

Fish motivation was also influenced by their size, as well as by environmental variables such as diel periods, water velocity and number of conspecifics in the cage below the barrier. This result is consistent with previous findings (Goerig and Castro-Santos, 2017, Maynard et al., 2017), and highlights the complexity of fish interactions with barriers. Even after those variables of importance have been taken into account, fish motivation to pass the culverts differed among streams, with trout from the Bécancour watershed exhibiting an overall higher attempt rate. This may be due to variables not considered in the analysis, for instance differences in movements and habitat use patterns among the studied populations or water quality factors. Habitat-based polymorphism has been observed in lakes and fluvial environments (Senay et al., 2015, Samways et al., 2015, Walker, 1997), with fish body shape differing for individuals found in riffles, runs and pools, as well as with migratory range, predation or prey availability, and other factors (Schaffer and Elson, 1975, Quinn et al., 2001, Quinn and Buck, 2001). Abiotic factors such as water depth and velocity are known to shape morphology (Drinan et al., 2012, Pease et al., 2012, Zastavniouk et al., 2017). However, stream fishes often move among habitats within stream reaches, and thus may exhibit high plasticity in morphological traits (Senay et al., 2015).

We also found evidence for individual variability in motivation, which may arise from various sources. Brook trout, like many species of fish, can be sexually dimorphic, both with respect to body shape and size, but also to behavior (Proulx and Magnan, 2004, Hutchings and Gerber, 2002). Although we were not able to determine sex, it is likely that some of the morphological diversity we observed is due to sex differences, and the same can be said for motivation and performance. Sex may influence dispersal, and thus motivation to pass a barrier to access upstream habitat (Hutchings and Gerber, 2002). Likewise, some trout may exhibit differential response to stress or the presence of conspecifics below the culvert.

While body shape is clearly related to brook trout motivation to enter and ascend culverts, it also had an effect on passage success once attempts were initiated. Successful attempters were characterized by shallower bodies, and shortened caudal peduncles, traits that minimize drag and enhance steady swimming (Langerhans and Reznick, 2010). Small heads, short fins, deeper caudal region and a streamlined body have also been linked to high swimming and acceleration performance in salmonids (Rouleau et al., 2010, Hawkins and Quinn, 1996, Ojanguren A.F., 2003). Similar traits were found in two fish species (*Prochilodus lineatus* and *Leporinus elongatus)* ascending a fishway in Brazil (Assumpção et al., 2012). In the current study, highly motivated trout had an increased probability of passing the culvert. These fish shared traits typical of a strong ability to accelerate and reach high swimming speeds, such as a streamlined body and a short caudal peduncle (Webb, 1994). However, four of the six studied culverts were made of corrugated metal, which creates low velocity areas inside the pipes and allows fish to rest during ascents (Goerig et al., 2016, Goerig et al., 2017). This factor may have partially offset the negative effect of water velocity on passage success and may explain why morphological traits associated with higher swimming ability did not have even greater impact on passage success. This result highlights that culverts are more than just simple challenges to swimming performance. They are complex barriers that demand a combination of behavioral and morphological traits to enable successful passage.

We deliberately used caged fish in this study so it was possible to know at any moment how many fish were present and attempting to pass, as well as the environmental conditions to which they were being exposed. By allowing 48 h for passage, we were able to observe diel effects, while giving fish ample time to recover from handling. Although free-ranging fish may have greater opportunity to pass a barrier than we provided here, our design provides an appropriate and meaningful approximation to natural conditions. Future work, however, should consider using unconstrained fish. Telemetry studies using PIT or active techniques have great power to characterize behaviors for free-ranging fish (Castro-Santos et al., 1996).

The current findings provide evidence that, in addition to reducing connectivity between riverine habitats, culverts may be exerting selective pressures on the behavioural and morphological traits of wild fish populations. We found that body shape and size are related to the willingness of trout to enter the culverts, as well as their passage success. Culverts have become ubiquitous riverine features, but the effects of such barriers are usually regarded as minimal as long as the barrier is deemed permeable to fish movement under some hydraulic conditions. However, passable barriers have been shown to drive landscape-scale patterns in the frequency of migration-associated alleles in steelhead trout (*Oncorhynchus mykiss*) (Apgar et al., 2017) .

Our results show that passable culverts may be imposing large-scale selection on wild brook trout populations that move throughout river networks. These findings likely apply to other fish species and types of in-stream barriers such as fishways, tide gates, and small dams. Selection depends on the features of the barriers, the environment, and the standing trait variation in the population. Depending on the situation, selection may favor highly dispersive phenotypes that can overcome barriers and move between stream fragments, or conversely non-dispersive phenotypes that remain isolated within fragments. Such factors deserve greater consideration as potentially widespread impacts of river fragmentation on the ecology and evolution of fish populations.

Authors' contributions

E.G designed the study and performed all the field experiments. E.G and B. W processed and analysed the data. All authors helped with statistical interpretation, as well as with writing and editing the manuscript. All authors gave final approval for publication.

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Ethics

The fish collection and tagging procedures were in conformance with the guidelines of the Canadian Council of Animal Care in science (CCPA).

Data availability statement

Data available via the Dryad Digital Repository https://doi.org/10.5061/dryad.9tf3hr5 (Goerig et al, 2019).

Tables and figures

Table 1. Correlation Coefficient (rPLS), p-value of PLS from resampling, effect size (Z), for each PLS model, and p-value of the difference between the two models, after Adams & Collyer (2016).

Model	rPLS	p-value	Z	p-value (Z difference)
1. Attempt	0.2296	0.0171	-1.6802	0.0036
2. Success	0.1502	0.9619	2.2665	

Table 2: Model describing effects of covariates on attempt rate (A; Cox regression) and passage success (B; Logistic regression).

A

ATTEMPT RATE

Parameter	β ± SE	HR	p-value
Number of fish in the cage	-0.090 ± 0.017	0.914	< 0.0001
Diel period			
Dawn	—	—	—
Day	-0.401 ± 0.166	0.669	0.016
Dusk	-0.139 ± 0.194	0.870	0.470
Night	-0.258 ± 0.169	0.772	0.130
Mean velocity (m s^{-1})	0.626 ± 0.286	1.870	0.029
Log centroid size	0.005 ± 0.002	1.005	0.017
Body shape (PLS scores)	-30.046 ± 6.622	0,00	< 0.0001
Random effects	**SD**	**Variance**	
Stream of origin │ID	0,777	0.605	
ID	0,765	0.585	
No of available fish	362		
No of events	1071		

B

PASSAGE SUCCESS

Parameter	β ± SE	* β	p-value
Intercept	3.330 ± 0.712		< 0.0001
Mean velocity (m s^{-1})	-3.356 ± 0.660	-2.51	< 0.0001
Motivation	1.696 ± 0.451	1.478	0.0002
Body shape (PLS score)	-26.309 ± 13.790	-0.71	0.0564
No of attempters	179		

*Note: Estimates ± standard error (β ± SE) and hazard ratios (HR) of parameters for the best-fitting model. HR are computed for each parameter by exponentiating the estimates. For the passage success model, standardized coefficients (*β) are obtained by converting ordinary coefficients (β) to standard deviation units. They measure the relative importance of the explanatory variables, regardless of the metrics in which the variables have been measured.*

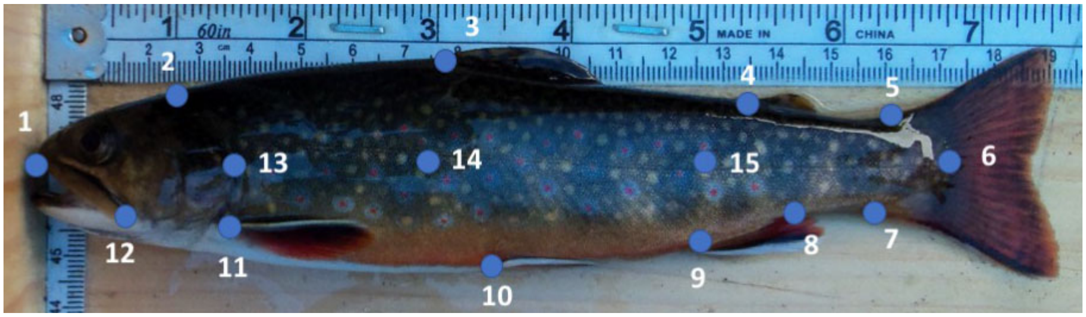

Figure 1. Landmark placement, modified from Varian & Nichol 2010. (1) Anterior tip of the snout, posterior edge of the cranium, (3) anterior dorsal fin insertion, (4) anterior adipose fin insertion, (5) dorsal caudal fin insertion, (6) medial dorsal fin insertion, (7) ventral dorsal fin insertion, (8) posterior anal fin insertion, (9) anterior anal fin insertion, (10) anterior pelvic fin insertion, (11) anterior pectoral fin insertion, (12) posterior extent of maxillary, (13-15) semi-landmarks along the medial axis of the fish

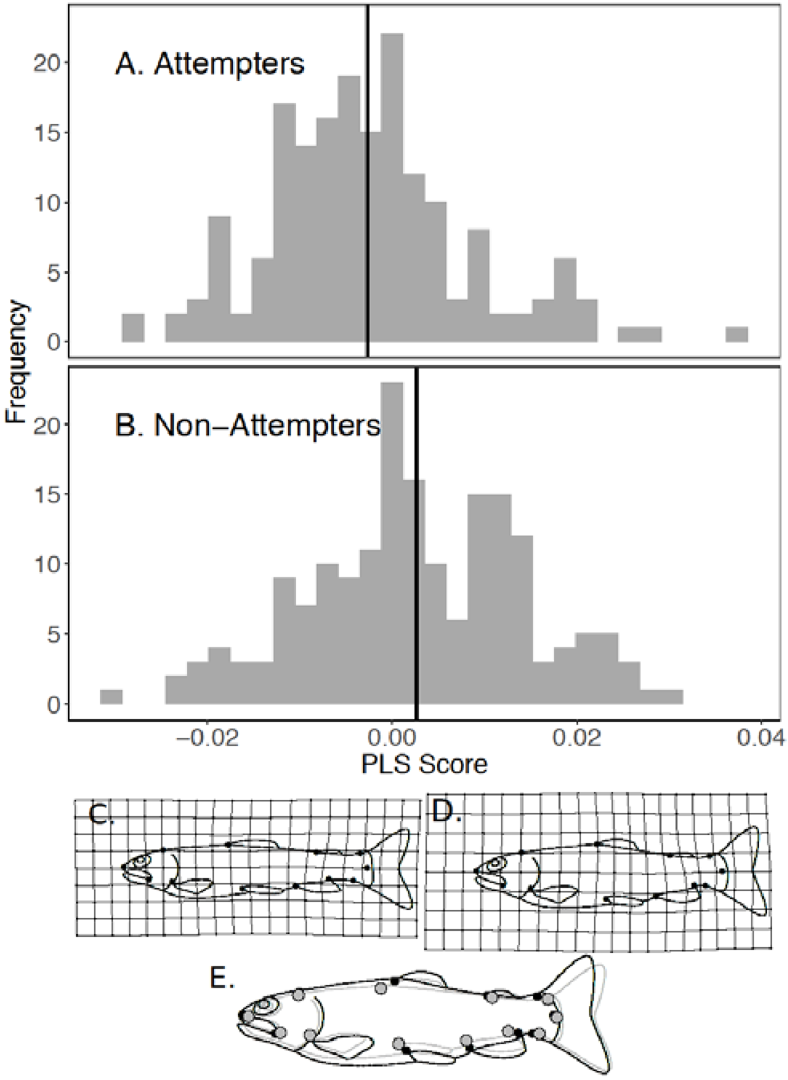

Figure 2. Histograms of PLS scores associated with attempt status, vertical black bars represent the group means. Underneath we use thin-plate-splines and transformation to represent the predicted shape of individuals with the most extreme PLS scores: most extreme attempter (C), and most extreme non-attempter (D) shapes. These shapes are then superimposed (E), with gray representing the shape of attempter and black of non-attempter. Note that differences in the outlines are based on extrapolation of the differences in landmarks and is meant as a visual aid only. Areas which are outside of the landmark coverage, such as the caudal fin, are based entirely on extrapolation and as such are not included in our interpretation.

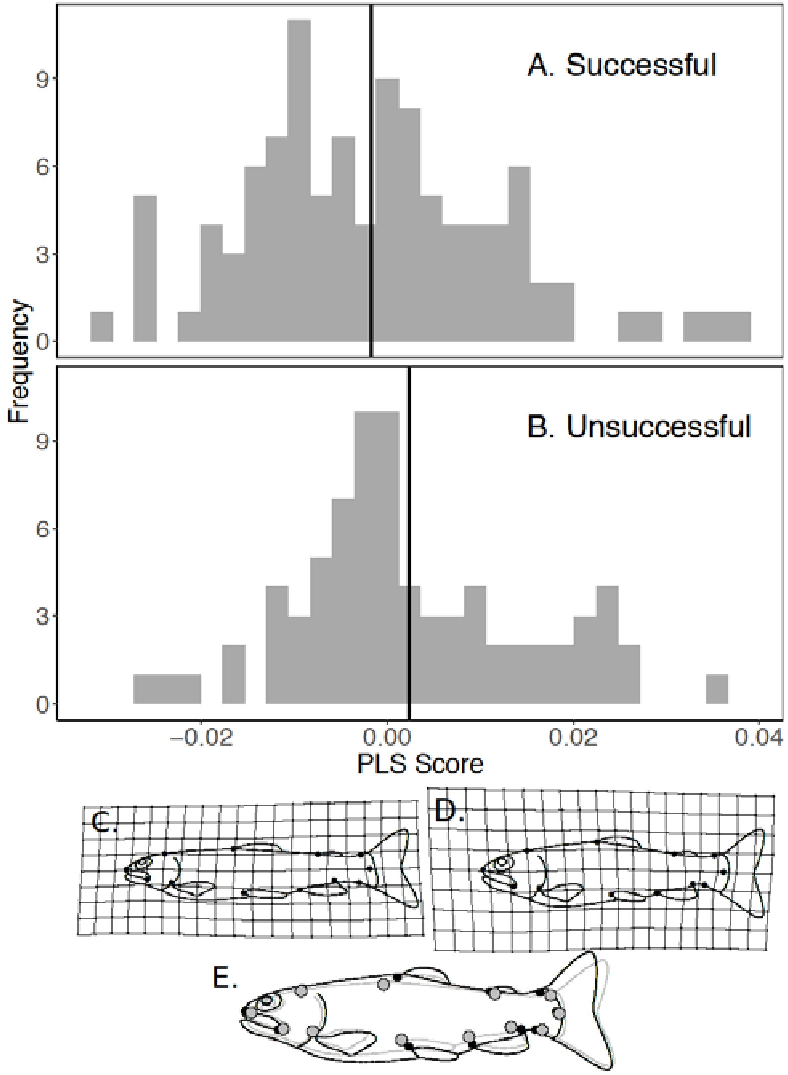

Figure 3. Histograms of PLS scores associated with success, vertical black bars represent the group means. Underneath we use thin-plate-splines and transformation to represent the predicted shape of individuals with the most extreme PLS scores: most extreme successful (C), and most extreme unsuccessful (D) shapes. These shapes are then superimposed (E), with gray representing the shape of successful fish and black of unsuccessful one

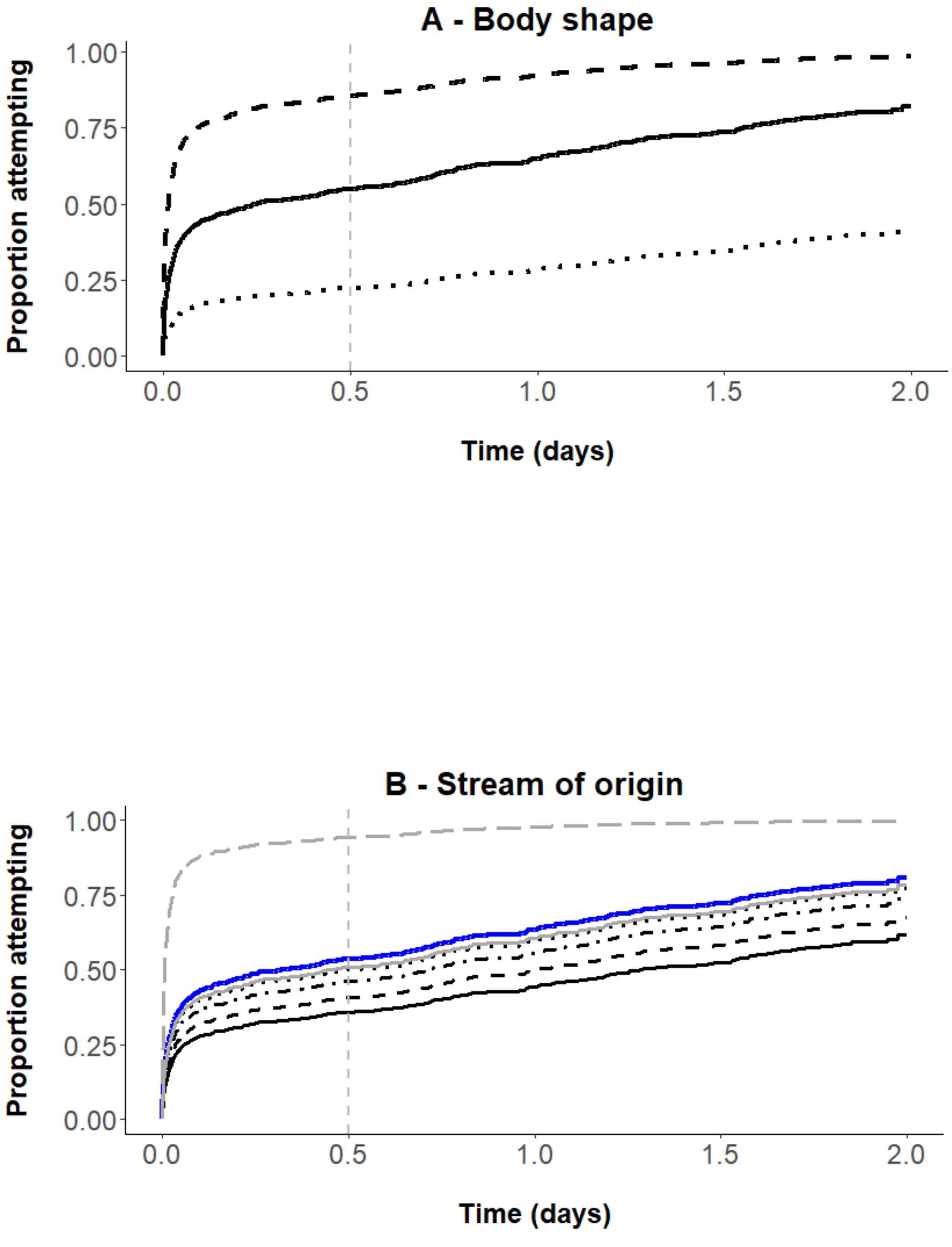

Figure 4: Proportion of fish attempting to pass the culvert as a function of A) body shape and B) stream of origin, modeled from the estimated Cox model.

In A, attempt rate increases with a decrease in PLS scores. Dotted line represents the attempt rate for a fish with a maximal PLS score (0.03), solid line for a mean PLS score (-0.0003) and dashed line for a minimal PLS score (-0.03). The proportion of released fish having staged attempt after 12h (vertical dashed line) was 25% for fish with the highest PLS scores, while 75% for fish with the lowest PLS scores.

In B, the curves represent the mean attempt rate for all fish in the study (solid blue line), attempt rate from fish from Grégoire Stream (dotted grey line), Tardif (two-dashed grey line), Adolphe (dotted black line), Raquette (dot dashed black line), Femmes (dashed black line), and Saumons (solid black line). The Adolphe curve is however superposed to the curve for the mean attempt rate. Other parameters of the model are set to their mean values. The hazard of staging an attempt is highest at stream Grégoire and lowest at stream Saumons. The proportion of released fish having staged attempts after 12 h (vertical dashed line) was 85% at Grégoire, ~ 45-55% at Adolphe, Raquette and Tardif, but only 30-35% at Saumons and Femmes Streams. Except for the fish from Adolphe Stream, fish from the Bécancour watershed (grey curves) had a higher attempt rate than those from the Saint-Louis watershed (black curves).

References

ADAMS, D. C., ROHLF, F. J. & SLICE, D. E. (2004). Geometric morphometrics: Ten years of progress following the 'revolution'. Italian Journal of Zoology, 71**,** 5-16.

ALLISON, P. D. 2014. *Event history and survival analysis*, SAGE.

APGAR, T. M., PEARSE, D. E. & PALKOVACS, E. P. (2017). Evolutionary restoration potential evaluated through the use of a trait-linked genetic marker. Evolutionary applications, 10**,** 485-497.

ASSUMPÇÃO, L. D., MAKRAKIS, M. C., MAKRAKIS, S., WAGNER, R. L., SILVA, P. S. D., LIMA, A. F. D. & KASHIWAQUI, E. A. L. (2012). The use of morphometric analysis to predict the swimming efficiency of two Neotropical long-distance migratory species in fish passage. Neotropical Ichthyology, 10**,** 797-804.

CASTRO-SANTOS, T. (2004). Quantifying the combined effects of attempt rate and swimming capacity on passage through velocity barriers. Canadian Journal of Fisheries and aquatic Sciences, 61**,** 1602-1615.

CASTRO-SANTOS, T. (2012). Adaptive fishway design: a framework and rationale for effective evaluations. 2. Kolloquium zur Herstellung der ökologischen Durchgängigkeit der Bundeswasserstraßen. Koblenz, Germany. 76-89.

CASTRO-SANTOS, T. & HARO, A. (2003). Quantifying migratory delay: a new application of survival analysis methods. Canadian Journal of Fisheries and Aquatic Sciences, 60**,** 986-996.

CASTRO-SANTOS, T. & HARO, A. (2006). Biomechanics and fisheries conservation. Fish physiology, 23**,** 469.

CASTRO-SANTOS, T., HARO, A. & WALK, S. (1996). A passive integrated transponder (PIT) tag system for monitoring fishways. Fisheries Research, 28**,** 253-261.

CASTRO-SANTOS, T. & PERRY, R. W. 2012. Time-to-event analysis as a framework for quantifying fish passage performance. *In:* ADAMS, N. S., BEEMAN, J. W. & EILER, J. H. (eds.) *Telemetry techniques: a user guide for fisheries research.* Bethesda, Maryland: American Fisheries Society.

COMTE, L. & OLDEN, J. D. (2018). Evidence for dispersal syndromes in freshwater fishes. Proc. R. Soc. B, 285**,** 20172214.

DRINAN, T. J., MCGINNITY, P., COUGHLAN, J. P., CROSS, T. F. & HARRISON, S. S. C. (2012). Morphological variability of Atlantic salmon Salmo salar and brown trout Salmo trutta in different river environments. Ecology of Freshwater Fish, 21, 420-432.

GALLAGHER, A. (1999). Barriers. Aquatic Habitat Assessment.

GIBSON, R. J., HAEDRICH, R. L. & WERNERHEIM, C. M. (2005). Loss of Fish Habitat as a Consequence of Inappropriately Constructed stream Crossings. Fisheries, 30, 10-17.

GOERIG, E., BERGERON, N. E. & CASTRO-SANTOS, T. (2017). Swimming behaviour and ascent paths of brook trout in a corrugated culvert. River Research and Applications, 33, 1463-1471.

GOERIG, E. & CASTRO-SANTOS, T. (2017). Is motivation important to brook trout passage through culverts? Canadian Journal of Fisheries and Aquatic Sciences, 74, 885-893.

GOERIG, E., CASTRO-SANTOS, T. & BERGERON, N. E. (2016). Brook trout passage performance through culverts. Canadian Journal of Fisheries and Aquatic Sciences, 73, 94-104.

GOERIG ET AL. (2019). Data from: Body shape is related to the attempt rate and passage success of brook trout at in-stream barriers. Dryad Digital Repository.https://doi.org/10.5061/dryad.9tf3hr5

HARO, A., CASTRO-SANTOS, T., NOREIKA, J. & ODEH, M. (2004). Swimming performance of upstream migrant fishes in open-channel flow: a new approach to predicting passage through velocity barriers. Canadian Journal of Fisheries and Aquatic Sciences, 61, 1590-1601.

HAWKINS, D. & QUINN, T. (1996). Critical swimming velocity and associated morphology of juvenile coastal cutthroat trout (Oncorhynchus clarki clarki), steelhead trout (Oncorhynchus mykiss), and their hybrids. Canadian Journal of Fisheries and Aquatic Sciences, 53, 1487-1496.

HOSMER, D., LEMESHOW, S. & MAY, S. (1999). Applied survival analysis: Regression modelling of time to event data. John Wiley & Sons. New York.

HUTCHINGS, J. A. & GERBER, L. (2002). Sex–biased dispersal in a salmonid fish. Proceedings of the Royal Society of London. Series B: Biological Sciences, 269, 2487-2493.

LANGERHANS, R. B. & REZNICK, D. N. (2010). Ecology and evolution of swimming performance in fishes: predicting evolution with biomechanics. Fish locomotion: an eco-ethological perspective, 200-248.

MAYNARD, G. A., KINNISON, M. T. & ZYDLEWSKI, J. D. (2017). Size selection from fishways and potential evolutionary responses in a threatened Atlantic salmon population. River Research and Applications, 33, 1004-1015.

OJANGUREN A.F., B. F. (2003). Effects of size and morphology on swimming performance in juvenile brown trout (Salmo trutta L.). Ecology of Freshwater Fish, 12, 241-246.

PEASE, A. A., GONZALEZ-DIAZ, A. A., RODILES-HERNANDEZ, R. & WILLEMILLER, K. O. (2012). Functional diversity and trait–environment relationships of stream fish assemblages in a large tropical catchment. Freshwater Biology, 57, 1060-1075.

PROULX, R. & MAGNAN, P. (2004). Contribution of phenotypic plasticity and heredity to the trophic polymorphism of lacustrine brook charr (Salvelinus fontinalis M.). Evolutionary Ecology Research, 6, 503-522.

QUINN, T. & BUCK, G. (2001). Size- and Sex-Selective Mortality of Adult Sockeye Salmon: Bears, Gulls, and Fish Out of Water. Transactions of the American Fisheries Society, 130, 995-1005.

QUINN, T., HENDRY, A. & BUCK, G. (2001). Balancing natural and sexual selection in sockeye salmon: interactions between body size, reproductive opportunity and vulnerability to predation by bears. Evolutionary Ecology Research, 3, 917-937.

R CORE TEAM (2015). R: A language and environment for statistical computing. Vienna, Austria: R Foundation for Statistical Computing.

RODRIGUEZ, M. A. (2002). Restricted movement in stream fish: the paradigm is incomplete, not lost. Ecology, 83, 1-13.

ROHLF, F. (2015). The tps series of software. Hystrix-Italian Journal Of Mammalogy, 26, 9-12.

ROHLF, F. J. & SLICE, D. (1990). Extensions of the Procrustes Method for the Optimal Superimposition of Landmarks. Systematic Zoology, 39, 40-59.

ROHLF, J. F. & MARCUS, L. F. (1993). A revolution morphometrics. Trends in Ecology & Evolution, 8**,** 129-132.

ROULEAU, S., GLÉMET, H. & MAGNAN, P. (2010). Effects of morphology on swimming performance in wild and laboratory crosses of brook trout ecotypes. Functional Ecology, 24**,** 310-321.

SAMWAYS, K. M., LEAVITT, P. R., MAGNAN, P., RODRÍGUEZ, M. A. & PERES-NETO, P. R. (2015). Convergent polymorphism between stream and lake habitats: the case of brook char. Canadian Journal of Fisheries and Aquatic Sciences, 72**,** 1406-1414.

SCHAFFER, W. M. & ELSON, P. F. (1975). The adaptive significance of variations in life history among local populations of atlantic salmon in North America. Ecology, 56**,** 577-590.

SENAY, C., BOISCLAIR, D., PERES-NETO, P. R. & RASMUSSEN, J. (2015). Habitat-based polymorphism is common in stream fishes. Journal of Animal Ecology, 84**,** 219-227.

THERNEAU, T. M. (2015). Package 'coxme': Mixed effects Cox models. R.

THERNEAU, T. M., GRAMBSCH, P. M. & PANKRATZ, V. S. (2003). Penalized Survival Models and Frailty. Journal of Computational and Graphical Statistics, 12**,** 156-175.

WALKER, J. A. (1997). Ecological morphology of lacustrine threespine stickleback Gasterosteus aculeatus L.(Gasterosteidae) body shape. Biological Journal of the Linnean Society, 61**,** 3-50.

WEBB, P. (1994). Exercise performance of fish. Advances in veterinary science and comparative medicine, 38**,** 1.

ZASTAVNIOUK, C., WEIR, L. K. & FRASER, D. J. (2017). The evolutionary consequences of habitat fragmentation: Body morphology and coloration differentiation among brook trout populations of varying size. Ecology and Evolution, 7**,** 6850-6862.