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Brook trout passage performance through culverts

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31 ABSTRACT

32 Culverts can restrict access to habitat for stream-dwelling fishes. We used PIT telemetry
33 to quantify passage performance of > 1000 wild brook trout attempting to pass 13 culverts of
34 Quebec under a range of hydraulic and environmental conditions. Several variables influenced
35 passage success, including complex interactions between physiology and behavior, hydraulics,
36 and structural characteristics. The probability of successful passage was greater through
37 corrugated metal culverts than through smooth ones, particularly among smaller fish. Trout
38 were also more likely to pass at warmer temperatures, but this effect diminished above 15°C.
39 Passage was impeded at higher flows, through culverts with steep slopes and those with deep
40 downstream pools. This study provides insight on factors influencing brook trout capacity to
41 pass culverts as well as a model to estimate passage success under various conditions, with an
42 improved resolution and accuracy over existing approaches. It also presents methods that could
43 be used to investigate passage success of other species, with implications for connectivity of the
44 riverscape.

45 Keywords: fishes, hydraulics, movement, culvert, habitat

46 RÉSUMÉ

47 Les ponceaux peuvent limiter l'accès à l'habitat pour les espèces d'eau douce. Nous
48 avons utilisé la technologie des transpondeurs passifs intégrés (PIT-tags) afin de quantifier la
49 performance de passage de > 1000 ombles de fontaine tentant de traverser 13 ponceaux du
50 Québec sous une gamme de conditions hydrauliques et environnementales. Plusieurs variables
51 influencent le succès de passage, incluant des interactions complexes entre la physiologie et le
52 comportement, l'hydraulique et les caractéristiques structurales des ponceaux. Les ponceaux de
53 métal ondulé augmentent la probabilité de passage et ce particulièrement pour les petits

ombles. Les ombles sont plus susceptibles de franchir le ponceau lorsque la température de l'eau s'élève mais cet effet diminue à partir de 15°C. À l'opposé, le succès de passage est moindre à des vitesses d'écoulement élevées, dans les ponceaux avec des pentes fortes ainsi que dans ceux avec des fosses profondes à l'aval. Cette étude apporte de nouvelles connaissances sur les facteurs influençant la capacité de l'omble de fontaine à franchir les ponceaux ainsi qu'un modèle pour estimer le succès de passage sous des conditions variées, ceci avec une résolution et une précision améliorée par rapport aux approches existantes. Elle présente également des méthodes pouvant être utilisées pour étudier le succès de passage de d'autres espèces, avec des implications pour la connectivité du paysage fluvial.

Mots-clés : poissons, hydraulique, déplacement, ponceau, habitat

INTRODUCTION

Access to habitat is a fundamental metric of habitat quality. Fish need to move among different habitats to optimally complete the stages of their life cycle; these include spawning, feeding, rearing and seeking refuge from temporary harsh environmental conditions. Depending on the heterogeneity and spatial arrangement of habitats, these may be located at variable distances from each other. As a result, freedom of movement among these habitats plays a critical role in fish life history and fitness (Fausch et al. 2002, Schlosser 1991).

Natural and human-derived elements of the riverscape such as falls, dams or road crossings can reduce the degree of connectivity in river systems, affecting habitat availability for fish and species dispersal. Moreover, at a population level, reduced fluvial connectivity causes

partial or complete isolation of populations, a reduction in gene flow and an increased risk of extirpation (Letcher et al. 2007, Whiteley et al. 2013, Wofford et al. 2005).

Culverts, one of the most widespread anthropogenic riverine features, can restrict longitudinal movements of fish in small streams. Barriers to movements that result from culverts can come in many forms. These include factors limiting the physiological ability of the fish to enter the structure and swim upstream, but also factors influencing its behavior and level of motivation to pass in an upstream or downstream direction (Gibson et al. 2005, Kemp and Williams 2008).

Because culvert hydraulics vary over time, passage performance is likewise variable. The ability to cope with challenging hydraulic conditions is closely related to the species behavior and swimming capacity. Individual variability in fish populations brings an additional level of complexity and makes assessment of culvert passability particularly challenging (Kemp and O'Hanley 2010). In the case of brook trout (*Salvelinus fontinalis*), a species displaying both potamodromous and anadromous life histories, movements over long distances are not unusual (Gowan and Fausch 1996, Kanno et al. 2014, Rodriguez 2002, Petty et al. 2012). This highlights the potential negative impact of barriers.

Previous studies addressing the issue of fish passage through culverts have used various methods. These include the development of flowcharts or classification systems in order to assess the degree of culvert passability and consequently the extent of watershed fragmentation (Bourne et al. 2011, Coffman 2005, Poplar-Jeffers et al. 2009). These so-called coarse filters mostly use static variables such as culvert length and slope, height of outlet drop or presence of roughness elements in the structure. Although inexpensive to use, these

methods have not been extensively validated with biological data and can lead to highly variable results when compared to each other (Bourne et al. 2011).

Other methods have related the hydraulic conditions within the culvert with fish leaping and swimming performance data from laboratory settings in order to predict passage (Castro-Santos 2005, Kondratieff and Myrick 2006, Neary 2012). The software FishXing (Furniss et al. 2006) uses this method to generate predictions of ascent distances and passage success. Some authors have emphasized that FishXing overestimates the proportion of impassable culverts for various species (Burford et al. 2009, Mahlum et al. 2013, Solcz 2007). This is partly because these models are derived from swimming performance data obtained in controlled laboratory environments that underestimated actual performance (Castro-Santos et al. 2013, Peake and Farrell 2006, Tudorache et al. 2007).

Studies have examined the effects of culverts by comparing fish abundance (MacPherson et al. 2012, Morita and Yamamoto 2002, Ppino et al. 2012) or genetic diversity (Neville and Peterson 2014, Nislow et al. 2011, Torterotot et al. 2014) in streams with presence of road crossings. These methods tell whether the culvert is passable but do not measure passage performance itself. An experimental culvert test bed has otherwise been used to study leaping capacity of juvenile fish (Mueller et al. 2008) as well as culvert passability (Peterson et al. 2013). In more natural conditions, fish movements in relation with the presence of culverts have also been studied with telemetry or mark-recapture techniques (Burford et al. 2009, Coffman 2005, Mahlum et al. 2013). These studies focused on comparing movements between stream reaches with culverts and natural reference reaches and were conducted on a single watershed.

Surprisingly, very few studies have sought to understand which variables are influencing successful passage upstream, once the fish enter a culvert. Such an objective requires

knowledge of individual passage attempts as well as current environmental and hydraulic conditions. This knowledge is nevertheless essential to a thorough understanding of culvert passability. Here we describe field observations and analysis of wild brook trout movements through several culverts and model the effect of environmental, biological and hydraulic variables on success.

METHODS

Study sites

Brook trout attempts and passage through culverts were recorded in field trials conducted from 2009 to 2012 in nine culverts located in three watersheds of southern Quebec: Sainte-Marguerite, Saint-Louis and Bécancour rivers (Table 1). Native brook trout is the dominant species in the study areas, mostly exhibiting a potamodromous life history. Three main criteria governed the choices of the study sites: 1) an outlet drop < 5 cm, 2) absence of substratum or roughness elements inside the culvert and 3) presence of high quality habitat upstream. Culverts were randomly selected from among all sites (n=15) that met these criteria.

The selected culverts comprised circular culverts made of metal, concrete or polyethylene and one box culvert made of concrete. Metal culverts had annular or helical (spiral) corrugations of 3-5 cm amplitude and 15 cm wavelength corresponding to a Manning's roughness coefficient of 0.03 (Chow, 1959). Concrete or polyethylene culverts had no corrugations and a coefficient of ~0.010 (Barfuss and Tullis, 1988). We will now refer to corrugated metal culverts as "rough" and concrete or polyethylene culverts as "smooth". In case of crossings with multiple pipes, each pipe was considered a separate site because their respective characteristics (length, diameter or slope) were not identical. This increased the total number of study sites to 13. The length and slope of the culverts were measured with a

theodolite TC705 (Leica Geosystems, Heerbrugg, Switzerland) by taking points at the upstream and downstream extremities as well as at several locations along the culvert.

Hydraulic conditions

Distributions of flow velocity and water depth were quantified before each trial using an electromagnetic (Marsh-McBirney Flow-Mate 2000) or propeller-type velocimeter (Swoffer, model 3000) at lateral transects spaced ~ 2 m along the culvert. At each transect, flow depth and mean flow velocity were measured at 25%, 50% and 75% of the flow cross-section width (Figure 2). These locations capture most of the range of velocities the fish are likely to encounter while ascending the culvert. Depth was measured from the surface to the crest of the corrugations and the corrugation's amplitude (3-5 cm) was considered as the boundary roughness height. Velocity at each location was calculated by averaging instantaneous velocities measured over a 30 second time interval, at a location corresponding to 40% of flow depth from the bottom of the culvert. This location corresponds to the approximate mean flow velocity on the vertical profile, according to the logarithmic distribution of velocities in turbulent flows in open channels (Chow 1959, Von Karman 1931). Average flow depth and velocity for the culvert were computed by averaging the mean values for each transect. Discharge was measured inside the culvert by using cross-sectional area and velocities taken with the velocimeter.

Reynolds number and Froude numbers were respectively computed relative to the culvert flow depth as

$$(1) \quad Re = Uy/\nu$$

$$(2) \quad Fr = \frac{U}{\sqrt{gy}}$$

where U is velocity (cm/s), y is mean flow depth (cm), ν is kinematic viscosity ($\text{cm}^2 \text{s}^{-1}$) and g is acceleration due to gravity (cm/s) (Chow 1959, Vogel 1994) .

Flow area, wetted perimeter and hydraulic radius for each trial were back-calculated using culvert dimensions and mean flow depth as

(3)
$$Rh = \frac{A}{P}$$

where hydraulic radius (Rh) is equal the flow area (A) divided by the wetted perimeter (P). For rectangular culverts, flow area and wetted perimeter are estimated as

(4)
$$A = width \times y$$

(5)
$$P = width + 2y$$

For circular culverts, flow area and wetted perimeter are estimated as

(6)
$$A = r^2(\theta - \cos \theta \sin \theta)$$

(7)
$$P = 2r(\theta)$$

where r is the culvert radius and θ is the characteristic angle (radians) estimated as

(8)
$$\theta = 6 \cos^{-1}(1 - \frac{y}{r})$$

Detailed information about culvert characteristics and hydraulics can be found in (Normann et al. 1985).

Fish collection and tagging

Native brook trout were caught by electrofishing (Smith-Root backpack electrofisher, model 15-C, Vancouver WA, USA), 0-500 m upstream of the culverts, within 48 h of the trials. When the densities upstream of the culvert were low, additional brook trout were caught

downstream or in connected tributaries. Voltage and waveforms were adjusted to account for variation in water conductivity and to minimize risks of injury to the fish (DC varying width pulses, voltage range: 800-1100, frequency: 45/60 Hz, duty cycle range: 0.9-72%).

Fish were anesthetized with a solution of 1 part of clove oil for 10 parts of 95% ethanol diluted in water (0.8-1.2 ml of solution in 1400 ml water; higher concentrations were used at colder water temperatures). Fish were then measured (FL, mm), weighed (wet mass, g) and surgically tagged with 23 mm PIT-tags (Texas Instrument, 23 mm in length, 3 mm in diameter; mass in air: 0.6 g; tag-to-fish mass ratio: 0.42-8.22%). Cyanoacrylate glue (Vetbond 3M) was used to close the incision and fish were kept in holding pens placed in the stream for a recovery period ranging from 2 to 26h (mean recovery time: 15 h). All fish were inspected before release in order to detect any sign of injury or unusual behaviour. Such cases were rare and these fish were not used in the trials. When possible, three tagged fish were also kept in holding pens for the duration of the trial in order to control for tagging-induced mortality. Fish were cared for with conformity to the guidelines of the Canadian Council of Animal Care in science (CCPA) and the experimental protocol was reviewed and approved by the animal care review committee of the research institution.

Study design

Passage trials were conducted between June and October during continuous time periods ranging from 24 to 48h. Water temperature was recorded at a time interval of 15 minutes by a thermograph (Onset, HOBO 020-001-04) deployed in each stream near the culvert. Fish were released in a cage (2m x 1.5m x 1.5m, Figure 1) secured to the downstream extremity of the culvert and allowed to stage attempts at their own volition. A few large rocks were placed in the cage to provide rest areas. As an alternate treatment for some trials, fish were released in

the pool downstream of the culvert, without the use of a cage, and the trial duration was extended to 72h. When a trial was conducted on a culvert with multiple pipes, the cage was fixed to a single pipe or, in case of an uncaged trial, the other pipes were blocked. From now on, trials will be identified as “caged” or “uncaged” to refer to these two groups. When a trial was conducted on a culvert with multiple pipes, the cage was fixed to a single pipe or, in case of an uncaged trial, the other pipes were blocked. This ensured that fish could only access the pipe of interest.

Instrumentation

Movements within the culvert were monitored with a passive integrated transponder (PIT) telemetry system consisting of four antennas located inside the culvert at equal distance from each other (Figure 1). The antennas were made of wire fixed to a rectangular plastic frame. The dimensions vary with the culverts diameter, ranging from 0.45 X 1 m to 0.45 X 2 m. The antennas were located above the water surface to avoid flow disturbance, optimized for 23 mm PIT-tags and interfaced with a half-duplex PIT reader (Technologie Aquartis, control module Quatro, multi-antennas system HDX-134.2 KHz) configured to charge and read tags at 10 Hz (2.5 Hz for each antenna). Horizontal and vertical detection ranges were recorded and adjusted if necessary before each trial to ensure optimal system efficiency and cover the full water depth. The vertical detection fields ranged from 15 to 60 cm from the plane of the antenna and horizontal fields ranged from 5 to 15 cm upstream and downstream of the antennas. The reader recorded tag number, antenna number and time to the nearest 1 s and stored this information in a flash memory card. Detections within 1 second were grouped together, representing discrete exposure to an antenna for a given fish.

The direction of movement was assessed by the order of detection at the four antennas. An attempt was defined as an upstream movement beginning at the furthest downstream antenna (antenna 1) and was considered successful if fish reach the upstream-most antenna (antenna 4) before the end of the trial. Conversely, it was considered a failed attempt if the fish did not reach the fourth antenna during the trial time period and/or moved downstream. In case a fish exited the culvert downstream and made multiple successive attempts, we applied a threshold of 30 seconds between detections at the first antenna to differentiate among attempts. Tagged fish returning from a previous trial and ascending the culvert were excluded from the analysis. Detection efficiency of the PIT system was assessed by quantifying the maximal antenna for every attempt and the detection by the previous antennas. This allowed us to calculate a probability of successful detection for antennas 1, 2 and 3.

Statistical analysis

Logistic regression (Proc Logistic, SAS 9.3) was used to assess the effect of various variables on the probability of passage success of caged fish. Fish that staged attempts were counted. Their best attempt in terms of ascent distance was used to classify them as successful or unsuccessful, depending on whether or not they reached the upstream end. The design allowed fish to stage more than one attempt during a trial but only one observation per attempting fish was used in the statistical analysis.

Culvert length, type and slope, average water temperature, mean flow velocity, mean hydraulic radius, depth of downstream pool, fish length, spawning period and trial duration were included as independent explanatory variables (Table 2). Discharge, Reynolds number and mean flow depth were not used as explanatory variables due to strong correlation with hydraulic radius ($R > 0.70$ in all cases). Culvert type was included as a categorical variable with

value of 0 for rough and 1 for smooth culverts. Spawning period was also a categorical variable with 0 and 1 being respectively more and less than two weeks and within two weeks from the expected spawning time of the source population.

The set of candidate models ($n=208$) included models comprising reasonable combinations of the covariates. In order to minimize the number of candidate models, the set was developed using the following criteria: 1) maximum of six main effects, 2) two-way interactions only, 3) no interactions after five main effects and 4) use water temperature with its quadratic term due to expected non-linearity in its effect on swimming performance in sustained and prolonged mode (Beamish et al. 1978, Brett 1971, Lee et al. 2003). The duration of the trial was included in all models with $\Rightarrow$ three main effects to account for unequal trial duration in the experimental design. Flow velocity, being expected to have an important effect on passage success, was also included in all models with $\Rightarrow$ three main effects. Culvert slope can have an additional effect on performance. Because slope was correlated with flow velocity ($R=0.54$), it was only included in models that already included flow velocity. When slope and flow velocity were together in a given model, a companion model comprising their interaction term was also included. In this way, we explicitly tested for effects of slope other than those associated with increased velocity.

Separate regression models were estimated using Standard International (SI) units and normalized distance units. Normalization (division of distance metrics by body length) was done to control for the fact that perception of distance and swimming ability is often correlated with body size (Goolish 1991). Thus in the normalized regressions culvert length, depth of pool, and hydraulic radius were converted to body lengths (BL) and flow velocity to BL/s. One effect of this

276 transformation was that conditions were no longer fixed at each culvert or trial, but instead
277 varied by individual.

278 During model selection, any model with a positive effect of culvert length or culvert
279 slope on passage success was rejected as it would not make sense biologically. For regressions in
280 SI units as well as for those in normalized distance units, the best model was selected based on
281 minimum of Akaike information criterion (AIC), computed as

282 (9)
$$AIC = -2 \log L + 2K$$

283 where L is the model's likelihood and K the number of parameters

284 AIC allows the selection of the most parsimonious model providing a good fit to the data. Lower
285 AIC values indicate a better fit for the model. When comparing AIC values between the model
286 with minimum AIC and the others in the set, models with a delta AIC of less than 4 were
287 considered viable candidates for the best model (Burham and Anderson 2002).

288 The predictive power of the selected model was assessed on two datasets: caged fish
289 used to develop the model and a new dataset consisting of attempts and passage observations
290 for uncaged fish released freely in the stream. In both datasets, a subsample comprising fish
291 that reached at least the second antenna was also considered, in order to discriminate between
292 truly motivated individuals and those showing only exploratory behaviors. A method derived
293 from the *leave-one-out* principle (Proc logistic, Predprobs = X, SAS 9.3) was used to compute
294 cross-validated individual probability of passage for the caged fish. Tjur's R^2 and c statistic, used
295 to assess the predictive power of the model, are measures of predictive power based on the
296 association between predicted probabilities and observed responses (Allison 2012, Hosmer et al.
297 2013). The c statistic, equivalent to the area under the Receiver Operating Characteristic (ROC)

curve, which is obtained by plotting the sensitivity (proportion of success correctly predicted) against the inverse of the specificity (proportion of failures correctly predicted) for each probability level. It ranges from 0.5 to 1. Tjur's R^2 is a similar statistic useful to compare predictive power between models or for a model applied to different datasets. It measures the difference between the mean of the predicted values for observations with success = 1 and the mean of the predicted values for observations with success = 0. For both statistics, a value of 1 indicates a perfect fit between predicted and observed values.

RESULTS

Trials conditions

A total of 1090 fish (FL 85-240 mm) was captured, pit-tagged and tested in 50 trials: 25 trials in rough culverts and 25 in smooth ones. Each trial consisted of a group of 15 to 30 fish (mean: 22), equally distributed in three size classes (85-119 mm; 119-149 mm; $\pm$ 150 mm). A total of 833 fish were used in caged trials and 257 in uncaged trials. Trial durations ranged from 24 to 48 h (mean = 48; SD =14) for caged fish and 42 to 72 h (mean =55; SD= 14) for uncaged fish. Trials were conducted from mid-June to mid-October, at mean water temperatures between 3 to 18 °C. Mean flow velocity conditions ranged from 0.4 to 2 m/s while the mean flow depth ranged from 0.03 to 0.46 m. For all trials, Reynold's numbers were well within the full turbulent flow range (Chow 1959). Trials conducted in rough culverts were however characterized by higher Reynold's numbers (median=139400; 5th-95th pctl range=54900-332600) than those in smooth culverts (median=55700; 5th-95th pctl range =19600-177000). A likely explanation for this is that for a given velocity, depth was greater in rough culverts than in smooth ones. Froude number was < 1 for rough culverts and $\geq$ 1 for smooth culverts, respectively indicating subcritical and supercritical flows.

Five mortalities were observed among the 77 control tagged fish held in holding pens during the trials, for a survival of 94.5 %. The exact cause of death remained unknown but it could have been induced by the tagging procedure. Eight additional fish (on 1098) died during the surgery or the recovery period and were not used in the trials. The proportion of fish attempting to pass the culverts differed greatly between caged and uncaged fish: 60 % (496) of caged fish staged at least one attempt while only 14 % (36) of uncaged fish did ($P = < 0.001$, t -test in SAS 9.3). Caged fish had only two choices: stay in the cage or stage attempts to pass the culvert, which may have increased the proportion of attempters compared to free-ranging fish facing a wider range of alternatives. For example, a proportion of uncaged fish could have moved downstream and thus were not available to stage attempts. An additional antenna located downstream of the culvert for uncaged trials would have allowed to know the number of fish available. Unfortunately, this would have required a second PIT system at each site and would have significantly increased the cost of the study. The higher density of individuals in the cage, compared to the downstream pool during uncaged trials, may have also stimulated fish to move upstream. Attempting fish had fork length located between 85 and 240 mm (median: 126 mm; 10th-90th pctl range: 102-175 mm). Passage success was higher for caged fish (logistic regression in SAS 9.3, $P < 0.01$), with 51 % of attempters passing the culvert compared to 25% for uncaged attempters. Successful fish had fork lengths ranging from 92 to 206 mm (median: 129 mm; 10th-90th pctl range: 105-175 mm).

Detection efficiency by the PIT system was high in this study. The probability of successful detection of a fish moving upstream was superior to 97% for antennas 1, 2 and 3. It was not possible to quantify detection efficiency for antenna 4, although we can infer a high value from the other antennas. When looking at returning fish moving downstream, we found only two individuals with a maximal distance of ascent equivalent to antenna 3 and

subsequently detected at antenna 4. These fish have exited the culvert without being detected at antenna 4 but returned downstream later in the study.

Model of passage success

Among all 208 models tested, only one emerged as the most parsimonious and providing a good fit to the data (Table 3). This best-fitting model included mean water temperature, mean flow velocity, culvert slope, culvert type (rough vs smooth), depth of the downstream pool and duration of the trial. This model is expressed as

(10)
$$P(success = 1) = \frac{e^{\beta_0 + \beta_1 x_{i1} + \beta_2 x_{i2} + \dots + \beta_k x_{ik}}}{1 + e^{\beta_0 + \beta_1 x_{i1} + \beta_2 x_{i2} + \dots + \beta_k x_{ik}}}$$

where β_0 is the intercept and β is the coefficient for each explanatory variable (x_i) included in the model

After careful observation of the diagnostic statistics, three observations had influence over both model's fit and estimation of parameters. These observations, corresponding to fish having failed to pass the culvert in relatively favorable conditions, were excluded from the estimation of best model's parameters in order to get more reliable estimates. All culverts were circular except one, a smooth box culvert with a low slope. In order to see if this culvert had a particular effect on model selection, it was a-posteriori removed from the analysis. The results remained unchanged and the same model was chosen as the best one. When modeling $P_{success}$ with explanatory variables normalized to body length, the same model was selected as the best one. However, the model in SI units had a reduced AIC with respect to the one in body length

units (417.02 vs 437.48), thus maximizing the likelihood that this model is the best to approximate reality given the data.

Initially, candidate models with six main effects were not allowed to have two-way interactions. The best-fitting model includes culvert type and, based on field observations, we hypothesized that the effect of roughness in culvert may be different depending on the fish body size. Therefore, we included a-posteriori an interaction between culvert type and fish length. This interaction further improved the model's AIC (389.17 vs 417.02) and was then kept in the selected model.

Standardized coefficients (β) measure the relative importance of the explanatory variables, regardless of the metrics in which the variables have been measured (Table 4). Culvert type had the greatest effect on success, followed by its interaction with fish length, culvert slope, depth of downstream pool, water temperature, average water velocity and trial duration.

Body length had contradictory effects on fish passage performance, depending on type of culvert ascended (Figure 3, panels A, B and C). Shorter fish performed better in rough culverts while in smooth culverts performance increased with the size of the fish.

Slope had an evident negative impact on passage success (Figure 4, panels A, B and C), a 1-unit increase (1%) in slope being associated with a 73% decrease in passage success (odds ratio = 0.27, Table 4). This effect was however less pronounced in rough culverts. Slope is the measure of change in height per distance and so relates to the rate of working required to elevate a mass. It also has important effects on hydraulics. Slope was correlated to flow velocity ($R=0.54$, $p<.001$) with steep slope associated with faster flow velocities. Slope was also correlated with hydraulic radius ($R=0.22$ for rough and $R=0.63$ for smooth culverts, $p<.0001$),

which was itself highly correlated with flow depth ($R=0.99$, $p<.0001$). Steeps slopes were therefore associated with shallow depths in smooth culverts but not necessarily in rough ones.

Depth of the staging area also affected P_{success} , with poorer success associated with deeper pools (Figure 5, panel A).

Passage success declined with increasing flow velocity, decreasing by 95% per m/s (odds ratio = 0.05, Table 4). Mean flow velocity had a negative effect on P_{success} (Figure 5, panel B), and this was much more pronounced in smooth than in rough culverts for a median-size fish (126 mm). In a smooth culvert, P_{success} falls under 0.5 at ~ 0.8 m/s while in a rough one it occurs at 1.5 m/s.

The probability of success increased with water temperature towards an optimum around 14-15°C, afterwards it decreased slowly until 18° (Figure 5, panel C), which is the upper limit of the range of tested temperatures.

Trout that were exposed to longer trials had greater opportunity to stage attempts. This led to an increase of 8% per hour in the predicted odds of success (odds ratio = 1.08, Table 4). This effect is however limited to 48h, which is the longest trial duration for caged fish.

Validation of model's predictive power

The c -statistic and Tjur's R^2 were high for the full training dataset and for the dataset comprising only the uncaged fish. This was true both for the model with variables in SI units and for the model with variables normalized to body lengths (Table 5). However, when only the fish that swam further than the first antenna were considered, the predictive power decreased in both datasets.

When using predicted probabilities to assess passage success, a cut-off point is required to switch from a prediction of failure to one of success. The ideal cut-off point is one maximizing both sensitivity and specificity (Allison 2012, Hosmer et al. 2013). For our study, this cut-point occurred at a probability level of 0.82 (Figure 6). The choice of the cut point value depends, however, on the assessment of relative costs of the two types of errors in a given context: predicting a passable culvert which in reality is not or predicting a barrier which is actually passable.

DISCUSSION

This study describes passage performance of >1000 PIT-tagged wild brook trout in their native streams through 13 culverts. The study design provided a unique ability to assess effects of design, hydraulics and behavior on passage performance with some surprising results. These highlight how successful passage is linked to several variables and is often the result of interactions between behavioral and physiological aspects of fish swimming performance. Type of culvert and its interaction with fish body length had the greatest effects on passage success. These results offer improved tools for estimating habitat fragmentation for brook trout, for prioritizing removal and retrofits of existing culverts, and for planning of future roadways and stream crossings.

We used PIT telemetry to obtain these results, which is a cost-effective method that allows continuous monitoring and recording of individual movement events. This contrasts with indirect methods like mark-recapture or genetics tools that are useful to demonstrate that movement has occurred (Neville and Peterson 2014, Whiteley et al. 2014) but have low potential to quantify rate of movement for a population. Ultimately it is both the rate of movement and passage success that determines connectivity. Thus the use of a direct method

such as PIT telemetry or a combination of direct and indirect techniques is valuable to supply the two different types of information. PIT telemetry can have effects on survival and swimming performance, due to the surgery procedure (Bateman and Gresswell 2006, Gries and Letcher 2002, Ombredane et al. 1998) or the tag burden (Perry et al. 2013). 23 mm tags would still be acceptable for salmonids of ≥ 80 mm (Bateman and Gresswell 2006). In the current study, some fish had high tag-to-fish mass ratio, which can have negatively impacted their performance. However, small fish showed good passage success in the culverts. Moreover, as the probability of success was computed on attempting fish, mortalities during the trials would have reduced the number of attempters but not the passage success itself. The probability of successful detection at each PIT antenna was superior to 97% in this study. Some failed detections might have happen at antennas 1 and 4, with effects such as underestimating the number of attempters or the probability of successful passage. However, the high detection efficiency makes these negligible effects with regards to the overall results.

Our results differ from existing literature where culvert passability has been mainly related to the height of outlet drop (Kondratieff and Myrick 2006, Park et al. 2008) or the average flow velocity inside the structure (Burford et al. 2009, Johnson et al. 2012, Warren and Pardew 1998). In contrast our results suggest that culvert type was the most important factor driving passability, with superior passage through rough culverts, especially for smaller fish.

The hydraulic complexity of rough culverts may explain this. Velocities in corrugated culverts do not conform to the expected log law distribution (Chow 1959, Von Karman 1931). Instead, the reduced velocity zone extends further away from the walls and floor of the culvert, particularly on the right side, facing upstream. (Ead et al. 2000, Powers et al. 1997, Richmond et al. 2007). Flow separation on the downstream side of the corrugations also creates very low

velocity zones. These can allow fish to achieve greater ascent distances by alternating between resting and active swimming behaviors. Because of this, any model relating fish swimming capacity to mean flow velocity ($\bar{U}_f$) to predict passage success will underestimate passage performance. Instead the ability to find and use these low velocity zones becomes a key element for fish passage success.

The scaling of the roughness elements with the fish length might explain the increased performance of small fish. The corrugation's characteristics in the studied rough culverts may have allowed fish less than 15 cm to rest in the lee of a corrugation, where the flow velocity is close to zero. Anecdotal observations of small fish resting in the lee of corrugations have been made in the present study as well as in fishways and culverts (Belford and Gould 1989, Bunt et al. 1999, Powers et al. 1997). This resting behavior might help them to recover from anaerobic activity such as sprinting. Such resting behavior can improve passage success, but can also reduce it, particularly if it reduces rates of upstream movement (Castro-Santos 2012, Wagner et al. 2012). More work is needed to understand how hydraulic complexity influences swimming ability and behaviors.

The effect of flow velocity is intuitive: as the mean flow velocity increases, fish fatigue more rapidly and ascent distance decreases. Flow velocity is well-known to limit passage performance (Haro et al. 2004, Peterson et al. 2013, Weaver 1963). In the current study, however, flow velocity alone was not sufficient to adequately predict success.

Likewise, the length of the culvert was not an important predictor of passage success. If swimming capacity is the dominant driver of success then one would expect success to decline with culvert length (Castro-Santos et al. 2013, Haro et al. 2004). The absence of this variable in the best model suggests that fatigue may not have been the primary cause of failure. A

proportion of failed fish may have abandoned their ascents for reasons related to motivation. Another explanation could be that, even in long culverts and fast flows, some successful fish were able to avoid relying exclusively on their anaerobic metabolism, either by using the corrugations to rest or low velocity zones to achieve greater ascent distances under aerobic processes. It may also be important that our longest culverts all had relatively low slopes, and there may have been some confounding interaction between these features. Finally, because we quantified passage and not actual ascent distance it may be that the logistic regression approach applied here lacked the power to accurately measure the effect of culvert length. Therefore our results should not be interpreted as meaning that culvert length is unimportant, but instead that other factors were also important and the combination of this, the study design and the binary passage metric applied failed to detect an effect of culvert length.

We observed passage under a wide range of water temperature during the study and found that P_{success} is maximized at an average temperature of $\sim 15^{\circ}\text{C}$. Interestingly, $14\text{--}15^{\circ}\text{C}$ is the average water temperature of the studied streams during the period between June and September, when most of the trials were conducted. Aerobic performance of salmonids has been observed to follow a bell-shaped curve (Brett 1971, Brett and Glass 1973), with an optimum that approximates the average temperature of natal streams (Farrell 2007, Lee et al. 2003). For brook trout, maximal aerobic capacity occurs at 15°C (Tudorache et al. 2010). At low temperature, the power production of red muscles is depressed. This requires early recruitment (at lower swim speeds) of white muscle fibers that use anaerobic metabolism (Rome 1990). As temperature approaches the optimum, aerobic function and power generation are maximized, leading to a higher swimming performance (Brett 1971). Anaerobic metabolism is much less affected by temperature (Beamish et al. 1978); fatigue occurs rapidly, reducing passage success against fast flows in all but the shortest culverts (Haro et al. 2004; Castro-Santos et al. 2013).

The critical flow velocity (U_{crit}) at which fish will transition from one metabolism to the other decreases at low temperatures, which should be considered in fish passage issues. Temperatures are usually colder during spawning, when brook trout motivation to move is at its highest level. It may then impede success at a critical stage of their life cycle. The current study has been done both outside and during the spawning period and it would be worth exploring further passage success with regards to cool water temperatures during spawning.

Culverts with steeper slopes are generally associated with poorer passage success due to the positive relationship between slope and flow velocity (Belfort and Gould 1989, Coffman 2005, Powers and Orsborn 1985). However, independently of flow, slope may have effects on passage performance. Indeed, it was an important predictor of passage success in the selected model, even when flow velocity was already accounted for. One reason for this may be that steep slopes affect the relationship between buoyancy and weight forces acting on the fish. These forces cancel each other at a zero slope and in static flow. This requires the fish to generate more power in order to deliver the propulsive force necessary to overcome the slope (Behlke 1991). Although this is an interesting concept, further work is needed to demonstrate its occurrence on swimming fish and to assess the magnitude of the effect.

The effect of slope can also be related to its correlation with flow depth. The unequal correlation between slope and flow depth in rough and smooth culverts may have implications for passage success under a range of slopes and flow velocities. Our findings indicate that success decreases with increase of slope, especially in smooth culverts (Figure 4). Even at high flow (1.7 m/s), passage success is possible in rough culverts of various slopes, perhaps due to the fact that these structures retain deeper flow. A deeper flow inside the culvert has been associated to greater swimming and leaping performance (Kondratieff and Myrick 2006, Powers

and Orsborn 1985). Nevertheless, depth might not always be an important constraint to fish upstream movements. In the present study, we observed fish ascending culverts at very shallow depths (< 5 cm), although it was against flow velocities < 1.2 m/s. Certainly, a deeper flow means more space for the fish to swim, recruit various muscles groups and optimally use its fins for propulsion and balance. Swimming near the surface generates waves and increase drag compared to submerged swimming (Videler 1993). For a similar mean flow velocity ($\bar{U}_f$), the gradient of velocities in the cross-section will be less pronounced at a deeper flow, which means that the size of the areas where $U_f < \text{or} > \bar{U}_f$ will be increased. A deeper flow may then allow the fish to benefit from reduced velocity zones by swimming close to the culvert's bottom and walls while simultaneously avoiding the surface. This might increase the probability of successful passage at high flows.

Passage performance decreased with increasing depth of the downstream pool. This variable can influence the perception by the fish of the oncoming flow as well as the level of comfort in the cage. A deeper pool means more space and refugia for the fish in the cage. Overall, caged fish staged more attempt than uncaged ones, which suggests that the behavior is partly an escape response. The density of individuals in the cage was higher at shallow depths, which may have increased their motivation to move upstream. Such pattern was observed for Coho salmon in an experimental culvert (Johnson et al. 2012) and for alewives exiting pools in fishways (Dominy 1973). The latter however considered the number of fish exiting rather than the proportion exiting versus the number of fish available, which makes the results ambiguous.

Longer trials improved passage success, probably because they offered more opportunities for fish to ascend the culvert. More than half (60%) of the caged fish staged attempts during the trials and we modeled overall success, regardless of the number and timing

of attempts. The proportion of attempters increases over time, perhaps influenced by variations of flow, temperature or diurnal patterns. Moreover, the number of attempt per individual could have an influence on performance. Castro-Santos (2004, 2006) demonstrated that fish staging multiple attempts increase their ascent distance over time, each new attempt being an opportunity for the fish to select an optimal swim speed and so maximize distance. In the event the model is applied to predict passage of free-range fish, the trial duration should be the period of time required for fish to pass the culvert or, from a management perspective, the acceptable delay in upstream movement induced by the structure. Further analysis is needed to understand better the effects of structural, biological and environmental variables on attempt rate of brook trout.

Other factors have not been taken into account when modelling P_{success} . For instance, we did not consider prior knowledge about the connectivity of sampled streams. Despite the fact that most of the fish have been caught upstream of the studied culverts, some of them may have interacted with the culvert before being tested and so acquired a certain learning of the structure. Besides, fish had been collected from deep pools to shallow riffles and may have developed various body morphologies and life histories in response to their habitat. When modelling success, we did not consider the characteristics of the stream where the fish came from. It is possible that individuals from fast-flowing or turbulent habitats had an increased ability to face challenging areas such as culverts (Castro-Santos and Haro 2006, Clausen 1931). Nonetheless, the fact that the proposed model has been developed with wild brook trout from different populations, each of them occupying watersheds with distinct geomorphological and ecological characteristics, increases the model's robustness and scope. This model was developed with data integrating various behavioral responses to the presence of a culvert: serious passage attempts as well as exploratory behaviors. Thus, it performed better at

predicting outcomes for fish exhibiting different behaviors, which will likely be the case in the field. The fact that the validation statistics remained high when the model was used to predict success for the uncaged fish is interesting as such a model is intended to predict passage success of wild, free-ranging fish.

This study provides new insight on underlying mechanisms of fish passage success through culverts, interactions between physiological and behavioral components and the beneficial effect of rough culverts. This means that replacing or relining corrugated metal culverts with smooth ones, a practice that is gaining popularity to increase culvert's lifespan, will have a detrimental effect on river connectivity. The increased ability of small fish to negotiate rough culverts is also particularly important. It may indicate a unique adaptability to local conditions in order to increase their capacity to move, which can have a high value from an ecological point of view. In conclusion, basing predictions of culvert passability and design criteria solely on fish physiological capacity can be misleading. The model developed here will improve accuracy of passage predictions for brook trout ascending culverts under the range of conditions described in Table 2. Although extensive work remains to be done, this is a first step towards a more comprehensive approach to understand fish passage at road crossings.

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REFERENCES

Allison, P.D. 2012. Logistic Regression Using SAS: Theory and Application, Second Edition. SAS Institute.

Bateman, D.S., and Gresswell, R.E. 2006. Survival and Growth of Age-0 Steelhead after Surgical Implantation of 23 mm Passive Integrated Transponders. *North American Journal of Fisheries Management* **26**(3): 545-550. doi: 10.1577/M05-111.1.

Beamish, F.W.H., Hoar, W.S., and Randall, D.J. 1978. 2 Swimming Capacity. *In Fish Physiology*. Academic Press. pp. 101-187.

Behlke, C.E. 1991. Power and energy implications of passage structures for fish. *American Fisheries Society Symposium* **10**: 289-298.

Belford, D.A., and Gould, W.R. 1989. An Evaluation of Trout Passage through Six Highway Culverts in Montana. *North American Journal of Fisheries Management* **9**(4): 437-445. doi: 10.1577/1548-8675(1989)009<0437:aeotpt>2.3.co;2.

Belfort, D.A., and Gould, W.R. 1989. An Evaluation of trout Passage through Six Highway Culverts in Montana. *North American Journal of Fisheries Management* **9**: 437-445.

Bourne, C., Kehler, D., Wiersma, Y., and Cote, D. 2011. Barriers to fish passage and barriers to fish passage assessments: the impact of assessment methods and assumptions on barrier

621 identification and quantification of watershed connectivity. *Aquat. Ecol.* **45**(3): 389-403. doi:
622 10.1007/s10452-011-9362-z.

623

624 Brett, J.R. 1971. Energetic Responses of Salmon to Temperature. A Study of Some Thermal
625 Relations in the Physiology and Freshwater Ecology of Sockeye Salmon (*Oncorhynchus nerka*).
626 *Am. Zool.* **11**(1): 99-113. doi: 10.1093/icb/11.1.99.

627 Brett, J.R., and Glass, N.R. 1973. Metabolic Rates and Critical Swimming Speeds of Sockeye
628 Salmon (*Oncorhynchus nerka*) in Relation to Size and Temperature. *J. Fish. Res. Board Can.*
629 **30**(3): 379-387. doi: doi:10.1139/f73-068.

630

631 Bunt, C.M., Katopodis, C., and McKinley, R.S. 1999. Attraction and Passage Efficiency of White
632 Suckers and Smallmouth Bass by Two Denil Fishways. *North American Journal of Fisheries*
633 *Management* **19**(3): 793-803. doi: 10.1577/1548-8675(1999)019<0793:aapeow>2.0.co;2.

634

635 Burford, D.D., McMahon, T.E., Cahoon, J.E., and Blank, M. 2009. Assessment of trout passage
636 through culverts in a large Montana drainage during summer low flow. *North American Journal*
637 *of Fisheries Management* **29**: 739-752. doi: 10.1577/M07-175.1.

638

639 Burham, K., and Anderson, D. 2002. Model Selection and Multivariate Inference: A Practical
640 Information-Theoretical Approach. Springer, New York.

641

642 Cahoon, J., MacMahon, T., and Stein, O. 2004. Fish passage in Montana Culverts; phase II-
643 Passage Goals. Montana State University. p. 26.

644

- 645 Castro-Santos, T. 2004. Quantifying the combined effects of attempt rate and swimming
646 capacity on passage through velocity barriers. *Can. J. Fish. Aquat. Sci.* **61**: 1602-1615. doi: doi:
647 10.1139/F04-094.
- 648
- 649 Castro-Santos, T. 2005. Optimal swim speeds for traversing velocity barriers: an analysis of
650 volitional high-speed swimming behavior of migratory fishes. *J Exp Biol* **208**(3): 421-432. doi:
651 10.1242/jeb.01380.
- 652 Castro-Santos, T. 2006. Modeling the effect of varying swim speeds on fish passage through
653 velocity barriers. *Trans. Am. Fish. Soc.* **135**(5): 1230-1237. doi: 10.1577/t05-262.1.
- 654
- 655 Castro-Santos, T. 2012. Adaptive fishway design: a framework and rationale for effective
656 evaluations. *In* Monitoring, Funktionskontrollen und Qualitätssicherung an
657 Fischaufstiegsanlagen, 2. Kolloquium zur Herstellung der ökologischen Durchgängigkeit der
658 Bundeswasserstraßen. Koblenz, Germany, pp. 76-89.
- 659
- 660 Castro-Santos, T., and Haro, A. 2006. Biomechanics and fisheries conservation. *In* Fish
661 Physiology, volume 23: Fish Biomechanics. *Edited by* R.E. Shadwick and G.V. Lauder. Academic
662 Press, New York. pp. 469-523.
- 663
- 664 Castro-Santos, T., Sanz-Ronda, F.J., and Ruiz-Legazpi, J. 2013. Breaking the speed limit —
665 comparative sprinting performance of brook trout (*Salvelinus fontinalis*) and brown trout (*Salmo*
666 *trutta*). *Can. J. Fish. Aquat. Sci.* **70**(2): 280-293. doi: doi:10.1139/cjfas-2012-0186.
- 667
- 668 Chow, V.T. 1959. Open-channel hydraulics. McGraw Hill Book Company.

- 669 Clausen, R.G. 1931. Orientation in Fresh Water Fishes. *Ecology* **12**(3): 541-546. doi:
670 10.2307/1928999.
- 671
- 672 Coffman, J.S. 2005. Evaluation of a predictive model for upstream fish passage through culverts,
673 Biology, James Madison University.
- 674
- 675 Dominy, C.L. 1973. Effect of Entrance-Pool Weir Elevation and Fish Density on Passage of
676 Alewives (*Alosa pseudoharengus*) in a Pool and Weir Fishway. *Trans. Am. Fish. Soc.* **102**(2): 398-
677 404. doi: 10.1577/1548-8659(1973)102<398:eoewea>2.0.co;2.
- 678
- 679 Ead, S.A., Rajaratnam, N., Katopodis, C., and Ade, F. 2000. Turbulent open-channel flow in
680 circular corrugated culverts. *Journal of Hydraulic Engineering-Asce* **126**(10): 750-757. Available
681 from <Go to ISI>://000089579200004.
- 682
- 683 Farrell, A.P. 2007. Cardiorespiratory performance during prolonged swimming tests with
684 salmonids: a perspective on temperature effects and potential analytical pitfalls. *Philosophical*
685 *Transactions of the Royal Society B: Biological Sciences* **362**(1487): 2017-2030. doi:
686 10.1098/rstb.2007.2111.
- 687
- 688 Fausch, K.D., Torgersen, C.E., Baxter, C.V., and Li, H.W. 2002. Landscapes to Riverscapes:
689 Bridging the Gap between Research and Conservation of Stream Fishes: A Continuous View of
690 the River is Needed to Understand How Processes Interacting among Scales Set the Context for
691 Stream Fishes and Their Habitat. *BioScience* **52**(6): 483-498. doi: 10.1641/0006-
692 3568(2002)052[0483:ltrbtg]2.0.co;2.

693

694 Gibson, R.J., Haedrich, R.L., and Wernerheim, C.M. 2005. Loss of Fish Habitat as a Consequence
695 of Inappropriately Constructed stream Crossings. *Fisheries* **30**(1): 10-17.

696

697 Goolish, E.M. 1991. Aerobic and Anaerobic scaling in Fish. *Biological Reviews* **66**(1): 33-56. doi:
698 10.1111/j.1469-185X.1991.tb01134.x.

699

700 Gowan, C., and Fausch, K.D. 1996. Mobile brook trout in two high elevation Colorado streams:
701 re-evaluating the concept of restricted movements. *Can. J. Fish. Aquat. Sci.* **53**: 1370-1381.

702

703 Gries, G., and Letcher, B.H. 2002. Tag retention and survival of age-0 atlantic salmon following
704 surgical implantation with passive integrated transponder tags. *North American Journal of*
705 *Fisheries Management* **22**(1): 219-222. doi: 10.1023/a:1017022026937.

706

707 Haro, A., Castro-Santos, T., Noreika, J., and Odeh, M. 2004. Swimming performance of upstream
708 migrant fishes in open-channel flow: a new approach to predicting passage through velocity
709 barriers. *Can. J. Fish. Aquat. Sci.* **61**: 1590-1601.

710

711 Hosmer, D.W., Lemeshow, S., and Sturdivant, R.X. 2013. Applied logistic regression. John Wiley
712 & Sons.

713

714 Johnson, G.E., Pearson, W.H., Southard, S.L., and Mueller, R.P. 2012. Upstream Movement of
715 Juvenile Coho Salmon in Relation to Environmental Conditions in a Culvert Test Bed. *Trans. Am.*
716 *Fish. Soc.* **141**(6): 1520-1531. doi: 10.1080/00028487.2012.699013.

717

718 Kanno, Y., Letcher, B.H., Coombs, J.A., Nislow, K.H., and Whiteley, A.R. 2014. Linking movement
719 and reproductive history of brook trout to assess habitat connectivity in a heterogeneous
720 stream network. *Freshwater Biol.* **59**(1): 142-154.

721

722 Kemp, P.S., and Williams, J.G. 2008. Response of migrating Chinook salmon (*Oncorhynchus*
723 tshawytscha) smolts to in-stream structure associated with culverts. *River Research and*
724 *Applications* **24**(5): 571-579. doi: 10.1002/rra.1140.

725

726 Kemp, P.S., and O'Hanley, J.R. 2010. Procedures for evaluating and prioritising the removal of
727 fish passage barriers: a synthesis. Blackwell Publishing Ltd. pp. 297-322.

728 Kondratieff, M.C., and Myrick, C.A. 2006. How High Can Brook Trout Jump? A Laboratory
729 Evaluation of Brook Trout Jumping Performance. *Trans. Am. Fish. Soc.* **135**(2): 361-370. doi:
730 10.1577/t04-210.1.

731

732 Lee, C.G., Farrell, A.P., Lotto, A., MacNutt, M.J., Hinch, S.G., and Healey, M.C. 2003. The effect of
733 temperature on swimming performance and oxygen consumption in adult sockeye
734 (*Oncorhynchus nerka*) and coho (*O. kisutch*) salmon stocks. *J. Exp. Biol.* **206**(18): 3239-3251.
735 doi: 10.1242/jeb.00547.

736

737 Letcher, B.H., Nislow, K.H., Coombs, J.A., O'Donnell, M.J., and Dubreuil, T.L. 2007. Population
738 Response to Habitat Fragmentation in a Stream-Dwelling Brook Trout Population. *PLoS ONE*
739 **2**(11): e1139. doi: 10.1371/journal.pone.0001139.

740

- 741 MacPherson, L.M., Sullivan, M.G., Foote, A.L., and Stevens, C.E. 2012. Effects of Culverts on
742 Stream Fish Assemblages in the Alberta Foothills. *North American Journal of Fisheries*
743 *Management* **32**(3): 480-490. doi: 10.1080/02755947.2012.686004.
744
- 745 Mahlum, S., Cote, D., Wiersma, Y.F., Kehler, D., and Clarke, K.D. 2013. Evaluating the Barrier
746 Assessment Technique Derived from FishXing Software and the Upstream Movement of Brook
747 Trout through Road Culverts. *Trans. Am. Fish. Soc.* **143**(1): 39-48. doi:
748 10.1080/00028487.2013.825641.
749
- 750 Morita, K., and Yamamoto, S. 2002. Effects of Habitat Fragmentation by Damming on the
751 Persistence of Stream-Dwelling Charr Populations. *The Journal of the Society for Conservation*
752 *Biology* **16**(5): 1318-1323. doi: 10.1046/j.1523-1739.2002.01476.x.
753
- 754 Mueller, R.P., Southard, S.S., May, C.W., Pearson, W.H., and Cullinan, V.I. 2008. Juvenile coho
755 salmon leaping ability and behavior in an experimental culvert test bed. *Trans. Am. Fish. Soc.*
756 **137**(4): 941-950. doi: 10.1577/t06-244.1.
757
- 758 Neary, V.S. 2012. Binary Fish Passage Models for Uniform and Nonuniforms Flows. *River*
759 *Research and Applications* **28**(4): 418-428. doi: 10.1002/rra.1564.
760
- 761 Neville, H.M., and Peterson, D.L. 2014. Genetic monitoring of trout movement after culvert
762 remediation: family matters. *Can. J. Fish. Aquat. Sci.* **71**(11): 1680-1694. doi: doi:10.1139/cjfas-
763 2014-0138.
764

- 765 Nislow, K.H., Hudy, M., Letcher, B.H., and Smith, E.P. 2011. Variation in local abundance and
766 species richness of stream fishes in relation to dispersal barriers: implications for management
767 and conservation. *Freshwater Biol.* **56**(10): 2135-2144. doi: 10.1111/j.1365-2427.2011.02634.x.
768
- 769 Normann, J.M., Houghtalen, R.J., and Johnston, W.J. 1985. Hydraulic design of highway culverts.
770 *Edited by* U.D.o. Transportation. Federal Highway Administration, Washington, DC. p. 272.
771
- 772 Ombredane, D., Bagliniere, J., and Marchand, F. 1998. The effects of Passive Integrated
773 Transponder tags on survival and growth of juvenile brown trout (&i&t;Salmo trutta L.) and
774 their use for studying movement in a small river. *Hydrobiologia* **371-372**(0): 99-106. doi:
775 10.1023/a:1017022026937.
776
- 777 Park, D., Sullivan, M., Bayne, E., and Scrimgeour, G. 2008. Landscape-level stream fragmentation
778 caused by hanging culverts along roads in Alberta's boreal forest. *Canadian Journal of Forest*
779 *Research-Revue Canadienne De Recherche Forestiere* **38**(3): 566-575. doi: 10.1139/x07-179.
780
- 781 Peake, S.J., and Farrell, A.P. 2006. Fatigue is a behavioural response in respirometer-confined
782 smallmouth bass. *J. Fish Biol.* **68**(6): 1742-1755. doi: 10.1111/j.0022-1112.2006.01052.x.
783
- 784 Ppino, M., Rodrguez, M.A., and Magnan, P. 2012. Impacts of highway crossings on density of
785 brook charr in streams. *J. Appl. Ecol.* **49**(2): 395-403. doi: 10.1111/j.1365-2664.2012.02108.x.
786
- 787 Perry, R.W., Plumb, J.M., Fielding, S.D., Adams, N.S., and Rondorf, D.W. 2013. Comparing Effects
788 of Transmitters within and among Populations: Application to Swimming Performance of

- 789 Juvenile Chinook Salmon. Transactions of the American Fisheries Society **142**(4): 901-911. doi:
790 10.1080/00028487.2013.788556.
- 791
792 Petty, J.T., Hansbarger, J.L., Huntsman, B.M., and Mazik, P.M. 2012. Brook Trout Movement in
793 Response to Temperature, Flow, and Thermal Refugia within a Complex Appalachian Riverscape.
794 Transactions of the American Fisheries Society **141**(4): 1060-1073. doi:
795 10.1080/00028487.2012.681102.
- 796
797 Peterson, N.P., Simmons, R.K., Cardoso, T., and Light, J.T. 2013. A Probabilistic Model for
798 Assessing Passage Performance of Coastal Cutthroat Trout through Corrugated Metal Culverts.
799 North American Journal of Fisheries Management **33**(1): 192-199. doi:
800 10.1080/02755947.2012.750633.
- 801
802 Poplar-Jeffers, I.O., Petty James, J.T., Anderson, T., Kite, S.J., Strager, M.P., and Fortney, R.H.
803 2009. Culvert Replacement and Stream Habitat Restoration: Implications from Brook Trout
804 Management in an Appalachian Watershed, U.S.A. Restoration Ecology **17**(3): 404-413. doi:
805 10.1111/j.1526-100X.2008.00396.x.
- 806
807 Powers, P.D., and Orsborn, J.F. 1985. Analysis of Barriers to Upstream Migration: An
808 Investigation of the Physical and Biological Conditions Affecting Fish Passage Success at Culverts
809 and Waterfalls. Albrook Hydraulics Laboratory Washington State University, Pullman, WA.
- 810
811 Powers, P.D., Bates, K., Burns, T., Gowen, B., and Whitney, R. 1997. Culvert hydraulics related to
812 upstream juvenile salmon passage. *Edited by* W.D.o.F.a. Wildlife.

813

814 Richmond, M.C., Deng, Z.Q., Guensch, G.R., Tritico, H., and Pearson, W.H. 2007. Mean flow and
815 turbulence characteristics of a full-scale spiral corrugated culvert with implications for fish
816 passage. *Ecological Engineering* **30**(4): 333-340. doi: 10.1016/j.ecoleng.2007.04.011.

817

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

820

821 Schlosser, I.J. 1991. Stream fish ecology: a landscape perspective. *Bioscience* **41**(10): 704-712.

822

823 Solcz, A.A. 2007. Assessment of culvert passage of Yellowstone cutthroat trout in a Yellowstone
824 river tributary using a passive integrated transponder system, Fish and Wildlife management,
825 Montana State University, Bozeman.

826

827 Torterotot, J.-B., Perrier, C., Bergeron, N.E., and Bernatchez, L. 2014. Influence of Forest Road
828 Culverts and Waterfalls on the Fine-Scale Distribution of Brook Trout Genetic Diversity in a
829 Boreal Watershed. *Trans. Am. Fish. Soc.* **143**(6): 1577-1591. doi:
830 10.1080/00028487.2014.952449.

831

832 Tudorache, C., Viaenen, P., Blust, R., and De Boeck, G. 2007. Longer flumes increase critical
833 swimming speeds by increasing burst–glide swimming duration in carp *Cyprinus carpio*, L. J. Fish
834 Biol. **71**(6): 1630-1638. doi: 10.1111/j.1095-8649.2007.01620.x.

835

- 836 Tudorache, C., O'Keefe, R.A., and Benfey, T.J. 2010. The effect of temperature and ammonia
837 exposure on swimming performance of brook charr (*Salvelinus fontinalis*). *Comp. Biochem.*
838 *Physiol., Part A: Mol. Integr. Physiol.* **156**(4): 523-528. doi:
839 <http://dx.doi.org/10.1016/j.cbpa.2010.04.010>.
- 840
- 841 Videler, J.J. 1993. *Fish swimming*. Chapman & Hall, London.
- 842
- 843 Vogel, S. 1994. *Life in Moving Fluids: The Physical Biology of Flow*. Princeton University Press.
- 844
- 845 Von Karman, T. 1931. Mechanical similitude and turbulence.
- 846
- 847 Wagner, R.L., Makrakis, S., Castro-Santos, T., Makrakis, M.C., Dias, J.H.P., and Belmont, R.F.
848 2012. Passage performance of long-distance upstream migrants at a large dam on the Paraná
849 River and the compounding effects of entry and ascent. *Neotropical Ichthyology* **10**: 785-
850 795. Available from [http://www.scielo.br/scielo.php?script=sci_arttext&pid=S1679-](http://www.scielo.br/scielo.php?script=sci_arttext&pid=S1679-62252012000400011&nrm=iso)
851 [62252012000400011&nrm=iso](http://www.scielo.br/scielo.php?script=sci_arttext&pid=S1679-62252012000400011&nrm=iso).
- 852
- 853 Warren, M.L., and Pardew, M.G. 1998. Road crossings as barriers to small-stream fish
854 movement. *Trans. Am. Fish. Soc.* **127**(4): 637-644. Available from <Go to
855 [ISI>://000075350600011](http://www.jstor.org/stable/1566611).
- 856
- 857 Weaver, C.R. 1963. Influence of water velocity upon orientation and performance of adult
858 migrating salmonids. *Fisheries Bulletin* **63**(1): 97-121.
- 859

- 860 Whiteley, A.R., Coombs, J.A., Hudy, M., Robinson, S.C., Colton, A.R., Nislow, K.H., and Letcher,
861 B.H. 2013. Fragmentation and patch size shape genetic structure of brook trout populations.
862 Can. J. Fish. Aquat. Sci. **70**(5): 678-688. doi: doi:10.1139/cjfas-2012-0493.
863
- 864 Whiteley, A.R., Coombs, J.A., Letcher, B.H., and Nislow, K.H. 2014. Simulation and empirical
865 analysis of novel sibship-based genetic determination of fish passage. Can. J. Fish. Aquat. Sci.
866 **71**(11): 1667-1679. doi: doi:10.1139/cjfas-2014-0137.
867
- 868 Wofford, J.E.B., Gresswell, R.E., and Banks, M.A. 2005. Influence of Barriers to Movement on
869 Within-Watershed Genetic Variation of Coastal Cutthroat Trout. Ecological Applications **15**(2):
870 628-637. Available from <http://www.jstor.org/stable/4543380>.

871 (1) Table 1: Study sites characteristics.

Site	Watershed	Latitude	Longitude	Material	Shape	Diameter	Length	Slope
Resimond	Sainte-Marguerite	48°25'52"N	70°26'03"W	Corrugated metal	Circular	1600	44,6	0.92
MorinA	Sainte-Marguerite	48°20'50"N	70°03'39"W	Corrugated metal	Circular	1500	33,2	1.38
MorinB	Sainte-Marguerite	48°20'50"N	70°03'39"W	Corrugated metal	Circular	2200	32,3	1.38
MorinC	Sainte-Marguerite	48°20'50"N	70°03'39"W	Corrugated metal	Circular	2200	33	1.38
MorinD	Sainte-Marguerite	48°20'50"N	70°03'39"W	Polyethylene	Circular	2200	32,4	1.38
Allaire	Sainte-Marguerite	48°21'19"N	70°07'07"W	Concrete	Box	2000 x 2000	18,4	0.28
Femmes	Saint-Louis	48°43'10"N	70°55'26"W	Corrugated metal	Circular	2000	17,9	2.4
Adolphe	Saint-Louis	48°46'38"N	70°49'25"W	Corrugated metal	Circular	2000	14,3	1.6
Raquette	Saint-Louis	48°38'59"N	70°55'22"W	Corrugated metal	Circular	2700	8,6	1.8
Saumons	Saint-Louis	48°47'38"N	70°47'59"W	Corrugated metal	Circular	1900	18,1	3.9
SA	Bécancour	46°05'40"N	71°25'58"W	Concrete	Circular	2100	17,5	4.5
SA2	Bécancour	46°05'40"N	71°25'58"W	Concrete	Circular	2200	18,2	4.5
SJ	Bécancour	46°18'55"N	71°18'49"W	Concrete	Circular	1500	19,2	1.15

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873 *Diameter is in mm, length in m and slope in %.

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874 (2) Table 2: Measured range of explanatory variables in their standard units and in body
 875 lengths (BL)

Conditions	Measured range	Median
Fish length (FL)	85-240 mm	126
Mean water temperature	3.3-18°C	14
Length of culvert	9-45 m or 67-360 BL	19 or 167
Slope of culvert	0.25-4.5%	1.5
Mean flow velocity	0.4-2 m/s or 1.9-23 BL/s	0.8 or 6.5
Hydraulic radius	0.2-0.27 or 0.1-2.6 BL	0.09 or 0.6
Depth of downstream pool	0.25-1 m or 1-11.5 BL	0.6 or 4.5
876 Trial duration or delay	24-48h	48

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(3) Table 3: Model selection based on the Akaike information criterion (AIC)

Model _i	-2 log (L)	K	AIC _i	Δ _i AIC	Δ _i AIC null	w _i
Null	687.49	1	691.5	691.5	0.0	0.000
Uf+T+T ² +P+D+Type+Rh	415.31	8	431.31	14.3	260.2	0.001
Uf+S+P+D+Type+Rh	416.62	7	430.62	13.6	260.9	0.001
Uf+S+P+D+Type+Uf*S	416.43	7	430.43	13.4	261.1	0.001
Uf+Spawn+T+T ² +P+D+Type	404.88	8	420.88	3.9	270.6	0.127
Uf+S+T+T²+P+D+Type	401.03	8	417.03	0.0	274.5	0.870

Table 3: Subset of tested models (n=208) showing the null model and the 5 models with the lowest -2 log-likelihood and AIC values. Explanatory variables are mean water temperature (Tc), mean flow velocity (Uf), hydraulic radius (Rh), depth of downstream pool (P), spawning period (Spawn), culvert type (Type), culvert slope (S), and trial duration (D). K represents the number of parameters in the model, Δ_i AIC the difference between AIC of model _i and AIC of the best model, Δ_i AIC null the difference between the AIC of model _i and AIC of the null model and w_i the Akaike weight, interpreted as the probability that model _i is the best-model given the data. Only one model emerged as providing the best fit to the data. This model, in bold, has an Akaike weight of 0.87.

888 (4) Table 4 : Estimation of parameters for the selected model

Variables in standard units					
Parameters		β	β	$\pm SE$	OR
β_0	Intercept		-4.563	4.411	
β_1	Water temperature	2.744	1.436	0.722	
β_2	Water temperature ²	-2.022	-0.048	0.026	
β_3	Culvert type (rough v/s smooth)	1.646	2.985	0.761	
β_4	Culvert slope	-0.846	-1.304	0.363	0.270
β_5	Mean flow velocity	-0.581	-2.985	0.625	0.050
β_6	Depth of downstream pool	-0.845	-8.159	1.376	0.000
β_7	Trial duration	0.395	0.078	0.022	1.080
β_8	Culvert type * fish length	0.869	-0.012	0.005	

889
 890 Table 4: Standardized estimates (β), estimates (β), standard error (SE), chi-square p-values (P^*)
 891 and odds ratio (OR) of parameters for the best-fitting model for a dataset with variables in
 892 standard units (SI). Odds ratios are computed for main effects with no interactions by
 893 exponentiating the estimates. Standardized coefficients are obtained by converting ordinary
 894 coefficients (β), from which individual probabilities of success can be computed, to standard
 895 deviation units. The units are Celsius for temperature, millimeters for fish length, meters per
 896 second for flow velocity, % for culvert slope, meters for depth of downstream pool and hours for
 897 trial duration. Culvert type is a categorical variable with rough =1 and smooth = 0.

(5) Table 5: Validation statistics for the selected model

Scored dataset	Variables in standard units			Variables normalized in BL	
	N	c	Tjur R ²	c	Tjur R ²
Caged fish	496	0.89	0.49	0.88	0.45
Caged fish = > 2 nd antenna	312	0.86	0.46	0.87	0.43
Uncaged fish	36	0.95	0.58	0.94	0.54
Uncaged fish = > 2 nd antenna	21	0.89	0.5	0.9	0.45

Table 5: C and Tjur’s R² statistics evaluating best model’s predictive power for 4 datasets, in standards and body lengths units (BL): caged fish, caged fish that swam = > 2nd antenna, uncaged fish and uncaged fish that swam = > 2nd antenna. A c value between 0.8 and 0.9 means that the model is excellent for predicting outcome while a value > 0.9 means that the predictive power of the model is outstanding (Hosmer et al. 2013).

(1) Figure 1

Figure 1 : Schematic representation of the stationary PIT system installed in culverts, with the cage downstream and the 4 PIT antennas (A1-A4). Adapted from Cahoon et al. (2004)

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(2) Figure 2

Figure 2: Schematic representation of culvert cross-section with dots representing the location of flow velocity measurements. At 25, 50 and 75% of flow width (w), flow depth (y) was measured, along with mean flow velocity.

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914 (3) Figure 3

915

916 Figure 2 : Panels show the predicted probability and 95% confidence intervals of success in
 917 rough (black line) and smooth (grey line) culverts with regards to fish length for a mean flow
 918 velocity of 0.4 m/s (A), 0.8 m/s (B) and 1.7 m/s (C), which correspond to the 5th, 50th and 95th
 919 percentiles of tested flow velocities. In smooth culvert longer fish had superior passage success,
 920 but in rough culverts shorter fish performed better, regardless of the flow velocity.

(4) Figure 4

Figure 3: Panels show the predicted probability and 95% confidence intervals of success in rough (black line) and smooth (grey line) culverts with regards to culvert slope for a mean flow velocity of 0.4 m/s (A), 0.8 m/s (B) and 1.7 m/s (C), corresponding to the 5th, 50th and 95th percentiles of tested flow velocities. Others parameters are set at their mean values (water temperature=14°C; flow velocity=0.8 m/s; depth of downstream pool=0.6 m and fish length=126 mm). In general, success decreased with increase of slope. However, it remained higher in rough culverts, regardless of flow velocity conditions. Caution should be applied when interpreting the combinations of slope and velocities. In the current study, the highest velocity was not encountered at the lowest slope and vice versa. More knowledge is needed to better understand the respective effect of slope and velocity on passage.

933 (5) Figure 5

934

935 Figure 4: Predicted individual probabilities and 95% confidence intervals of success for fish
 936 ascending rough (black lines) and smooth (grey lines) culverts. Panels show the effect of depth
 937 of the downstream pool (A), mean flow velocity (B) and trial mean water temperature (C) on the
 938 probability of success for a fish of 126 mm, swimming in culverts of 9-45 m during a 48 h trial.
 939 Others parameters are set at their mean values (water temperature=14°C; flow velocity=0.8
 940 m/s; depth of downstream pool=0.6 m and culvert slope=1.5%). For each parameter, the
 941 probability of success is higher in rough culverts. Passage performance of trout decreases with
 942 increasing depth of the downstream pool and flow velocity. Conversely, passage increases with
 943 water temperature to an optimum at 15°C. A limited number of fish (44) were tested at
 944 temperature below 7°C and panel C shows a large upper confidence interval for rough culvert.
 945 Caution should then be applied when predicting passage at low temperatures.

(6) Figure 6

Figure 6: Sensitivity and specificity under all possible cut-off points. When using the developed model to predict passage success of brook trout in culverts, sensitivity and specificity are both maximized at a probability cut-off of 0.82.