Is motivation important to brook trout passage through culverts?

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ABSTRACT

Culverts can restrict movement of stream-dwelling fish. Motivation to enter and ascend these structures is an essential precursor for successful passage. However, motivation is challenging to quantify. Here, we use attempt rate to assess motivation of 447 brook trout entering three culverts under a range of hydraulic, environmental and biological conditions. A passive integrated transponder system allowed for the identification of passage attempts and success of individual fish. Attempt rate was quantified using time-to-event analysis allowing for time-varying covariates and recurrent events. Attempt rate was greatest during the spawning period, at elevated discharge, at dusk, and for longer fish. It decreased during the day and with increasing number of conspecifics downstream of the culvert. Results also show a positive correlation between elevated motivation and successful passage. This study enhances understanding of factors influencing brook trout motivation to ascend culverts and shows that attempt rate is a dynamic phenomenon, variable over time and among individuals. It also presents methods that could be used to investigate other species' motivation to pass natural or anthropogenic barriers.

RÉSUMÉ

Les ponceaux peuvent limiter les déplacements des espèces d'eau douce. La motivation à entrer dans le ponceau constitue un élément essentiel au succès de passage. Elle est cependant difficile à quantifier. Dans la présente étude, nous utilisons la fréquence des tentatives pour évaluer la motivation de 447 ombles de fontaine tentant de franchir des ponceaux sous une gamme de conditions hydrauliques et environnementales. Un système à transpondeurs passifs intégrés a permis de quantifier les tentatives et le succès de passage des ombles sur une base individuelle. La fréquence des tentatives a été déterminée en utilisant des analyses de temps à l'événement permettant de considérer les variables fluctuant dans le temps et les événements récurrents. La fréquence des tentatives était plus élevée en période de reproduction, à un débit élevé, au crépuscule et pour les ombles de taille supérieure. À l'inverse, la fréquence des tentatives diminuait durant le jour et avec la présence d'un nombre élevé d'ombles en aval du ponceau. Les résultats démontrent également un lien entre une motivation accrue et le succès de passage. Cette étude procure une meilleure compréhension des facteurs influençant la motivation de l'omble de fontaine à franchir les ponceaux et montre que celle-ci est un phénomène dynamique, variable dans le temps et entre les individus. Elle présente par ailleurs des techniques pouvant être utilisées pour déterminer la motivation de d'autres espèces à franchir des obstacles d'origine naturelle ou anthropique.

INTRODUCTION

Connectivity plays a key role in the ecology of fish species (Fausch et al. 2002). Natural or anthropogenic features may limit the ability of fish to access fluvial habitats, thus impeding the persistence of healthy fish populations (Letcher et al. 2007, Morita and Yamamoto 2002, Perkin and Gido 2012). Road-stream crossings constitute some of the most ubiquitous structures that contribute to habitat fragmentation. Culverts can pose partial or complete barriers to fish movements by being perched, providing insufficient flow depth, or excessive velocities that fish are unable to negotiate. (Burford et al. 2009, Gibson et al. 2005, Goerig et al. 2016, Mahlum et al. 2013).

Assessments of fish passage through culverts have been based on coarse filters using culvert characteristics (Coffman 2005, Poplar-Jeffers et al. 2009), empirical studies of fish ascending culverts (Goerig et al. 2016) or experimental studies on swimming performance and maximal distances of ascent in controlled laboratory environments (Castro-Santos 2005, Sanz-Ronda et al. 2015). Many studies have focused on physiological limits of fish (Castro-Santos et al. 2013, Peake et al. 1997, Weaver 1963) but few have quantified behavioral factors that may also influence passage.

Motivation to enter a culvert is an essential step towards successful passage. Indeed, even a culvert with favorable conditions becomes a barrier if fish do not enter the structure and attempt to pass. This highlights the importance of considering causal mechanisms influencing their motivation and the implication for passage success. However, motivation is difficult to quantify, in part because it lacks a discrete and uniformly accepted definition. In general, motivation refers to conditions that prompt an individual to movement or action (Marriam-Webster 2006). It also refers to the internal condition influencing the relationship between stimulus and responses (Barnard 2012). Various models have been developed to explain and quantify motivation, with their respective strengths and drawbacks (Barnard 2004, 2012, McFarland 1999).In the context of culvert passage, we define motivation as the willingness to enter the structure and swim upstream. The rate at which fish attempt to surmount obstacles provides an index of motivation that is both intuitive and appropriate for understanding passage success.

Motivation to move upstream results both from the physiological condition of the fish and its response to external factors like flow, temperature, or predation (Agostinho et al. 2007, Castro-Santos et al. 2013, Hasler and Scholz 2012). In a fluctuating environment, fish motivation is likely to vary over time. Furthermore, fish may exhibit diversified and complex behavior in response to a new or challenging environment and so variability among individuals is to be expected (Adams et al. 2000, Magurran 1986). Nevertheless, the attraction exerted by the culvert, as well as environmental variables such as diel period or water temperature, may be important to stimulate fish to initiate an attempt.

The brook trout (*Salvelinus fontinalis*) is a widely distributed species that can exhibit long-distance movements (Gowan and Fausch 1996, Rodriguez 2002) and is negatively impacted by barriers. Attempt rate and swimming performance of brook trout has been studied in an open flume (Castro-Santos et al. 2013) but not in their natural habitat. A recent study described passage of brook trout through culverts (Goerig et al. 2016), but only the individuals that staged attempts were used in the analysis. Here we present field observations of brook trout attempting to pass culverts under a range of conditions, with the aim of developing a method to quantify their motivation and its importance on passage success. The methods we describe here could be readily applied to other species and locations.

To achieve our objectives, we use an analytical approach considering all available fish to model the effect of hydraulic, environmental and biological variables on the timing and rate of attempts, which we interpret as an index of motivation. We then consider the effect of these variables as well as that of individual variability in motivation, on passage success.

METHODS

Study sites

Brook trout passage attempts were recorded during field trials at three culverts located in the Sainte-Marguerite River watershed (Québec, Canada), on the Morin, Allaire and Résimond streams. Culverts were 18 to 45 m in length and 1.6 to 2.2 m in diameter. They were made of either corrugated metal or smooth material (Table 1). One culvert had multiple pipes, bringing the total number of tested pipes to six.

Fish collection and tagging

Fish were caught by electrofishing (Smith-Root backpack electrofisher, model 15-C, Vancouver, Washington, USA) 0-500 m upstream of the culverts. In order to increase sample size, some fish were also caught 0-500 m downstream of the Morin culvert and in a nearby stream, the Épinette. (Table 2; Figure 1). The Morin, Allaire and Épinette streams are located within 10 km of each other while the Résimond stream, by contrast, is > 26 km distant from the others.

Fish were anesthetized by immersion in a 1:9 solution of clove oil and 95% ethanol, diluted in water (0.8-1.2 ml of solution for 1400 ml of water). They were measured (fork length, mm), weighed (wet mass, gr) and surgically tagged with half-duplex passive integrated transponders (PIT) tags (Texas Instruments, 23 mm in length, 3 mm in diameter; mass in air: 0.6 g; tag-to-fish mass ratio:0.42%–8.22%). The PIT-tags were inserted in the fish peritoneal cavity and cyanoacrylate glue (Vetbond, 3M) was used to close the incision. Fish were placed in holding pens in the river for a recovery period of 2 (6.7%), 4 (86%) or 18h (7.6%). . After recovery, fish were transported in buckets and released in the cage below the culverts. The collection and tagging procedures were in conformance with the guidelines of the Canadian Council of Animal Care in science (CCPA).

Study design and instrumentation

Passage trials lasted 24-48h, and were conducted between July and October. Fish were released in a large cage (2 x 2 x 1 m) secured to the downstream extremity of the culverts and allowed to volitionally stage passage attempts. To ensure that entry into the culvert was truly volitional, each cage contained rocks and other substrate, providing ample resting areas under all tested conditions. Thus there was no coercion of fish to stage attempts. For the culvert with multiple pipes, the cage was fixed to a single pipe during a given trial and the other pipes were blocked. Flow depth and water temperature of each stream were recorded every 60 min by a data logger (Onset, HOBO 020-001-04) located 20 m upstream of the culvert. We derived discharge rating curves for each stream by correlating depth data with on-site flow measurements (Marsh-McBirney Flow-Mate 2000 electromagnetic velocimeter). Assuming no significant backflow or hydraulic loss, this method provided a reasonable approximate of the flow discharge inside the culvert (Chow 1959).

The tested pipes were instrumented with a telemetry system consisting of four antennas evenly spaced along the pipe. The first antenna was located at the downstream end of the culvert and the fourth was located at the upstream end. Antennas were placed above the water surface to avoid flow disturbances. Their dimensions varied with the culvert's diameter, ranging from 0.45 m × 1 m to 0.45 m × 2 m. The antennas interfaced with a half-duplex PIT reader via a multiplexer (Technologie Aquartis, control module Quatro, multi-antennas system HDX-134.2 kHz). The reader recorded tag number, antenna number, and time to the nearest 1 s. Detection efficiency of the PIT system was assessed by comparing detections at the upstream-most antenna with those downstream. This allowed us to quantify detection efficiency of antennas 1-3, but not antenna 4, which we assumed to be 100%.

Detections within 1 s were grouped together, representing discrete exposure to an antenna. The direction of the fish's movement was assessed by the order of detection at the four antennas, and an attempt was defined as an upstream movement beginning at the downstream-most antenna (antenna 1). The attempt was considered successful if the fish reached the upstream-most antenna (antenna 4) before the end of the trial. A threshold of 60 seconds between detections at the first antenna was used to differentiate among attempts. This threshold was identified based on the distribution of time intervals between successive detections at antenna 1 (Castro-Santos and Perry 2012). Data were screened for false readings, resulting from simultaneous detections at two antennas. These were very rare and were corrected before processing the data for statistical analysis.

Statistical analysis

We used time-to-event analysis (Allison 2014, Castro-Santos 2004, Hosmer et al. 1999) to quantify attempt rate of fish released downstream of culverts. Attempt rate refers to the percentage of fish staging an attempt per unit of time (% t^{-1}). In the context of the current study, it is the proportion of the fish available to stage a given attempt that a particular individual represents at the moment it stages an attempt. Each attempt constitutes a single event, and has an associated instantaneous event rate (or 'hazard'). Cox regression estimates the relative effect of covariates on the hazard function (Armstrong and Herbert 1997, Castro-Santos and Haro 2003). Cox regression assumes covariate effects on the hazard remain proportional, meaning that explanatory variables do not interact with time and so have a constant effect over the time interval considered.

Cox regression mixed models were fit to the data using the package Coxme in R 3.2.0 (R Core Team 2015, Therneau 2015a), by including fixed effects and nested random effects (e.g. frailty terms) for stream of origin and individual fish. This model structure accounted for the heterogeneity related to the stream of origin and the statistical dependence among repeated events from the same fish (Armstrong and Herbert 1997, Therneau et al. 2003). It is expressed by

(1) $$\lambda\ (t) = \lambda_0\,(t)\, e^{X\beta+Zb}$$

(2) $$b \sim G\ (0, \sum(\theta))$$

Where $\lambda\ (t)$ is the baseline hazard function (i.e., attempt rate) modeled as a function of time (*t*). The time interval preceding each attempt is considered in the analysis, along with *X* and *Z* representing the matrices of fixed and random effect values, respectively. *β* is the vector of fixed-effects coefficients and *b* is the vector of random effects coefficients. The distribution of random effects *G* is modeled as Gaussian with a mean of 0 and a variance matrix ∑, which depends a vector of parameters θ (Therneau 2015a). The random effects estimate the variance among streams of origin and individual fish in the baseline hazard function, that is, after controlling for fixed effects. The random effect for each individual measures its deviation from the baseline attempt rate. Negative values represent less-than-average attempt rate whereas positive values measure higher-than-average attempt rate.

Independent explanatory variables deemed likely to have an effect on attempt rate were considered in the analysis, representing the fixed effects in the model. These included fish fork length, fish condition factor ($k = 10^5$*weight/length^3), diel period (dawn, day, dusk or night), hourly discharge, relative change in discharge (Q_2-$Q_{1)}$/Q_1), hourly water temperature, change in water temperature (T_2-T_1) and number of fish in the cage. The spawning period was included as a categorical variable. It was coded 0 for periods greater than two weeks from the expected spawning time and 1 for periods within two weeks of expected spawning time. In the Ste. Marguerite watershed, spawning occurs in mid- September. The effect of independent variables on attempt rate was modeled as linear, since an analysis of the residuals of the full model did not detect any nonlinear trends (Fox 2002, Therneau et al. 1990) A suite of candidate models, each consisting of a reasonable combination of explanatory variables and the nested random effects, was developed according to the following criteria: i) minimum of one and maximum of six main effects ii) no interactions iii) change of temperature was always used along with water temperature iv) relative change in discharge was used with and without discharge v) water temperature and discharge were never used together in a model due to their correlation (*r*=-0.67, p<.0001), as well as fish fork length and fish condition factor (*r* = 0.30, p < .0001)

The time interval between the beginning of the trial and the beginning of the first attempt was recorded for each fish, corresponding to the pre-attempt interval. When fish returned to the cage and became available to stage a subsequent attempt, the time interval between the arrival in the cage and the beginning of the second attempt was recorded. The time interval between the end of the last attempt and the termination of the trial was also recorded. The occurrence of an event, as well as the sequence of event (attempt number), were indicated in the dataset. Right censoring, consisting in fish having not yet staged an attempt at the end of the trial, was indicated by 0 for censored and 1 for complete observations.

One of the strengths of time-to-event analysis is that it allows for explicit measurement of effects of covariates that change over time. These were integrated with the dataset so that each discrete value of the number of fish in the cage, diel period, flow discharge and water temperature had a distinct record, with an associated start and an end time(Castro-Santos and Perry 2012). Start and end times of diel periods (dawn, day, dusk and night) were determined for each trial using the sunrise/sunset calculator of the National Research Council of Canada (NSERC). The number of fish in the cage was set to a starting value corresponding to the number of fish released at the beginning of the trial. It was then allowed to vary instantaneously according to individuals staging attempts and others returning downstream after an attempt. Tagged fish returning downstream from previous trials, although not considered in the quantification of attempt rate, contributed to the number of fish in the cage. To account for eventual reverse causation created by the intrinsic link between the number of individuals in the cage and the attempt rate, we used in the analysis the most recent value observed prior to the attempt (Allison 2014).

Models were selected by minimizing the Akaike Information Criterion (AIC), defined as:

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

Where *L* is the model's likelihood, and *K* is the number of parameters.

Fixed and random effects coefficients, as well as standard errors, were extracted from the selected model. Hazard ratios were obtained by exponentiating the coefficients estimated for each covariate. Functions to extract residuals and plot Kaplan-Meier and survival curves were not available in the Coxme package. To test the assumption for proportionality of hazards, we used the Survival package (Therneau 2015b) to fit the same model with a random effect on stream and used it to extract residuals. We also extracted the baseline hazard and used it, along with the parameter coefficients estimated in the Cox mixed model, to plot survival curves adjusted for a given set of covariate values.

We modeled passage success for fish that staged attempts and assessed the relationship between individual motivation and passage performance. Individual variability in motivation was estimated by the random effect coefficients for each fish in the attempt rate model described above. The probability of successful passage was modeled as a function of a random effect on trial and fixed effects on fish fork length and motivation, using logistic regression (R 3.2.0, package Lme4, function glmer). The random effect accounted for most of the variability in passage performance due to the characteristic of the trials (water temperature, mean flow depth and velocity) and those of the culverts (culvert type, slope and length). The fixed effects allowed the assessment of the specific effects of fork length and motivation on passage success.

RESULTS

Trial conditions

A total of 447 fish were released during 19 passage trials: 14 in corrugated metal culverts and 5 in smooth-material culverts. Each trial consisted of a group of 15 to 25 tagged individuals, of fork length ranging from 90 to 263 mm (Table 2). Trials were conducted from late June to mid-October, at water temperatures from 3 to 20°C (Table 3). Flow discharge ranged from 55.5 to 715.5 L s^{-1} while the number of fish in the cage varied between 2 and 28 (Table 2). The detection efficiency of the PIT system for a fish moving upstream was greater than 97% for antennas 1, 2 and 3. Despite the fact that detection efficiency could not be quantified for antenna 4, we can infer a high value based on these results.

One hundred ninety three fish staged no attempts during the trials. This represents 43 % of the available fish, and these were included in the analysis as censored observations on the first attempt.

Some trout staged several attempts during the trials. The rate at which the first attempt occurred was slower than the rate of subsequent ones, as illustrated in the empirical cumulative incidence curves (Figure 2). The rate thereafter increased with subsequent attempts. Because trials were of finite duration, fish that staged more attempts necessarily staged them at a greater rate.

Model for attempt rate

Among the 191 models estimated, one model had an optimal fit to the data (Δ AIC from closest competing model = 2, Akaike weight =0.71, Table 4). This model includes proximity of the spawning period, flow discharge, diel periods, number of fish in the cage and fork length.

Examination of Schoenfeld residuals indicated that the selected model did not violate the proportional hazards assumption, meaning that covariate effects were consistent over time (Hosmer et al. 1999).

Fish staged attempts at a higher rate at the approach of spawning, the estimated hazard of attempt being 1.80 times higher within two weeks of the expected spawning time than outside this period (HR = 1.809, Table 5).

Discharge had a positive effect on the attempt rate: an increase of 1 L s^{-1} led to a 0.3 % increase in the hazard of staging an attempt (HR = 1.003, Table 5). This means that the attempt rate was ~ 7 times faster at the maximum discharge tested (715 L $s\text{-}^{1}$) compared with the minimum discharge (55 L s^{-1}). For an average culvert, ~ 60% of the released fish would have attempted to pass the culvert when there was 100 L s^{-1}, compared to ~ 80% at 300 L s^{-1} and ~ 90% at 500 L s^{-1} (Figure 3).

Attempt rate was 25% higher at dusk than at dawn (HR = 1.253, Table 5). Attempt rate was similar between night and dawn periods, but it was reduced during the day by ~ 15 % (HR = 0.841, Table5). Attempt rate also decreased with an increase of the number of conspecifics in the cage, each new fish in the cage leading to a decrease of 4 % in the attempt rate (HR = 0.963, Table 5). Longer fish had a higher attempt rate, each additional mm increasing the rate by 0.8% (HR = 1.008, Table 5). This means that the longest individual tested (263 mm) had an attempt rate ~ 3 times faster than the smallest one (85 mm).

After accounting for the fixed effects in the model, some unexplained variability in attempt rate remained, with the variance of the random effects for stream of origin and individual fish being respectively 0.472 and 1.158 (Table 5). Controlling for covariates, trout from Allaire and Épinette streams had greater attempt rates 42% greater than the average (HR = 1.427 and 1.362, Table 5). Trout from Résimond stream staged attempts at 0.37 times the average rate of the study, or a reduction of 63% (Table 4). The proportion of released fish having staged attempts after twelve hours was between 70 and 80 % for trout from Allaire, Épinette, Morin and Morin DS streams, but only 35% for trout from Résimond stream (Figure 4).

The estimated random effect coefficients for all fish follow a bimodal distribution, with lower values representing less motivated individuals, and higher values representing more motivated individuals, as indicated by reduced or elevated attempt rates, respectively (Figure 5). We hypothesize that the two modes correspond at least partially to the fish that did not stage attempts during the course of the trial and the ones that did. This does not respect the assumption of a normal distribution for the random effect in the Cox mixed model and may suggest that a bimodal unmeasured variable is influencing individual motivation. The random effects were not correlated to the distribution of other covariates, except for the number of fish in the cage (r = 0.22, p < 0.001). As fish were attempting and eventually passing the culvert, the number of conspecifics in the cage decreased. For a passable culvert, the number of fish in the cage was low at the end of the trial and the ones remaining were the less motivated fish (e.g. those that staged few or no passage attempts).

Effect of motivation on passage success

When estimating the probability of passage success in the study, we found a substantial variance for the random effect on trials (7.273, Table 5). This was to be expected as most of the variability in passage performance was due to differences in conditions in flow and water temperature during the trials, as well as in the characteristics of the culverts. The individual variability in motivation, represented by the coefficient estimated for each fish in the attempt rate model, has a significant positive effect on passage success (OR = 2.109, Table 6 & Figure 5). This means that a trout with a high level of motivation (coefficient = 1) had a probability of successful passage twice that of a fish with an average level of motivation (coefficient = 0). Fork length had a small positive impact on passage success, each additional cm increased the probability of success by ~ 1% (OR = 1.011, Table 6). A likelihood ratio chi-square test indicated that the model including motivation and fish fork length was better over the one comprising only the random effects on trial (chi-square = 5.697, df =2, p = 0.057).

DISCUSSION

This study used attempt rate as an index of the motivation of wild fish to pass culverts in their native environment. The study design offered the opportunity to assess the impact of environmental and biological variables on motivation, with results suggesting that motivation is a dynamic phenomenon, variable over time and among individuals. In this study, brook trout attempt rate in culverts was influenced by hydraulics, diel period and fish behavior and physiology. After accounting for these effects, individual variability in attempt rate was still observed in the study, with important implications for passage success.

Effect of covariates on attempt rate

Trout staged attempts more frequently at a higher discharge. Similar behavior was observed for brook trout and other species attempting to ascend experimental flumes (Castro-Santos 2004, Castro-Santos et al. 2013, Weaver 1963).This finding emphasizes the importance of providing attraction flow below culverts in order to stimulate fish to enter.

Trout showed greatest motivation to ascend the culvert at dusk. Motivation was similar at dawn and night but decreased during the day. These results are consistent with those of a study of fish passage in an experimental culvert (Peterson et al. 2013) and previous findings showing that salmonids are more active and moved greater distances at twilight and night, with a sharp decline in overall activity during the day (Bunnell et al. 1998, Roy et al. 2013, Young 1999). Such patterns may be the result of competition or predator avoidance. Fish are indeed less visible when light declines and can leave their shelter and move more safely. Reduced movement can also result from avoidance of sudden changes in luminosity, the difference between the open stream and the culvert being more pronounced during the day. Also, drift feeding is known to be more efficient for salmonids during the day (Fraser and Metcalfe 1997, Jenkins Jr 1969). Because they often restrict the flow area and increase the density of drifting invertebrates, culverts may constitute ideal feeding spots. This can increase the propensity of the fish to remain downstream of the culvert during daylight and explain the reduced attempt rate at this period. Considering all this, the higher attempt rate of brook trout at dusk and, to a lesser extent, at night and dawn, may represent an opportunistic behavior.

Trout became more motivated to pass when there were fewer fish present in the cage downstream of the culvert. Decreasing passage rates above a certain density has also been observed for alewife (Dominy 1973). Although a recent study with Coho salmon in an experimental culvert failed to detect this effect (Johnson et al. 2012), the phenomenon may be widespread. Salmonids are known to display a hierarchical social behavior (Höjesjö et al. 1998, Newman 1956, Sundström and Johnsson 2001), with larger individuals occupying the first-order positions related to drift feeding and cover (Hughes 1992).It may be that as density increases so does the number of social interactions, and these interactions could have the effect of suppressing attempt rate. This would lead to increased delay in passing the culvert.

Larger trout had a higher attempt rate than smaller individuals. A higher attempt rate in experimental flumes was reported previously for larger individuals of several species (Castro-Santos 2004, Peake 2008), as well as a higher propensity to move with regards to body size for brown trout (Bunnell et al. 1998, Young 1999). It is possible that larger and likely older individuals exhibited a stronger homing behavior or may have interacted with the culvert before, either of which might have affected motivation. Moreover, if they occupied forward positions (presumably preferred for feeding), they had greater opportunity to initiate attempts and enter the culvert in order to seek cover or more suitable habitat upstream.

Variability in motivation

There were noticeable differences in attempt rate of trout from different capture locations. We caught 75% of the fish upstream of the studied culverts, assuming that homing behavior would increase their propensity to move and attempt to pass the culvert (Armstrong and Herbert 1997). Fish caught upstream of the Résimond culvert had an overall lower attempt rate than those originating from the other streams while trout caught downstream of Morin culvert and in Épinette stream had a similar attempt rate than the ones caught upstream of Morin and Allaire culverts. According to these results, homing behavior is not a likely candidate to explain differences in attempt rate.t is more likely that unmeasured variables related to the streams of origin had some influence on the fish motivation. The Résimond stream is > 26 km distant from the others. Fish caught in this stream may display different movement patterns, which could in part explain the observed differences.

Most trout staged only one attempt, but some staged more. Overall, fish with greater attempt rates were more likely to pass, but sometimes individuals entered multiple times without passing, even under easily-passable conditions. This suggests that culvert entry may include behaviors not necessarily associated with passage attempts and that not all attempts are similar in terms of produced effort and potential for success. This individual variability in attempt rate highlights the fact that causal mechanisms may be missing from the current thinking about entry and passage behaviors. These may include individual differences in life history, responses to stimuli, physiology or personality traits. Differences in personality traits have been related to risk-taking behavior and mobility for brook trout (Farwell and McLaughlin 2009) as well as variability in dispersal for other species (Cote et al. 2010). Intraspecific variability in movement patterns has also been reported for brook trout, some individuals being more mobile than others (Rodriguez 2002). In the current study, motivated fish have expressed a higher willingness to take risks and stage fast attempts. Some of our study sites are also believed to hold sub-populations of anadromous brook trout. If these were present in the study, their behavior and motivation to pass culverts in order to access upstream spawning habitat may have been different from those of resident individuals. In the absence of data on sex, life history or social status, the random effects are useful to quantify the unexplained variability in the attempt rate that was not accounted for by other covariates.

Among all tested fish, the rate at which the first attempt occurred was markedly lower than the rate of subsequent attempts. This may be a result of the tagging procedures or simply the acclimation of the fish to a new environment. In laboratory studies, a lower rate for the first attempt was also observed for brook trout, walleye and white sucker (Castro-Santos et al. 2013).The importance of providing an acclimation period is broadly recognized, and is a standard feature of laboratory studies (O'Neal et al. 2016); however the magnitude and duration of the effect are typically not quantified in non-volitional studies. Our data provide clear evidence of both the magnitude of the effect and its duration, which varies among individuals, but can persist for days, even in a field-like situation.

Effect of motivation on passage performance

When facing a culvert, motivation to enter the structure is essential to achieve successful passage. In this study, this was shown by the fact that trout with a higher level of motivation had an increased probability of passage through the culverts. The individual variability in motivation was based on the attempt rate of each fish, and the influence of covariates on these rates was described using Cox regression. Trout with high attempt rates were fish that staged rapid and/or multiple attempts.

The current study focused on brook trout originating from different streams, yet all located within the same watershed. Trout from other locations may possibly react differently to hydraulics and environmental variables. Moreover, caged fish may differ in their behavior than free-ranging fish facing a wider range of alternatives. Nevertheless, the current study quantifies motivation of wild fish to pass existing culverts. The methods developed here can be applied to other species in order to better understand the effect of individual variability and time-varying covariates on attempt rate at culverts, fishways or natural obstacles.

A better understanding of factors influencing the species motivation to negotiate barriers has important implications for design and fish passage issues. Entry and passage are however two distinct phenomena on which covariates may have differential effects. In this study, we showed the positive effect of flow discharge on attraction at culverts. This poses a paradox, because flow velocity is known to negatively impact passage performance through barriers (Burford et al. 2009, Castro-Santos et al. 2013, Goerig et al. 2016). These findings point to the importance of culvert designs that are both attractive and passable.

TABLES

Table 1: Study site characteristics

Site	Latitude	Longitude	Material	Diameter (m)	Length (m)	Slope (%)	Openness ratio (m)
Resimond	48°25'52"N	70°26'03"W	Corrugated metal	1.6	44.6	0.92	0.16
MorinA	48°20'50"N	70°03'39"W	Corrugated metal	1.5	33.2	1.38	0.20
MorinB	48°20'50"N	70°03'39"W	Corrugated metal	2.2	32.3	1.38	0.29
MorinC	48°20'50"N	70°03'39"W	Corrugated metal	2.2	33	1.38	0.29
MorinD	48°20'50"N	70°03'39"W	Polyethylene	2.2	32.4	1.38	0.29
Allaire	48°21'19"N	70°07'07"W	Concrete	2 x 2	18.4	0.28	0.22

Note:

Openness ratio is calculated by dividing the cross-sectional area of the culvert by its length. Large values correspond to short culverts with large diameters while low values correspond to long culverts with small diameters.

Table 2: Origin of tested fish

Tested pipe	**Stream of origin**				
	Résimond	Morin	Morin DS	Allaire	Épinette
Résimond	33	—	—	—	—
Morin A	—	—	—	27	54
Morin B	—	84	18	—	15
Morin C	—	—	—	27	27
Morin D	—	—	—	54	—
Allaire	—	—	—	108	—

Note:

Number of fish caught in the different streams, for each tested pipe. Fish were caught upstream of the tested pipes for Résimond, Morin and Allaire streams, and downstream for Morin DS stream. Additional fish were caught in Épinette stream, a nearby tributary of the Sainte-Marguerite river.

Table 3: Measured range of the explanatory variables

Study site	**Allaire**				**Morin (A, B, C & D)**				**Resimond**			
n trial	**4**				**13**				**2**			
n fish	**108**				**305**				**34**			
Parameter	**Min**	**Max**	**Median**	**Mean**	**Min**	**Max**	**Median**	**Mean**	**Min**	**Max**	**Median**	**Mean**
Mean flow velocity (m s^{-1})	0	0.81	0.58	0.62	0.58	1.81	0.77	0.86	0.79	0.85	0.85	0.82
Flow discharge (L s^{-1})	94.00	715.50	321.50	347	55.5	642.5	195	266.3	281.5	290	289	288
Relative change in discharge (L s-1)	0	0.39	0.02	0.04	0	0.93	0.02	0.03	0	0.018	0.003	0.004
Water temperature (°C)	8.80	19.90	11.40	11.2	2.94	18.3	12.6	11.5	10.4	12.5	10.9	11.1
Change in water temperature (°C)	0	3.20	0.10	0.27	0	8.52	0.09	0.19	0	0.39	0.05	0.08
Number of fish in the cage	2	28	17	16	4	26	22	19	11	16	14	13.8
Fish body length (mm)	93	230	123	133	90	263	125	131	95	206	119	127
Fish condition factor (Fulton k)	0.74	1.5	1.02	1.03	0.71	1.5	1.01	1.01	0.77	1.4	1.06	1.08
Number of attempts per fish	0	66	1	5	1	58	1	2	1	3	1	1

Note:

Relative change in discharge is calculated as Q_2-$Q_{1)}$/Q_1 while change in water temperature is calculated as T_2-T_1. The number of fish in the cage varies according to the number of fish released at the beginning of the trial, fish staging attempts and fish returning downstream after an attempt or from a previous trial.

Table 4: Model selection based on the Akaike information criterion (AIC)

Model $_i$	**RE**	**-2 log (L)**	**K (df)**	**AIC $_i$**	**Δ_i AIC**	**w $_i$**	**w_i/w_j**
Spawn+ Q + DielPeriods + Nbcage+ BL	**(1 |Stream/ID)**	**-15011.2**	**242.0**	15495.36	**0.0**	**0.71**	
Spawn + Q+ dQr + DielPeriods + Nbcage+BL	(1 |Stream/ID)	-15011.2	243.0	15497.37	2.0	0.26	2.73
Q + DielPeriods + NbCage + BL	(1 |Stream/ID)	-15022.4	241.0	15504.79	9.4	0.01	71.00
k + Q + DielPeriods + NbCage + BL	(1 |Stream/ID)	-15022.7	241.0	15505.34	10.0	0.00	142.00

Note:

Subset of tested models (*n* = 191) showing the four models with the lowest−2 log-likelihood (penalized) and AIC values. Explanatory variables are proximity of the spawning period (spawn), flow discharge (Q), relative change in discharge (dQr), diel periods, number of fish in the cage (NbCage), fork length (BL) and Fulton condition factor (k). RE represents the nested random effects structure, *K* (df) the number of degrees of freedom in the model, Δ_i AIC is the difference between AIC of model$_i$ and AIC of the best model. Akaike weight of model$_i$ (w_i) is interpreted as the probability that model$_i$ is the best model given

472 the data and w_i/w_j is the evidence ratio for $model_i$ versus $model_j$. Two models emerged from the model

473 set as providing the best fit to the data. The first one, in bold, has an Akaike weight of 0.71. It is followed

474 by a second model with a weigth of 0.26. The evidence ratio between these two models is 2.73,

475 indicating evidence in favor of the first one (Burham and Anderson 2002).

Table 5: Estimation of parameters for the selected attempt rate model

Parameter		**β ± SE**	**HR**	**p-value**
Spawning		0.593 ± 0.203	1.809	0.004
Flow discharge (L s^{-1})		0.003 ± 0.000	1.003	0.000
Fish fork length (mm)		0.008 ± 0.003	1.008	0.002
Number of fish in the cage		-0.037 ± 0.009	0.963	0.000
Diel periods				
	Dawn	----	----	----
	Day	-0.173 ± 0.151	0.841	0.250
	Dusk	0.223 ± 0.190	1.253	0.240
	Nigth	0.035 ± 0.152	1.004	0.820
Random effects		**SD**	**Variance**	
Stream of origin/ ID		1.076	1.158	
Stream of origin		0.687	0.472	
		β	**HR**	
	Allaire	0.356	1.427	
	Épinette	0.309	1.362	
	Morin	0.165	1.180	
	Morin DS	0.161	1.175	
	Résimond	-0.991	0.371	
Number of available fish		447		
Number of events		1241		

Note:
Estimates ± standard error (β ± SE) and hazard ratios (HR) of parameters for the best-fitting model..

Hazard ratios (HR) are computed for each parameter by exponentiating the estimates. Spawning is a categorical variable with 1 = within 2 weeks of the expected spawning period and 0 = more than 2 weeks than the expected spawning period.

Table 6 : Estimation of parameters for the passage success model

Parameter	β ± SE	OR	p-value
Intercept	-2.501 ± 1.186	—	0.035
Individual motivation	0.746± 0.380	2.109	0.049
Fish body lenght (mm)	0.011 ± 0.006	1.011	0.079
Random effects	**Variance**	**SD**	
Trial	7.273	2.697	

Note: Estimates ± standard error (β ± SE), odds ratio (OR) and chi-square p-values of parameters for the best-fitting model. Odds ratios (OR) are computed by exponentiating the estimates. Individual motivation was based on the attempt rate of each fish, as described in the Cox regression, and had a positive effect on passage success.

FIGURES

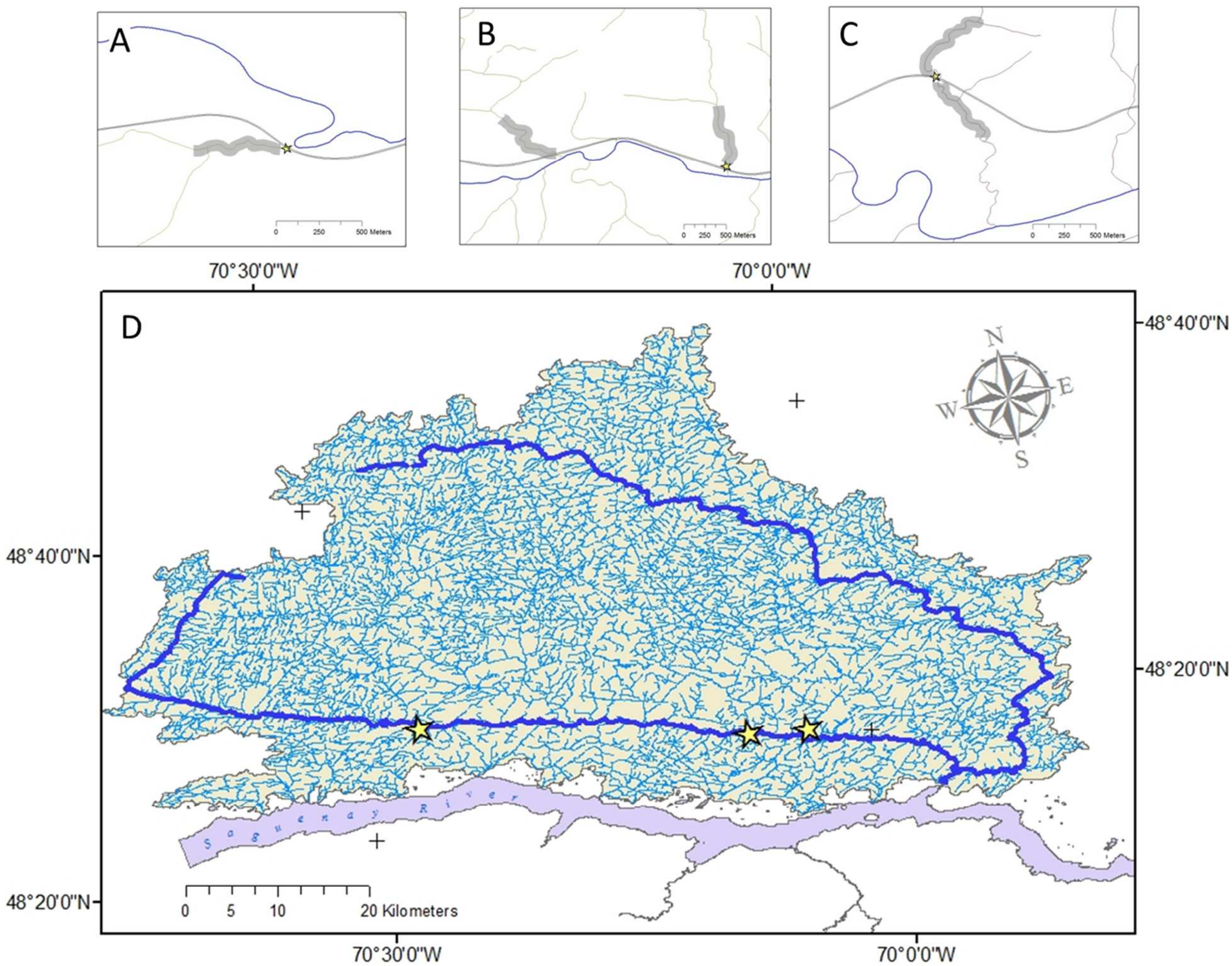

Figure 1. Study sites (stars) and their location within the Ste. Marguerite river watershed (Panel D). Details of studied culverts and collection locations (Tables 1 & 2) are shown in the upper panels (A: Résimond; B: Allaire; and C: Morin). Roads are shown as double-lines, and collection locations are indicated by transparent, heavy gray lines (Panels A, B &C). The Épinette stream collection site is shown in panel B, situated to the west of the Allaire study site.

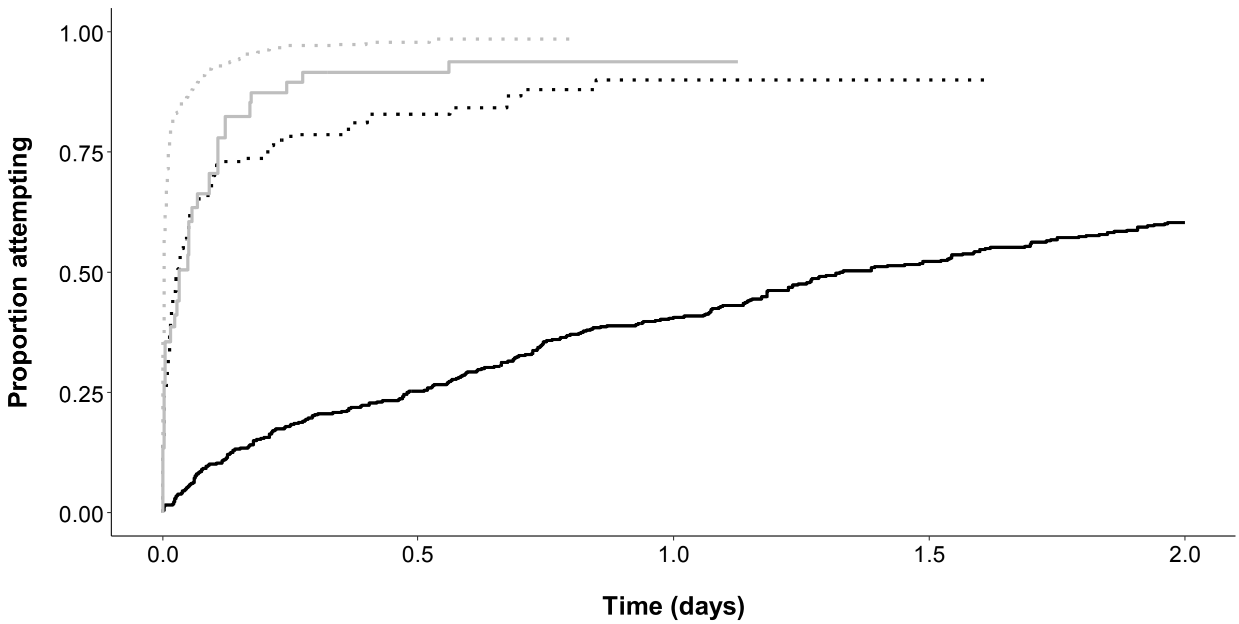

Figure 2: Cumulative incidence curves (1- empirical Kaplan-Meier curves) representing proportion of fish attempting to pass the culverts as a function of time. Data are stratified by attempts, the black curve representing the 1st attempts, the black dotted curve the attempts 2-5, the grey curve attempts 6-10, and the grey dotted curve attempts > 10. The rate of the first attempt is much slower than the one of subsequent ones. The rate thereafter increased with subsequent attempts.

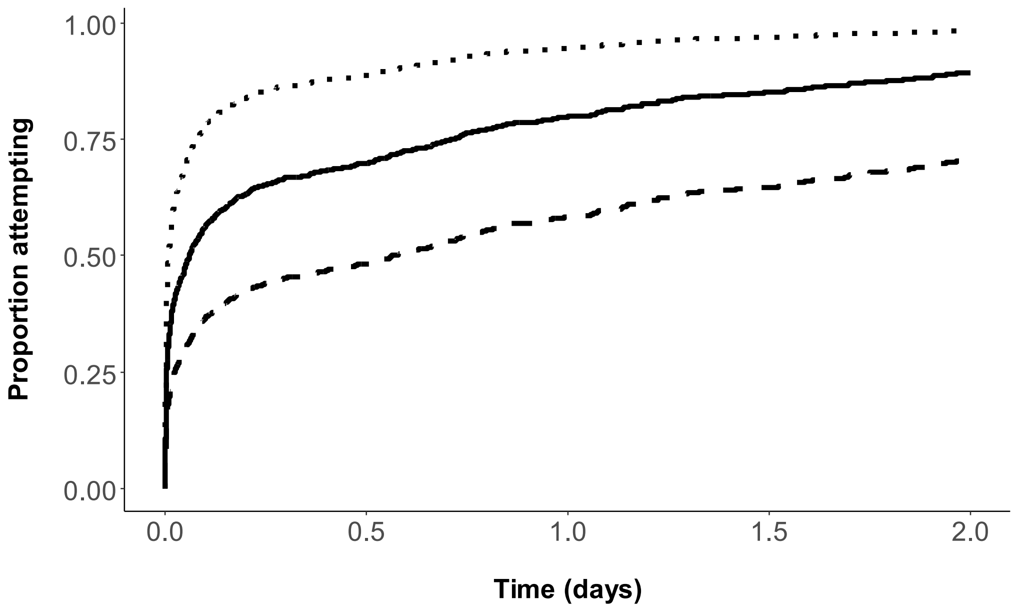

Figure 3: Proportion of fish attempting to pass the culvert as a function of time and flow discharge, modeled from the estimated Cox model. The attempt rate increases with higher values of discharge. Dashed line: 100 L s^{-1}; solid line: 300 L s^{-1} and dotted line: 500 L s^{-1}, which corresponds to the 25^{th}, 50^{th} and 75^{th} percentiles, respectively, of tested flow discharge. Others parameters are set at their mean values (number of fish in the cage = 28, and fork length = 131.6 mm).

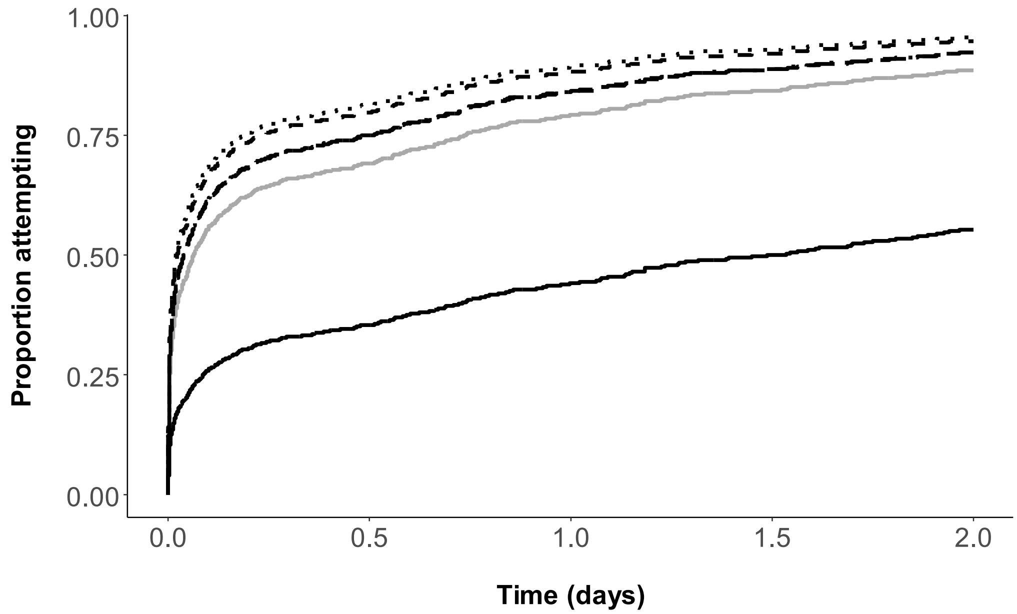

Figure 4: Proportion of fish attempting to pass the culvert as a function of time and stream of origin, modeled from the estimated Cox model. The curves represent the average attempt rate (solid grey line), fish from the stream Allaire (dotted line), Épinette (dashed line), Morin (dotdashed line), Morin DS (longdashed line) and Résimond (twodashed line). The Morin and Morin DS curves are however superposed as fish from those streams have similar average attempt rate. Other parameters of the model are set to their mean values (Q = 294 L s^{-1}, number of fish in the cage = 28, and fork length = 131.6 mm). The hazard of staging an attempt is highest at stream Allaire and lowest at stream Résimond. The proportion of released fish having staged attempts after twelve hours was between 70 and 80 % at Allaire, Épinette, Morin and Morin DS streams, but only 35% at Résimond stream.

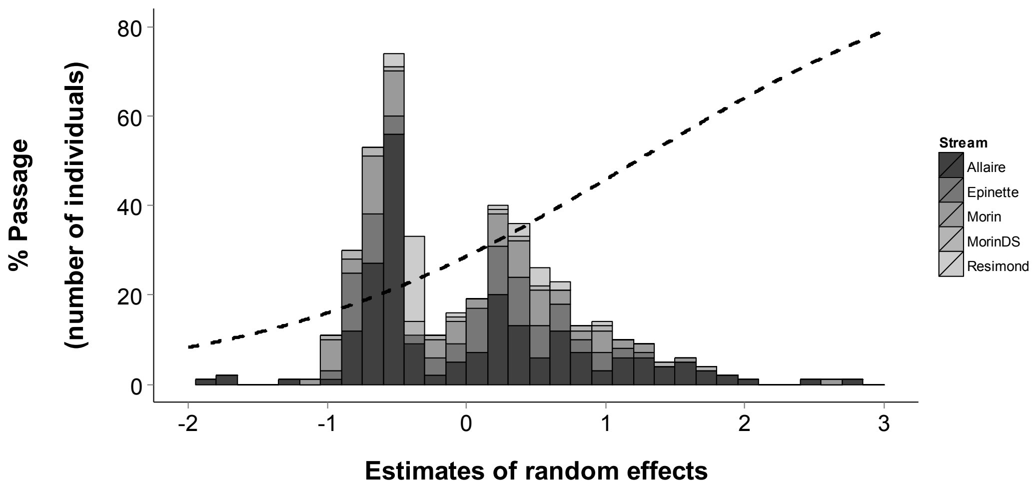

Figure 5: Estimates of random effect coefficients for individual fish in the Coxme model, as a function of stream of origin. The random effects coefficients are an index of the fish individual motivation. Each stream includes trout with low, average and high level of motivation. The dashed curve represents the predicted passage probability as a function of the fish motivation, as estimated by the logistic passage model.

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Table 1: Study site characteristics

Site	Latitude	Longitude	Material	Diameter (m)	Length (m)
Resimond	48°25'52"N	70°26'03"W	Corrugated metal	1.6	44.6
MorinA	48°20'50"N	70°03'39"W	Corrugated metal	1.5	33.2
MorinB	48°20'50"N	70°03'39"W	Corrugated metal	2.2	32.3
MorinC	48°20'50"N	70°03'39"W	Corrugated metal	2.2	33
MorinD	48°20'50"N	70°03'39"W	Polyethylene	2.2	32.4
Allaire	48°21'19"N	70°07'07"W	Concrete	2 x 2	18.4

Note:
Openness ratio is calculated by dividing the cross-sectional area of the culvert by its length. Large values correspond to short culverts with large diameters while low values correspond to

Slope (%)	Openness ratio (m)
0.92	0.16
1.38	0.20
1.38	0.29
1.38	0.29
1.38	0.29
0.28	0.22

long culverts with small diameters.

Table 2: Origin of tested fish

Tested pipe	**Stream of origin**				
	Résimond	Morin	Morin DS	Allaire	Épinette
Résimond	33	—	—	—	—
Morin A	—	—	—	27	54
Morin B	—	84	18	—	15
Morin C	—	—	—	27	27
Morin D	—	—	—	54	—
Allaire	—	—	—	108	—

Note:
Number of fish caught in the different streams, for each tested pipe.
Fish were caught upstream of the tested pipes for Résimond, Morin and Allaire strea
Additional fish were caught in Épinette stream, a nearby tributary of the Sainte-Mar

ams, and downstream for Morin DS stream.
guerite river.

Table 3: Measured range of the explanatory variables

Tested pipes	**Allaire**			
n trial	**4**			
n fish	**108**			
Parameter	**Min**	**Max**	**Median**	**Mean**
Mean flow velocity (m s^{-1})	0	0.81	0.58	0.62
Flow discharge (L s^{-1})	94.00	715.50	321.50	347
Relative change in discharge (L s-1)	0	0.39	0.02	0.04
Water temperature (°C)	8.80	19.90	11.40	11.2
Change in water temperature (°C)	0	3.20	0.10	0.27
Number of fish in the cage	2	28	17	16
Fish fork length (mm)	93	230	123	133
Fish condition factor (Fulton k)	0.74	1.5	1.02	1.03
Number of attempts per fish	0	66	1	5

Note:

Relative change in discharge is calculated as Q_2-$Q_{1)}$/Q_1 while change in water temperatu

The number of fish in the cage varies according to the number of fish released at the be

Morin (A, B, C & D)				**Resimond**			
13				**2**			
305				**34**			
Min	**Max**	**Median**	**Mean**	**Min**	**Max**	**Median**	**Mean**
0.58	1.81	0.77	0.86	0.79	0.85	0.85	0.82
55.5	642.5	195	266.3	281.5	290	289	288
0	0.93	0.02	0.03	0	0.018	0.003	0.004
2.94	18.3	12.6	11.5	10.4	12.5	10.9	11.1
0	8.52	0.09	0.19	0	0.39	0.05	0.08
4	26	22	19	11	16	14	13.8
90	263	125	131	95	206	119	127
0.71	1.5	1.01	1.01	0.77	1.4	1.06	1.08
1	58	1	2	1	3	1	1

ıre is calculated as T_2-T_1.

ginning of the trial, fish staging attempts and fish returning downstream after an attempt or from a previous trial.

Table 4: Model selection based on the Akaike information criterion (AIC)

Model $_i$	RE	-2 log (L)	K (df)
Spawn+ Q + DielPeriods + Nbcage+ BL	**(1 |Stream/ID)**	**-15011.2**	**242.0**
Spawn + Q+ dQr + DielPeriods + Nbcage+BL	(1 |Stream/ID)	-15011.2	243.0
Q + DielPeriods + NbCage + BL	(1 |Stream/ID)	-15022.4	241.0
k + Q + DielPeriods + NbCage + BL	(1 |Stream/ID)	-15022.7	241.0

Note:

Subset of tested models (*n* = 191) showing the four models with the lowest−2 log-likelihood (pe

Explanatory variables are proximity of the spawning period (spawn), flow discharge (Q), relative

RE represents the nested random effects structure, K (df) the number of degrees of freedom in

Akaike weight of model$_i$ (w$_i$) is interpreted as the probability that modeli is the best model giver

Two models emerged from the model set as providing the best fit to the data. The first one, in b

AIC_i	Δ_i AIC	w_i	w_i/w_j
15495.36	**0.0**	**0.71**	
15497.37	2.0	0.26	2.73
15504.79	9.4	0.01	71.00
15505.34	10.0	0.00	142.00

enalized) and AIC values.

e change in discharge (dQr), diel periods, number of fish in the cage (NbCage), fish body length (BL) and Ful

the model, Δi AIC is the difference between AIC of modeli and AIC of the best model.

n the data and w_i/w_j is the evidence ratio for modeli versus $model_j$.

bold, has an Akaike weight of 0.71. He is followed by a second model with a weigth of 0.26. The evidence ra ton condition factor (k).

atio between these two models is 2.73, indicating evidence in favor of the first one (Burham and Ande erson 2002).

Table 5: Estimation of parameters for the selected attempt rate model

Parameter		**β ± SE**	**HR**
Spawning		0.593 ± 0.203	1.809
Flow discharge (L s^{-1})		0.003 ± 0.000	1.003
Fish fork length (mm)		0.008 ± 0.003	1.008
Number of fish in the cage		-0.037 ± 0.009	0.963
Diel periods			
	Dawn	----	----
	Day	-0.173 ± 0.151	0.841
	Dusk	0.223 ± 0.190	1.253
	Nigth	0.035 ± 0.152	1.004
Random effects		**SD**	**Variance**
Stream of origin/ ID		1.076	1.158
Stream of origin		0.687	0.472
		β	**HR**
	Allaire	0.356	1.427
	Épinette	0.309	1.362
	Morin	0.165	1.180
	Morin DS	0.161	1.175
	Résimond	-0.991	0.371
Number of available fish		447	
Number of events		1241	

Note:

Estimates ± standard error (β ± SE) and hazard ratios (HR) of parameters for th
Hazard ratios (HR) are computed for each parameter by exponentiating the es

p-value
0.004
0.000
0.002
0.000

0.250
0.240
0.820

ne best-fitting model.
stimates. Spawning is a categorical variable with 1 = within 2 weeks of the expected spawning peri

od and 0 = more than 2 weeks than the expected spawning period.

Table 6 : Estimation of parameters for the passage success model

Parameter	β ± SE	OR	p-value
Intercept	-2.501 ± 1.186	—	0.035
Individual variability in motivation	0.746± 0.380	2.109	0.049
Fish fork lenght (mm)	0.011 ± 0.006	1.011	0.079
Random effects	**Variance**	**SD**	
Trial	7.273	2.697	

Note: Estimates ± standard error (β ± SE), odds ratio (OR) and chi-square p-values of parameters for the
Individual motivation was based on the attempt rate of each fish, as described in the Cox regression, an
The random effect on trial took into account all variability in passage performance due to the trial condi

best-fitting model. Odds ratios (OR) are computed by exponentiating the estimates.
d had a positive effect on passage success.
tions or the characteristics of the culvert.

Table 4: Estimation of parameters for the selected attempt rate models for all attempts, the first atte

	ALL ATTEMPTS			FIRST ATTEMPT		
Number of a	447			447		
Number of e	1241			254		
Parameter	**β ± SE**	**HR**	**p-value**	**β ± SE**	**HR**	**p-value**
Fulton condit	----	----	----	----	----	----
Spawning	0.593 ± 0.203	1.809	0.004	0.599 ± 0	1.820	0.008
Flow discha	0.003 ± 0.000	1.003	0.000	0.005 ± 0	1.005	0.000
(Relative ch	0.109 ± 0.499	1.115	0.830	2.377 ± 1	10.782	0.090
Fish fork ler	0.008 ± 0.003	1.008	0.002	0.010 ± 0	1.010	0.000
Number of f	-0.037 ± 0.009	0.963	0.000	----	----	----
Diel periods						
Dawn	----	----	----	----	----	----
Day	-0.173 ± 0.151	0.841	0.250	1.140 ± 0	3.126	0.014
Dusk	0.223 ± 0.190	1.253	0.240	1.774 ± 0	5.897	0.001
Nigth	0.035 ± 0.152	1.004	0.820	0.774 ± 0	2.167	0.093
Random ef	**SD**	**Variance**		**SD**	**Variance**	
Stream of o	1.076	1.158		0.894	0.799	
Stream of o	0.687	0.472		0.370	0.137	
	β	**HR**		**β**	**HR**	
Allaire	0.356	1.427		0.09	1.09	
Épinette	0.309	1.362		0.39	1.47	
Morin	0.165	1.180		-0.16	0.85	
Morin DS	0.161	1.175		0.09	1.10	
Résimond	-0.991	0.371		-0.41	0.67	

Note:

Estimates ± standard error (β ± SE) and hazard ratios (HR) of parameters for the best-fitting r

Hazard ratios (HR) are computed for each parameter by exponentiating the estimates. Spawı

For all attempts, the relative change in discharge is presented in () as this parameter was not

The relative change in discharge and the diel periods have large standard errors compared tc empt only and all subsequent attempts.

SUBSEQUENT ATTEMPTS		
170		
987		
β ± SE	**HR**	**p-value**
1.380 ± 0	3.976	0.004
----	----	----
0.001 ± 0	1.001	0.000
----	----	----
----	----	----
----	----	----
----	----	----
----	----	----
----	----	----
----	----	----
SD	**Variance**	
0.516	0.266	
0.592	0.350	
β	**HR**	
0.72	2.06	
-0.14	0.87	
0.06	1.06	
0.08	1.09	
-0.73	0.48	

nodel for all attempts, first attempt only and subsequent attempts.
ning is a categorical variable with 1 = within 2 weeks of the expected spawning period and 0 =
: included in the best-fitting model, but rather in a competing model with a lower Akaike weig
) their estimated coefficient, indicating some uncertainty with regards to in their effect on att

= more than 2 weeks than the expected spawning period.
ght.
tempt rate.

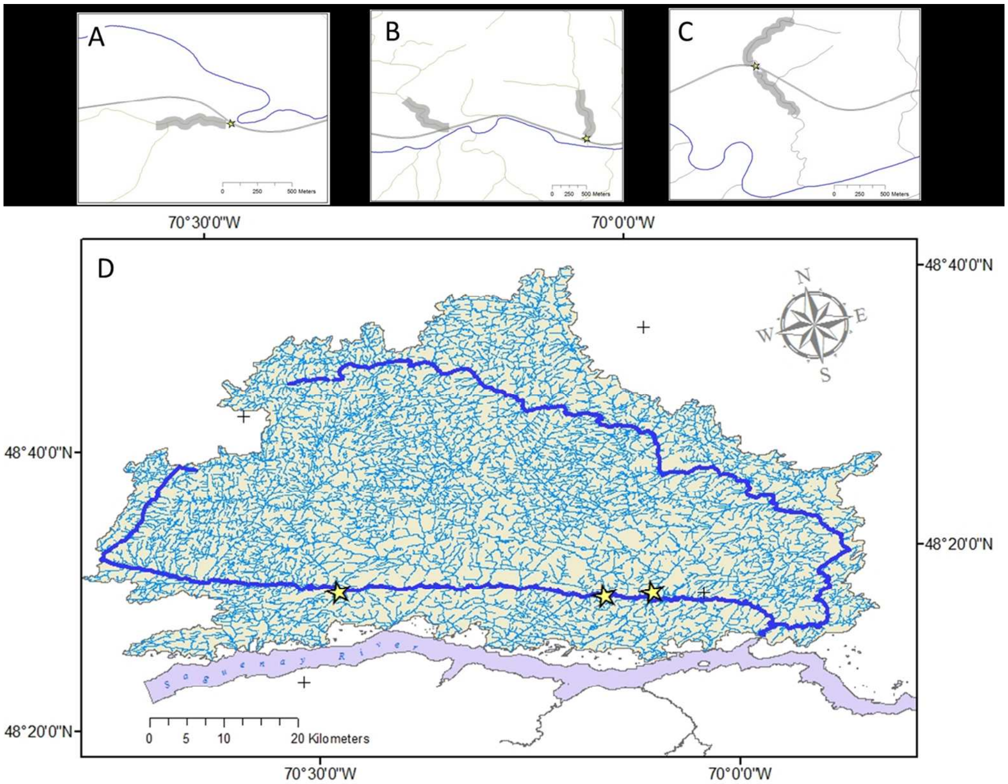

Figure 1. Study sites (stars) and their location within the Ste. Marguerite river watershed (Panel D). Details of studied culverts and collection locations (Tables 1 & 2) are shown in the upper panels (A: Résimond; B: Allaire; and C: Morin). Roads are shown as double-lines, and collection locations are indicated by transparent, heavy gray lines (Panels A, B &C). The Épinette stream collection site is shown in panel B, situated to the west of the Allaire study site.

237x185mm (150 x 150 DPI)

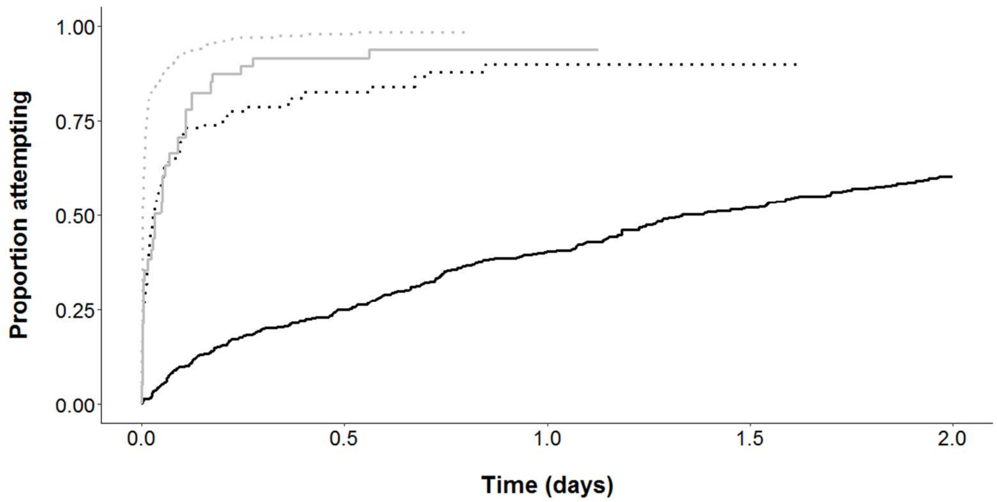

Figure 2: Cumulative incidence curves (1- empirical Kaplan-Meier curves) representing proportion of fish attempting to pass the culverts as a function of time. Data are stratified by attempts, the black curve representing the 1st attempts, the black dotted curve the attempts 2-5, the grey curve attempts 6-10, and the grey dotted curve attempts > 10. The rate of the first attempt is much slower than the one of subsequent ones. The rate thereafter increased with subsequent attempts.

409x204mm (72 x 72 DPI)

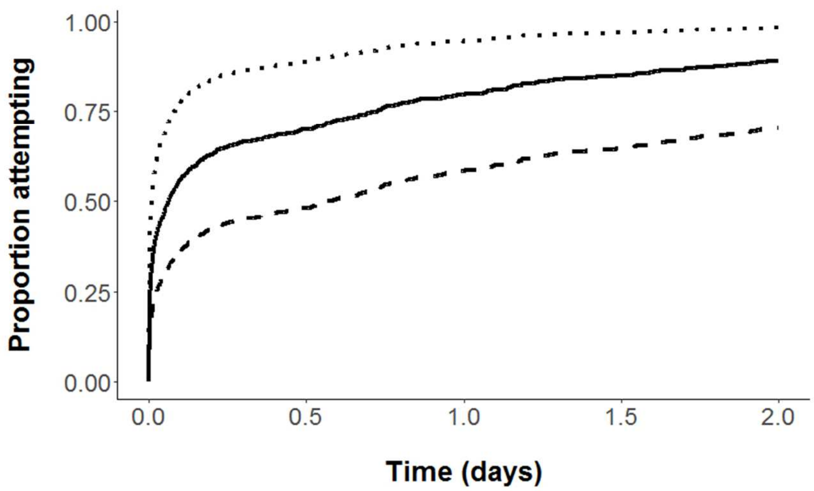

Figure 3: Proportion of fish attempting to pass the culvert as a function of time and flow discharge, modeled from the estimated Cox model. The attempt rate increases with higher values of discharge. Dashed line: 100 L s-1; solid line: 300 L s-1 and dotted line: 500 L s-1, which corresponds to the 25th, 50th and 75th percentiles, respectively, of tested flow discharge. Others parameters are set at their mean values (number of fish in the cage = 28, and fork length = 131.6 mm).

345x230mm (72 x 72 DPI)

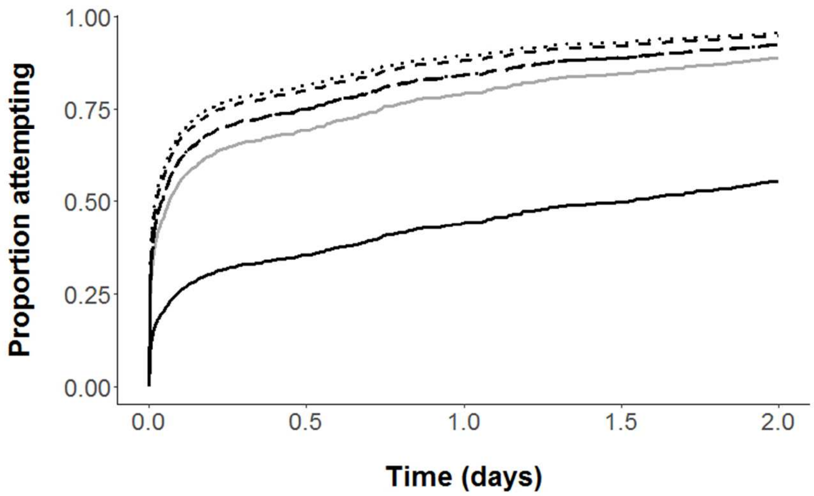

Figure 4: Proportion of fish attempting to pass the culvert as a function of time and stream of origin, modeled from the estimated Cox model. The curves represent the average attempt rate (solid grey line), fish from the stream Allaire (dotted line), Épinette (dashed line), Morin (dotdashed line), Morin DS (longdashed line) and Résimond (twodashed line). The Morin and Morin DS curves are however superposed as fish from those streams have similar average attempt rate. Other parameters of the model are set to their mean values (Q = 294 L s-1, number of fish in the cage = 28, and fork length = 131.6 mm). The hazard of staging an attempt is highest at stream Allaire and lowest at stream Résimond. The proportion of released fish having staged attempts after twelve hours was between 70 and 80 % at Allaire, Épinette, Morin and Morin DS streams, but only 35% at Résimond stream.

345x230mm (72 x 72 DPI)

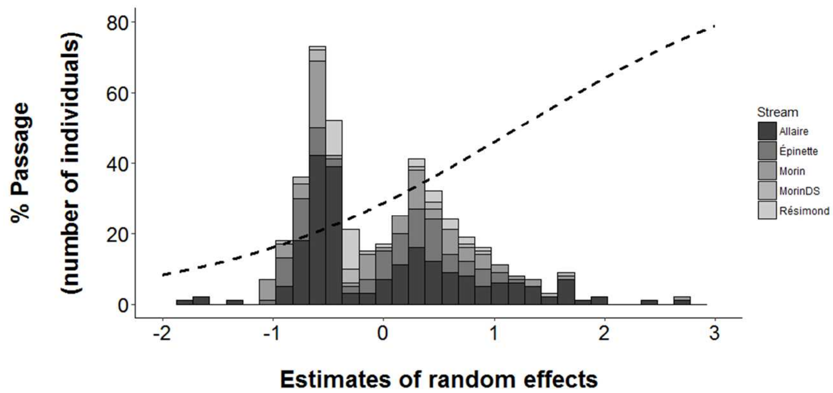

Figure 5: Estimates of random effect coefficients for individual fish in the Coxme model, as a function of stream of origin. The random effects coefficients are an index of the fish individual motivation. Each stream includes trout with low, average and high level of motivation. The dashed curve represents the predicted passage probability as a function of the fish motivation, as estimated by the logistic passage model.

409x223mm (72 x 72 DPI)