Université du Québec
Institut National de la Recherche Scientifique
Centre Eau Terre Environnement

MODÉLISATION DE LA CAPACITÉ DE L'OMBLE DE FONTAINE (*SALVELINUS FONTINALIS*) À FRANCHIR LES PONCEAUX

Par

Elsa M.C. Goerig

Thèse présentée pour l'obtention du grade de
Philosophiae doctor (Ph.D.)
en sciences de la terre

Jury d'évaluation

Président du jury et examinateur interne	Patrice Couture Institut National de la Recherche Scientifique
Examinateurs externes	Stephan James Peake University of New-Brunswick
	Marco A. Rodriguez Université du Québec à Trois- Rivières
Directeur de recherche	Normand E. Bergeron Institut National de la Recherche Scientifique
Codirecteur de recherche	Theodore Castro-Santos US Geological Survey

"An undisturbed river is as perfect as we will ever know, every refractive slide of cold water a glimpse of eternity."

- Thomas McGuane

“Everyday I wonder how many things I am dead wrong about.”

- Jim Harrison

REMERCIEMENTS

Je dédie cette thèse à mes enfants, ainsi que leurs amis qui, contrairement à bien des adultes, ont toujours considéré mon projet de thèse avec le plus grand enthousiasme. Grâce à leurs yeux qui pétillent et à leur incessante question : «Comment vont tes poissons ?», j'ai conservé intacte ma propre étincelle.

Un doctorat est une grande aventure personnelle, mais dont le succès repose sur la présence et l'implication de nombreuses personnes.

Je tiens tout d'abord à remercier François, qui m'a fait réaliser que j'avais la force et la confiance en moi nécessaire pour débuter cette aventure. Puis mon époux Marco, qui m'a soutenue pendant sa réalisation, a pris soin de nos enfants lors de mes absences et a écouté avec patience toutes mes doléances à propos du «code qui ne marche pas !», bien que je réalise maintenant ne lui avoir jamais expliqué ce que cela signifiait.

Je remercie mes parents et ma famille. Sans leur soutien inconditionnel, la réalisation de ma thèse aurait été impossible. Un grand merci à MC, qui m'a si généreusement et si souvent fourni un toit, d'excellents repas et son amitié. Sans toi, ma chère, le doctorat aurait tourné court il y a bien longtemps.

Je remercie mes directeurs de recherche, qui m'ont accompagnée dans cette aventure. Normand, pour ton accueil et ta confiance. Pour tes idées excellentes et ton enthousiasme, ainsi que pour m'avoir enseigné comment me faire une place et, je l'espère, réussir en recherche. Theodore, for your endless generosity, patience and rigor. For giving me the strength to push doors, think by myself and discuss my opinions. And for opening so many possibilities for my future.

Je tiens également à remercier tous les gens du S.O. Conte Anadromous Fish Research Center qui m'ont aidée ou soutenue pendants mes deux dernières années de doctorat, ainsi que ceux de l'INRS qui ont fait un excellent travail et ont contribué à leur façon à la réalisation de cette thèse. Un merci particulier à Suzanne qui m’a écoutée et soutenue dans les périodes plus difficiles.

Je remercie également tous les partenaires financiers qui ont rendu ce projet possible, notamment le Conseil de recherche en sciences et génie du Canada, le Fonds de recherche Nature et technologies du Québec, le Ministère des transports du Québec, le Fonds de la Recherche forestière du Saguenay-Lac-Saint-Jean, et le Groupe de recherche interuniversitaire en limnologie et environnements aquatiques (GRIL). Un grand merci à Martin Lafrance, pour son enthousiasme toujours renouvelé pour le projet!

Enfin, un immense merci à tous ceux du CIRSA et du Labo Bergeron («Là où on fait des champions !»). Que d’escapades au pays des épinettes et des mouches noires, de voyages, de conférences et de nuits quasi blanches, de dur travail mais aussi de plaisir fou. Merci d’avoir toujours été là pour moi et de m’avoir épaulée durant toutes ces années. Chacun à votre manière, vous êtes présent dans les pages qui suivent.

RÉSUMÉ

L’accès à l’habitat pour les poissons est un élément primordial de la qualité globale de l’habitat aquatique. Différents éléments d’origine naturelle ou anthropique peuvent limiter la connectivité du paysage fluvial et compromettre l’accès à des habitats complémentaires nécessaires au cycle de vie de certaines espèces. Les ponceaux sont largement distribués sur le territoire et constituent un des obstacles les plus fréquents à la libre circulation des poissons.

L’objectif principal de cette thèse est de mieux comprendre les facteurs qui influencent la capacité de l’omble de fontaine, une espèce native de l’est de l’Amérique du Nord, à franchir les ponceaux. Cet objectif sera atteint à travers cinq objectifs spécifiques, réalisés de façon chronologique.

Une approche permettant de recueillir, en milieu naturel, des données sur la capacité de passage de cette espèce dans les ponceaux, sera tout d’abord développée. Les données recueillies seront comparées avec les prédictions de passage produites par trois approches prédictives existantes. La motivation des ombles à franchir les ponceaux sera ensuite modélisée, de façon à prendre en compte l’effet de différents facteurs environnementaux, biologiques et hydrauliques sur l’occurrence d’une tentative de passage. La performance de passage en elle-même sera également abordée, avec comme objectif de produire un modèle prédictif de passage de l’omble de fontaine dans les ponceaux. Enfin, le comportement et les trajectoires de nage des ombles lors d’une tentative de passage seront caractérisés dans le cadre d’une expérience complémentaire.

Cette thèse apporte un nouveau regard sur la capacité de l’omble de fontaine à franchir les ponceaux et des méthodes pouvant facilement s’adapter à l’étude de d’autres espèces.

TABLE DES MATIÈRES

LISTE DES TABLEAUX

LISTE DES FIGURES

PARTIE 1: SYNTHÈSE

1 INTRODUCTION

Les besoins en espace et en ressources amènent l'homme à développer et à aménager le territoire autour de lui. Les besoins en déplacements, que ce soit pour l'accès aux ressources, pour relier des communautés éloignées ou simplement pour passer d'une sphère de la vie quotidienne à l'autre, sont multiples et diversifiés. Ils entraînent le développement d'infrastructures de transport, des composantes essentielles de l'aménagement du territoire.

Les routes, peu importe leur type et leur dimensions, permettent à l'homme de se mettre en mouvement et d'accéder à l'espace qui l'entoure. Le fait de se déplacer dans l'espace afin de combler différents besoins n'est toutefois pas le propre de l'homme. La plupart des espèces animales se déplacent sur des distances variables et utilisent des habitats complémentaires pour combler leurs différents besoins vitaux (Fausch *et al.*, 2002, Schlosser, 1991).

Paradoxalement, les voies de transport qui permettent l'interconnexion des territoires et l'utilisation de ceux-ci par l'homme peuvent réduire son accessibilité pour les autres espèces animales. En effet, l'aménagement du territoire peut fragmenter celui-ci en de multiples parcelles entrecoupées par des voies de transport diverses. Ces dernières peuvent dans certains cas constituer de véritables obstacles aux déplacements des espèces fauniques, réduisant ainsi la portion accessible de leur habitat (Forman *et al.*, 1998, Gibson *et al.*, 2005, Kemp *et al.*, 2008). Ce phénomène, assez visible dans le cas de la grande faune, s'avère souvent moins flagrant dans celui des espèces aquatiques. Les traverses de cours d'eau, ponts ou ponceaux, assurent dans l'imaginaire collectif la continuité fluviale. L'eau s'écoulant sous la route semble en effet ne rencontrer aucun obstacle à sa course. Pourquoi alors en serait-il autrement des espèces aquatiques présentes dans le cours d'eau?

Dans la réalité, les ponceaux peuvent constituer des obstacles aux déplacements des espèces aquatiques, particulièrement les poissons. Cela est d'autant plus fréquent pour les espèces largement distribuées sur le territoire ou qui parcourent de longues distances, telles les salmonidés.

2 MISE EN CONTEXTE

Il est connu dans la littérature que les salmonidés juvéniles ont tendance à migrer vers les petits tributaires (Curry *et al.*, 1993, Erkinaro *et al.*, 1997, Erkinaro *et al.*, 1998). Les petits cours d'eau produisent en effet plus d'invertébrés par unité de surface que les grands cours d'eau (Hynes *et al.*, 1970) et les salmonidés y retrouvent une alimentation plus abondante leur permettant d'obtenir de meilleurs taux de croissance que dans le tronçon principal d'une rivière (Erkinaro *et al.*, 1995). D'autres motivations aux mouvements vers l'amont des salmonidés sont liées à la reproduction, à la recherche d'une eau plus fraîche durant l'été (Meyers *et al.*, 1992) et, à l'approche de l'hiver, de substrat suffisamment grossier afin de leur permettre de s'enfouir dans les interstices (Bjornn, 1971, Young, 1998). Bien que les espèces non-anadromes se déplacent sur des distances moins grandes que celles anadromes, des études récentes indiquent que les déplacements de plus de cinquante mètres ne sont pas inhabituels chez ces espèces (Gowan *et al.*, 1996, Rodriguez, 2002). Ces déplacements peuvent avoir cours à différents moments de l'année et non pas seulement dans la période de reproduction. Ainsi, une étude réalisée au Montana a relevé un nombre élevé de déplacements vers l'amont durant la période d'étiage estival pour l'omble de fontaine et la truite fardée (Burford *et al.*, 2009). Ces études remettent en cause le paradigme du mouvement restreint chez certaines espèces d'eau douce (Gerking, 1959) et souligne l'éventuel impact négatif des barrières chez celles-ci.

Effet des ponceaux sur l'habitat du poisson

Le nombre de ponceaux sur un territoire est fonction de la densité des réseaux routiers et hydrographiques présents sur celui-ci. Il est difficile d'avancer un nombre précis, mais il est possible d'affirmer que plusieurs milliers de ponceaux sont installés ou remplacés chaque année au Québec (Prévost *et al.*, 2002). Aux États-Unis, le US Fish and Wildlife Service estime le nombre de traverses de cours d'eau sur le territoire américain à 1,4 millions (Castro, 2003). De dimensions allant de quelques dizaines de centimètres à plus de trois mètres de diamètre, les ponceaux peuvent être de formes (circulaire, rectangulaire, en arche), de longueurs et de matériaux (métal, béton, plastique) divers.

Les ponceaux sont susceptibles d'avoir des effets négatifs sur l'habitat du poisson. Il est connu qu'ils peuvent favoriser l'introduction de sédiments fins dans les cours d'eau (Prévost et al. 2002). Plusieurs études effectuées au Québec et ailleurs ont permis d'analyser cet aspect de la problématique et de proposer de nouvelles normes permettant de minimiser les impacts sur la faune aquatique. Le ponceau, en modifiant les conditions hydrauliques naturelles du cours d'eau, peut également constituer une barrière physique aux déplacements des espèces aquatiques. Une étude effectuée au Labrador a analysé quarante-sept nouveaux ponceaux dont la construction était soumise aux normes recommandées par Pêches et Océans Canada (Gibson *et al.*, 2005). Une proportion de 53 % de ces ponceaux ne répondaient pas à ces normes et constituaient un obstacle au passage des poissons en raison de problèmes de conception ou d'installation. Ainsi, la présence de ponceaux peut entraver, sous certaines conditions hydrauliques, les déplacements des poissons vers l'amont de façon permanente ou temporaire, ce qui a pour conséquence de fragmenter l'habitat disponible en réduisant l'accès aux portions de cours d'eau situées en amont du ponceau (Gibson *et al.*, 2005, Harper *et al.*, 2005, Langill *et al.*, 2002, Park *et al.*, 2008). Les principales causes connues de cette entrave sont une vitesse de l'eau élevée, de faibles profondeurs et une sortie surélevée créant une chute (Bates, 2003, Belford *et al.*, 1989, Boubée *et al.*, 1999, Fitch, 1995, Kahler *et al.*, 1998, Larinier, 2002, Zwirn, 2002). La présence d'obstructions à l'intérieur des ponceaux (accumulation de débris ligneux, effondrement du ponceau, etc.) peut constituer une source additionnelle d'entrave aux mouvements des poissons.

Des vitesses d'écoulement excédant la capacité de nage des poissons sont identifiées par certains auteurs (Matthew Blank *et al.*, 2009, Castro-Santos, 2005, Gibson *et al.*, 2005) comme la cause d'entrave dominante. Le fait que le diamètre (D) du ponceau soit souvent inférieur à la largeur plein-bords (w) du cours d'eau (ratio de constriction w/D < 1) a pour effet de restreindre l'aire d'écoulement et peut favoriser une augmentation des vitesses d'écoulement à l'intérieur du ponceau. L'augmentation des vitesses d'écoulement à l'intérieur du ponceau par rapport à celles ayant cours dans le cours d'eau est toutefois due à la combinaison de deux facteurs principaux : la pente du ponceau est souvent plus grande que celle du chenal et le matériau dont est constitué le ponceau a généralement un coefficient de rugosité inférieur à celui du lit naturel du cours d'eau.

La profondeur d'eau peut également jouer un rôle dans le fait qu'un ponceau soit difficilement franchissable pour un individu donné. Celle-ci a un impact direct sur la capacité physique du poisson d'entrer et de se déplacer à l'intérieur d'un ponceau. Une profondeur d'eau insuffisante en relation avec la taille du poisson rendra en effet sa progression difficile, particulièrement sous des conditions de vitesse d'écoulement élevée (Gibson *et al.*, 2005, Warren *et al.*, 1998).

La présence d'infrastructures routières peut avoir un impact sur la qualité et l'accessibilité de l'habitat pour les espèces aquatiques. Les traverses de cours d'eau constituent en effet, de par leurs caractéristiques propres et sous certaines conditions hydrauliques, des obstacles permanents ou temporaires aux déplacements vers l'amont des poissons. La restriction des mouvements dans le temps et dans l'espace peut avoir diverses conséquences sur les populations de salmonidés. Au niveau individuel, un ponceau agissant comme une barrière peut empêcher un individu d'accéder à des portions d'habitat de qualité ou induire un délai dans l'accès aux sites de reproduction (Belford and Gould. 1989, Gibson et al. 2005). Plusieurs ponceaux difficilement franchissables situés dans un même bassin-versant peuvent par ailleurs avoir un effet cumulatif sur la réduction de la connectivité des habitats, isolant les populations les unes des autres et réduisant les échanges génétiques entre elles (Letcher *et al.*, 2007, Morita *et al.*, 2002, Torterotot *et al.*, 2014, Wofford *et al.*, 2005). Les effets de cet isolement varieront toutefois selon la quantité et la qualité de l'habitat disponible dans les différents segments fragmentés du cours d'eau.

Modélisation de la capacité de passage

Dans le contexte actuel des connaissances, il demeure difficile de modéliser la capacité d'un poisson d'une espèce et d'une taille donnée à franchir un ponceau. Cette modélisation doit nécessairement être constituée de deux composantes : la détermination des conditions d'écoulement à l'intérieur et aux extrémités amont et aval du ponceau et la détermination du taux de succès d'un poisson (d'une espèce, d'un âge et d'une taille donnée) à franchir un ponceau d'une longueur donnée selon les conditions de vitesse et de profondeur d'eau observées à l'intérieur de celui-ci (Castro-Santos, 2004). La capacité d'un poisson à franchir un ponceau est fonction de critères biologiques tels que sa capacité de nage et de saut, eux-mêmes influencés par d'autres variables comme sa motivation à se déplacer, l'attraction exercée par le ponceau, la température de l'eau, etc. (Boubée *et al.*, 1999, Burford *et al.*, 2009, Castro-Santos, 2004). Il existe peu d'études qui fournissent des données quantitatives sur la performance de nage des poissons et cette lacune est problématique pour la conception des passes migratoires et des ponceaux (Haro *et al.*, 2004). De plus, lorsque des données décrivant la capacité de nage globale d'une espèce de poisson existent, elles proviennent habituellement d'expériences menées dans des environnements contrôlées de laboratoire et elles sont difficilement applicables, sur le terrain, à la détermination de la capacité de passage du poisson dans un ponceau. Il existe donc un important besoin d'obtenir, en conditions naturelles, les données permettant de modéliser la capacité biologique des poissons à franchir les ponceaux.

La capacité de saut, utile quant à elle pour entrer dans un ponceau dont l'extrémité aval est surélevée par rapport au cours d'eau, a fait l'objet d'une étude en laboratoire de (Kondratieff *et al.*, 2006). Ces auteurs ont déterminé que la capacité de l'omble de fontaine à franchir un obstacle vertical est influencée par la hauteur dudit obstacle, la profondeur du bassin situé immédiatement en aval, la longueur et la condition physique du poisson. Cette dernière est définie dans l'expérience par un score indiquant la présence ou l'absence de blessures aux nageoires, aux yeux, à l'opercule ou à la mâchoire de l'individu. Le modèle développé par les auteurs doit toutefois s'appliquer avec précaution sur le terrain, la morphologie des obstacles n'étant pas toujours identique à celle d'un mur vertical.

La motivation des individus à franchir un ponceau demeure par ailleurs un aspect comportemental incontournable. Une étude de (Castro-Santos, 2004) a mis en évidence l'importance de la fréquence des tentatives sur le succès de passage des meuniers et des dorés, la probabilité de succès étant plus élevée avec un nombre grandissant de tentatives. Dans cette étude, les tentatives étaient plus fréquentes lorsque les vitesses d'écoulement étaient élevées à l'extrémité aval du ponceau, mettant également en lumière l'importance de l'attraction exercée par les conditions hydrauliques en aval du ponceau en ce qui a trait à l'occurrence de tentatives et au succès de passage.

D'autres éléments sont également à prendre en considération, notamment le fait que l'écoulement est rarement uniforme dans un ponceau et que les gradients latéraux et verticaux des vitesses d'écoulement peuvent être prononcés (Clark *et al.*, 2011, Neary, 2012, Richmond *et al.*, 2007). La vitesse moyenne déterminée pour un segment ou l'ensemble d'un ponceau peut ainsi ne pas correspondre à la vitesse réelle affrontée par l'individu lors de sa progression dans le ponceau. House *et al.* (2005) ont développé une approche afin de déterminer, pour une coupe transversale dans un ponceau, le pourcentage de l'aire d'écoulement où la vitesse est égale ou inférieure à une vitesse d'écoulement seuil en regard de la capacité de nage de saumons juvéniles. La turbulence de l'écoulement constitue un autre aspect à prendre en considération au moment de comparer les vitesses moyennes d'écoulement avec la capacité de nage des poissons. L'étude de Clark *et al.* (2011) a mis en évidence l'existence de circulations secondaires de l'écoulement dans les ponceaux en métal ondulé. Celles-ci consistent en une cellule de circulation de chaque côté de la coupe transversale du ponceau, ces cellules n'étant toutefois pas symétriques. Le long de l'axe central, l'eau se déplace verticalement vers le fond du ponceau, puis en direction des côtés pour ensuite remonter vers la surface, transportant les masses d'eau à faible momentum vers le centre, près de la surface et vice-versa. Tous les profils de vitesses montraient une diminution près de la surface, l'endroit où se trouvait les vitesses maximales étant situé approximativement à mi-profondeur, au centre de la coupe transversale. Les caractéristiques de l'écoulement peuvent toutefois varier selon le degré de rugosité du matériel dont est constitué le ponceau (métal ondulé versus béton ou plastique) et la configuration de l'entrée amont.

L'aptitude des poissons à tirer parti des zones où la vitesse de l'écoulement est réduite joue certainement un rôle dans leur capacité à franchir les ponceaux (Castro-Santos, 2005, Powers *et al.*, 1997). Le comportement de nage des poissons constitue donc une variable d'importance, au même titre que leur capacité de nage proprement dite (Hinch *et al.*, 2000). Une étude a combiné des techniques de modélisation en trois dimensions de l'écoulement et des observations visuelles des trajectoires empruntés par des truites fardées lors de tentatives de remontée d'un ponceau (Blank et al. 2009). Les auteurs concluent que les trajectoires préférentielles empruntées par les individus ayant complété la remontée du ponceau correspondent aux zones de vitesses d'écoulement réduites présentes dans celui-ci. Ces zones permettent une dépense énergétique moindre pour les individus et leur utilisation augmente la probabilité de passage. La détermination des vitesses et des profondeurs préférentielles sélectionnées par les individus en fonction de celles disponibles lors de leurs tentatives de passage, constitue un aspect du comportement de nage à considérer lors de l'évaluation de la capacité d'une espèce à franchir les ponceaux. Cela pourrait permettre, en comparant ces vitesses avec la vitesse moyenne déterminée pour l'ensemble du ponceau, d'élaborer et d'appliquer des facteurs de correction aux paramètres de vitesse d'écoulement utilisés dans les modèles de passage. Des facteurs de correction allant de 0,4 à 0,8 ont été développés par Behlke (1991) pour les juvéniles de salmonidés et peuvent être utilisés dans des modèles de simulation de passage.

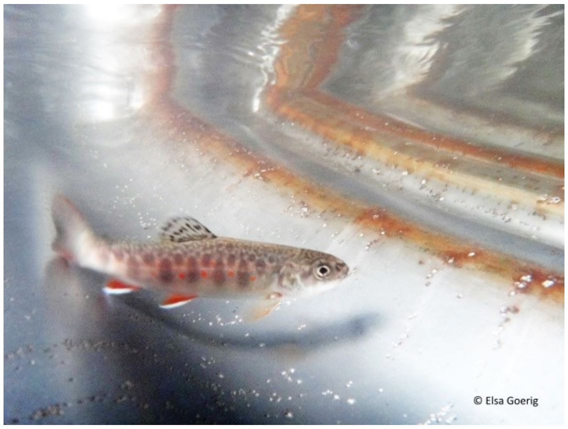

Figure 1 : Omble de fontaine dans une ondulation d'un ponceau

Source : Elsa Goerig (INRS), 2011

L'intérêt grandissant pour la question de la perméabilité des ponceaux aux déplacements des espèces aquatiques a mené à la conception de modèles de succès de passage afin de prédire si un poisson d'une espèce et d'une longueur donnée peut franchir un ponceau sous des conditions hydrauliques spécifiques. Deux types de modèles se retrouvent dans la littérature : le modèle de type «seuil d'épuisement» ou *exhaustion threshold* et celui de type «distance de remontée» ou *ascent distance* (Neary, 2011).

Modèle de type «seuil d'épuisement»

Le modèle de type seuil d'épuisement cherche à prédire le seuil de vitesse d'écoulement se traduisant par l'épuisement à une distance donnée de remontée dans le cas d'un individu progressant dans le ponceau à une vitesse optimale. La vitesse de nage optimale se définie comme la vitesse de déplacement au sol permettant à l'individu de maximiser la distance parcourue contre la vitesse d'écoulement à laquelle il fait face. Une vitesse d'écoulement égale ou supérieure au seuil se traduit par un échec de passage. Des exemples de courbes de seuil d'épuisement sont disponibles pour différentes espèces dans plusieurs études (Adams *et al.*, 2000, Benton *et al.*, 2008, Peake *et al.*, 1997).

FishXing (Furniss *et al.*, 2008), un logiciel permettant de simuler des tentatives de passage qui sera utilisé au cours de la thèse, fonctionne sur le mode «seuil d'épuisement». FishXing est actuellement le modèle le plus largement utilisé pour prédire la capacité d'un poisson d'une espèce donnée à franchir un ponceau sous des conditions hydrauliques variées. Il utilise, en premier lieu, des données de performance de nage par espèce et par gamme de taille afin de modéliser la capacité de passage. Ces données proviennent de diverses études majoritairement effectuées en laboratoire. En deuxième lieu, le modèle effectue des simulations hydrauliques afin de reconstituer, selon la gamme de débits envisagée et les caractéristiques du ponceau, la répartition des profondeurs et des vitesses moyennes d'écoulement à l'intérieur de celui-ci. La capacité de nage en modes prolongé et sprint du poisson est mise en relation avec ces données hydrauliques pour chacune des coupes transversales du ponceau. FishXing détermine, par un algorithme de nage, le temps à l'épuisement du poisson sous les conditions d'écoulement en vigueur et la distance maximale parcourue au moment de l'épuisement. Lorsque le poisson atteint le seuil d'épuisement dans un mode de nage (ex. prolongé), l'algorithme de nage recalcule le temps à l'épuisement pour le mode de nage supérieur (ex. sprint). Au terme des estimations, si la distance maximale atteinte au seuil d'épuisement en mode sprint est inférieure à la longueur du ponceau, FishXing prédit un échec et permet de visualiser jusqu'à quelle distance le poisson a réussi à remonter le ponceau.

Certains auteurs s'interrogent sur l'efficacité de FishXing à prédire adéquatement l'issue d'une tentative de passage pour certaines espèces. Solcz (2007) a observé pour la truite fardée une correspondance de 50% entre ses observations de terrain et les prédictions du modèle tandis que Burford et al. (2009) mentionne une correspondance de 17% et une tendance du modèle à surestimer le nombre de ponceaux infranchissables. Cahoon et al. (2009) ont observé, pour la truite fardée et l'omble de fontaine, une correspondance de 48% entre les prédictions de FishXing et des observations directes de passage effectuées sur le terrain. Selon cette étude, FishXing tend à être conservateur dans son évaluation de la perméabilité des ponceaux aux mouvements des poissons. Le fait que les données de nage utilisées par le modèle proviennent essentiellement de travaux effectués en laboratoire rend difficile leur application sur le terrain, les conditions d'écoulement et la motivation des individus pouvant y être très différentes (Castro-Santos, 2004, Gardner, 2006). Certains aspects peuvent par ailleurs être difficilement pris en compte dans une simulation de passage, par exemple l'utilisation par les poissons de zones de vitesses d'écoulement réduites dans les ponceaux et le comportement de nage des individus (ex : utilisation d'un ou de deux types de nage combinés, choix préférentiel de vitesse et de profondeur en fonction de celles disponibles lors de la remontée).

Modèle de type «distance de remontée»

Ce type de modèle estime une distance maximale de remontée sous des conditions hydrauliques données pour un individu nageant à une vitesse optimale. Castro-Santos (2005) a élaboré une approche permettant de déterminer la vitesse de nage optimale permettant à un poisson de maximiser la distance maximale parcourue contre une vitesse d'écoulement donnée. Cette distance est ensuite comparée à la longueur de la barrière de vitesse afin de prédire le succès ou l'échec d'une tentative. Les travaux de Peake et al. (1997) et de Castro-Santos (2005) constituent un bon exemple de modèle de type «distance de remontée». Peake et al. (1997) ont évalué les performances de nage de différentes espèces lors d'expériences de laboratoire et ont proposé un modèle permettant d'estimer la vitesse de nage de ces espèces, et ce pour différents types de nage. Ainsi, la vitesse de nage peut être estimée à l'aide de l'équation suivante :

$$S = a_0 + a_1X + a_2Y + a_3Z \qquad (1)$$

où S correspond à la vitesse de nage en m s^{-1}, a_0 correspond à l'ordonnée à l'origine, a_1 est le coefficient de longueur, X correspond à la longueur à la fourche en cm, a_2 est le coefficient de température, Y correspond à la température en degrés Celsius, a_3 est le coefficient de temps et Z représente le log du temps en minute. Ce modèle a été établi à partir de données obtenues pour des poissons dont la taille variait entre 6.3 et 25.9 cm et pour une température de l'eau variant entre 14.0 et 20.0 °C (Peake et al. 1997). Le temps à l'épuisement pour différentes vitesses de nage prolongée est estimé en isolant le terme Z dans l'équation 1. La relation entre le temps à l'épuisement et la vitesse de nage prolongée suit généralement un modèle log-linéaire tel que décrit à l'équation 2 (Brett, 1964).

$$\ln T = a + bU_s \qquad (2)$$

où T représente le temps à l'épuisement en secondes, U_s correspond à la vitesse de nage prolongée (en longueurs de corps s^{-1}), et a et b sont respectivement l'ordonnée à l'origine et la pente (Castro-Santos 2005).

Lorsqu'un poisson doit franchir une barrière de vitesse aux limites spatiales définies (ex. un ponceau), la distance maximale qu'un poisson peut nager avant de se fatiguer doit être exprimée en distance de progression au sol (D_g) et prendre en compte la vitesse de l'écoulement. Les coefficients a et b de la relation entre le temps à l'épuisement et la vitesse de nage prolongée ont par la suite été utilisés afin de déterminer la distance maximale qu'un poisson peut parcourir face à une vitesse moyenne d'écoulement (U_f) donnée. Selon Castro-Santos (2005), D_g peut être déterminée à l'aide de l'équation 3:

$$D_g = \left(U_s - U_f\right) \times e^{a+bU_s} \qquad (3)$$

où les vitesses sont en longueur de corps s^{-1} et la distance obtenue est exprimée en longueur de corps.

L'équation 3 est illustrée par la figure 2, sur laquelle il est possible d'observer que la distance maximale de remontée est maximisée à une certaine vitesse de nage. Cette vitesse de nage optimale permettant de maximiser la distance parcourue varie selon la vitesse de l'écoulement.

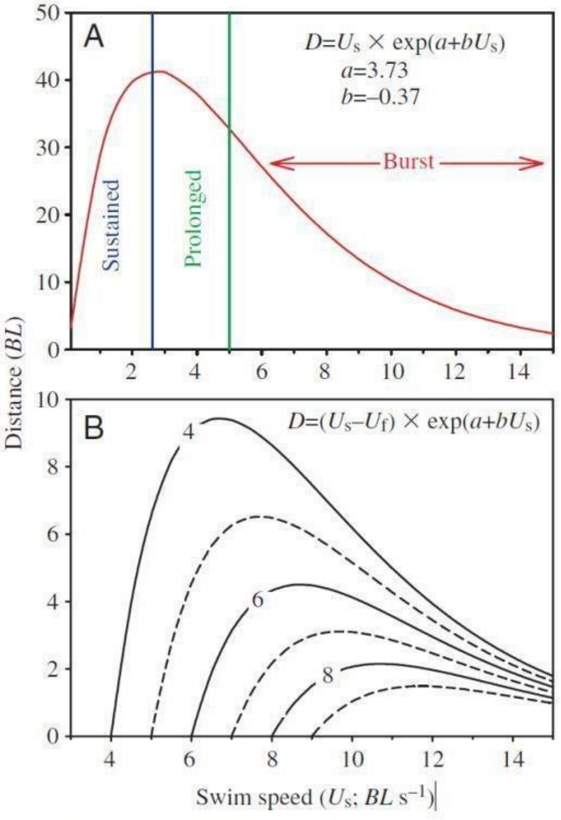

Figure 2: Distance maximale (en longueurs de corps) prédite par l'équation 6 en eau dormante (A) et en présence d'écoulement (B) pour la truite arc-en-ciel. Les contours indiquent la vitesse d'écoulement (m s^{-1}). Source : Castro-Santos (2005)

Pour un type de nage donné, la vitesse de nage au sol optimale (U_{opt}), c'est-à-dire la vitesse permettant de parcourir une distance au sol maximale pour une vitesse moyenne (U_f) donnée, est définie par l'équation 4 (les vitesses sont exprimées en longueur de corps s^{-1}) (Castro-Santos 2005).

$$U_{opt} = U_f - \frac{1}{b} \tag{4}$$

Ainsi, il est possible de remplacer le terme U_S de l'équation 3 par la vitesse optimale définie à l'équation 4 afin de déterminer la distance maximale pouvant être parcourue par un omble de fontaine de 6 cm pour une vitesse moyenne donnée en utilisant l'équation suivante (Castro-Santos 2005) :

$$D_g = \left[\left(U_f - {}^{1}\!/_{b}\right) - U_f\right] \times e^{a+b\left(U_f - {}^{1}\!/_{b}\right)} \tag{5}$$

où tous les paramètres de vitesse sont exprimés en longueur de corps s^{-1} et la distance obtenue en longueur de corps.

Une fois cette vitesse optimale estimée, le modèle calcule la distance maximale de remontée de l'individu et compare celle-ci avec la longueur de la barrière de vitesse donnée, en l'occurrence un ponceau. Si le poisson peut parcourir une distance supérieure à la longueur du ponceau avant de se fatiguer, le modèle théorique prédit un succès de passage pour cet individu. Dans le cas contraire, il prédit un échec.

Libre-passage du poisson, un phénomène complexe

Le passage des poissons dans les ponceaux constitue un phénomène complexe, ayant cours autant à des échelles spatiales que temporelles et influencé par des facteurs physiques et biologiques. Bien que les obstacles naturels tels les seuils, les chutes et les zones où les vitesses d'écoulement sont élevées contribuent également à fragmenter certaines portions de cours d'eau, les obstacles d'origine anthropique comme les ponceaux sont nombreux et largement distribués sur le territoire. Une meilleure compréhension de la capacité des espèces aquatiques à franchir les ponceaux est primordiale afin de concevoir et d'installer des structures perméables à leurs mouvements.

Malgré le fait que plusieurs études se soient intéressées au passage des poissons dans les ponceaux, les divers critères régissant la capacité des poissons à franchir ces structures ne sont pas encore pleinement connus et compris. La capacité de nage, par exemple, constitue un critère biologique d'importance pour déterminer le succès de passage d'un individu donné. Malheureusement, il existe peu d'études qui fournissent des données quantitatives sur la performance de nage en sprint des poissons et cette lacune est problématique pour la conception des passes migratoires et des ponceaux (Haro et al. 2004). De plus, lorsque des données décrivant la capacité de nage globale d'une espèce de poisson existent, elles proviennent habituellement d'expériences menées dans des environnements contrôlées de laboratoire et elles sont difficilement applicables, sur le terrain, à la détermination de la capacité de passage du poisson dans un ponceau (Castro-Santos, 2004, Coffman, 2005, Gardner, 2006). Il existe donc un important besoin d'obtenir, en conditions naturelles, les données permettant de modéliser la capacité biologique des poissons à franchir les ponceaux. Ce besoin est particulièrement important pour l'omble de fontaine, espèce présente sur une grande proportion du territoire et donc susceptible d'être grandement affectée par les ponceaux.

Il n'existait pas, jusqu'à récemment, de méthodes efficaces pour obtenir en conditions naturelles les données nécessaires à la modélisation de la capacité des poissons à franchir les ponceaux. Ces données devraient idéalement fournir des informations en continu sur les tentatives de passage de chacun des individus à l'étude, afin de suivre leur progression à l'intérieur d'un ponceau sous différentes conditions hydrauliques, ceci afin de déterminer non seulement le succès de passage du poisson mais également sa vitesse de nage au sol, le moment où il se fatigue et l'endroit dans le ponceau où il rebrousse chemin dans le cas d'un échec. Les techniques de marquage-recapture, par exemple celles utilisant des implants visibles d''élastomère (VIE-tag; Northwest Marine Technology) ou des marques sur les nageoires permettent de déterminer si des individus ont franchi un ponceau, mais sans connaissance exacte du moment. La détermination des conditions hydrauliques dans le ponceau au moment où l'individu l'a franchi est donc difficile. Des développements récents dans la technologie des transpondeurs passifs intégrés (PIT-tags) permettent dorénavant d'obtenir des données en continu sur les tentatives de passage de poissons de différentes tailles dans des ponceaux (Connolly *et al.*, 2008, Solcz, 2007). Couplée à des mesures directes des conditions hydrauliques ayant cours dans le ponceau au moment des tentatives de passage, une telle approche permettra d'accroître les connaissances sur la façon dont les salmonidés se déplacent à l'intérieur des structures routières et sur les facteurs régissant leur capacité à les franchir.

3 OBJECTIFS DE RECHERCHES

La thèse a comme objectif principal de mieux comprendre les facteurs qui régissent la capacité de l'omble de fontaine (*Salvelinus fontinalis*) à franchir les ponceaux. Afin d'atteindre cet objectif, plusieurs populations d'omble de fontaine ainsi que différents ponceaux aux caractéristiques distinctes ont été considérés, à travers quatre objectifs spécifiques.

Le premier objectif consiste à développer et à tester une nouvelle approche utilisant la technologie des transpondeurs passifs afin de déterminer, en milieu naturel, la capacité de l'omble de fontaine à franchir les ponceaux. La réalisation de cet objectif est une prémisse à celle des objectifs suivants.

Le deuxième objectif consiste à comparer les observations obtenues grâce à la nouvelle approche avec les prédictions de passage de deux approches prédictives existantes.

Le troisième objectif est de déterminer quels facteurs influencent la motivation des ombles de fontaine à franchir les ponceaux. J'émets l'hypothèse que la motivation est un phénomène dynamique dans le temps et variable selon les individus. Il est d'autant plus important de mieux en saisir les nuances.

Le quatrième objectif réside dans l'élaboration d'un modèle prédictif du succès de passage des ombles de fontaine dans les ponceaux intégrant des variables biologiques (ex. âge, taille, facteur de condition), hydrauliques (ex. vitesse de l'eau, profondeur d'eau, etc.), structurale (ex. type de ponceau) et environnementales (ex. luminosité, température de l'eau).

Enfin, le cinquième et dernier objectif est de caractériser les trajectoires de remontée des ombles de fontaine dans les ponceaux, ceci afin d'apporter un éclairage «de l'intérieur» sur le comportement de nage des ombles lors de leurs tentatives de passage.

Subdivision de la thèse

Cette thèse est constituée de deux parties distinctes. La première partie, rédigée en français, comprend l'introduction au sujet de recherche, les objectifs, un résumé des travaux de recherche et des méthodes utilisées ainsi que d'une conclusion mettant en contexte l'ensemble des résultats obtenus et les avenues de recherches futures.

La deuxième partie est constituée des articles issus de la thèse. Ces articles sont rédigés en anglais et ont été soumis à des revues scientifiques pour fins de publication.

4 RÉSUMÉ DES TRAVAUX DE RECHERCHE

Cette section a pour but de résumer, en français, les travaux de recherches effectués dans le cadre du doctorat. Pour chaque objectif de la thèse, les méthodes seront présentées de façon succincte ainsi que les principaux résultats. Pour de plus amples informations, ainsi que pour avoir une discussion détaillée des résultats reliés aux objectifs 3, 4 et 5, il est recommandé de consulter les articles de la partie 2 du présent document.

1. Une nouvelle approche afin de déterminer, en milieu naturel, la capacité des poissons à franchir les ponceaux.

METHODES

Approche générale

L'approche générale consiste à utiliser la technologie des transpondeurs passifs intégrés (PIT-tags) afin d'étudier, sur le terrain, la capacité de l'omble de fontaine à franchir les ponceaux.

Les transpondeurs passifs sont constitués d'une antenne hélicoïdale et d'un circuit intégré et ne possède pas de pile interne. Il est possible d'attribuer au transpondeur un code unique (Prentice *et al.*, 1990). Une antenne externe produisant un champ électromagnétique est nécessaire pour énergiser le transpondeur et lui permettre de transmettre son code. Les transpondeurs passifs intégrés varient en dimensions et fonctionnent à des fréquences d'interrogations de 125 à 400 kHz selon deux modes de transmission distincts : le *full-duplex* et le *half-duplex*. Le premier mode émet et reçoit des signaux simultanément tandis que le deuxième le fait en alternance. Bien que plus lents, les systèmes *half-duplex* ont une portée de détection plus grande et consomment moins d'énergie. Dans la présente étude, les transpondeurs utilisés était de type *half-*

duplex, d’une dimension de 23 mm et d’un poids de 0.6 gr (Texas Instrument Inc., figure 3).

Figure 3: PIT-tag 23 mm. Source : Biomark

Les ombles ont été capturés par pêche à l’électricité, de 0 à 500 m en amont des ponceaux étudiés. Le transpondeur était ensuite inséré dans la cavité abdominale du poisson par une chirurgie effectuée sous anesthésie (figure 4). Après une période de récupération d’environ 12h, les ombles ont été relâchés dans une large cage fixée à l’extrémité aval du ponceau et libres d’effectuer des tentatives de passage ou de rester dans la cage pour une période de 48h. Certains essais de passage ont également été effectués sans cage, en relâchant simplement les ombles en aval du ponceau. La durée de ces essais était de 72h. Lorsque possible, trois ombles étaient gardés dans un vivier en tant que témoins.

Figure 4 : Marquage d’un omble de fontaine avec un transpondeur passif 23 mm (à gauche)

Figure 5: Antenne PIT-tag installée dans un ponceau (à droite)

Des antennes PIT-tags, installées à l'intérieur des ponceaux (figure 5) et interrogées de façon séquentielle par un système de contrôle fonctionnant à 125 kHz, permettaient de détecter en continu les tentatives de passage dans le ponceau des poissons marqués, avec une résolution temporelle de 1 seconde. Chaque système était composé de quatre antennes disposées au-dessus de l’eau et de quatre condensateurs, le tout relié à un module de contrôle et d’acquisition des données (Technologie Aquartis, module Quatro). Le système était alimenté en énergie par des batteries et un panneau solaire. Les données étaient enregistrées sur une carte mémoire de type flash et pouvaient ensuite être transférées vers un ordinateur personnel. Des systèmes fixes similaires ont été utilisés avec succès dans des passes migratoires (Castro-Santos *et al.*, 1996) ou des ponceaux expérimentaux (Ice *et al.*, 2009).

Mesures des variables environnementales et hydrauliques

La température de l’eau a été mesurée grâce à des thermographes déployés dans les cours d’eau, en amont des ponceaux à l’étude. La luminosité à l’intérieur des ponceaux n’a pas été quantifiée mais les heures de début et de fin de chaque période circadienne (aube, jour, crépuscule et nuit) ont été déterminées pour chaque essai en utilisant la calculatrice des levers et couchers de soleil du Conseil national de recherches du Canada (www.nrc-cnrc.gc.ca/fra/services/levers/).

Le niveau d’eau a été mesuré à chaque heure à l’aide d’une sonde de pression hydrostatique installée en amont des ponceaux. Le débit a été déterminé en se basant sur des courbes de tarage développées à partir des données de niveau d’eau et de mesures ponctuelles de débit faite avec un courantomètre. De plus, les profondeurs et vitesses d’écoulement ont été mesurées à plusieurs stations de mesure dans le ponceau lors de chaque essai de passage. Le protocole d’échantillonnage des données hydrauliques est décrit en détail dans Goerig et al. (2016).

Localisation des sites d'études

Les sites d'étude sélectionnés sont situés dans deux régions du Québec : le Saguenay Lac-Saint-Jean et Chaudières-Appalaches (figure 6). Les premiers ponceaux instrumentés en 2009 et 2010 étaient situés sur des tributaires de la rivière Sainte-Marguerite, au Saguenay, les ruisseaux Résimond, Allaire et Morin. Les ponceaux sont de type circulaire en métal ondulé (Résimond et Morin) et rectangulaire en béton armé (Allaire). En 2011, quatre nouveaux sites ont été instrumentés dans le secteur des Monts Valin, au Saguenay. Ces quatre ponceaux, tous de type circulaire en métal ondulé, étaient situés sur les ruisseaux Saumons, des Femmes, Adolphe et Raquette, des tributaires de la rivière Saint-Louis. Durant la même période, deux ponceaux circulaires en béton armé ont été instrumentés en Chaudières-Appalaches, sur des tributaires des rivières Palmer et Bagot, elles-mêmes tributaires directs de la rivière Bécancour. Ces deux ponceaux ont aussi été utilisés en 2012.

Figure 6: Sites d'étude : les ponceaux Résimond, Morin, Palmer et Allaire

RESULTATS

Les tentatives et les succès de passage de 1090 ombles de fontaine ont été enregistrés entre 2009 et 2012. L'approche choisie a été un succès dans son ensemble. Le seul problème rencontré fut un défaut de fonctionnement d'une carte mémoire et la perte des données de deux essais de passage, soit cinquante individus. La mortalité associée aux procédures de capture et marquage fut faible, avec seulement 8 mortalités durant la procédure de marquage (sur 1098) et 5 mortalités sur les 77 ombles témoins.

L'alimentation en énergie solaire des systèmes à transpondeurs passifs a été suffisante. Je recommande toutefois deux panneaux solaires branchés en parallèle pour une utilisation en période automnale.

Les étendues de détection des antennes variaient entre 20 et 50 cm et étaient optimisées avant chaque essai de façon à couvrir la totalité de l'épaisseur d'eau dans le ponceau. L'efficacité de détection était de 97% pour les antennes 1, 2 et 3. Bien qu'il soit impossible d'obtenir un chiffre exact pour l'antenne 4, nous pouvons assumer une efficacité élevée (Goerig *et al.*, 2016).

DISCUSSION

L'approche utilisée permet de recueillir des données en continu sur la performance de passage des poissons dans des ponceaux existants, tout en mesurant en parallèle les variables hydrauliques et environnementales. Cette approche permet de quantifier l'effet de ces variables sur la motivation des poissons à franchir les ponceaux d'une part, et sur leur succès de passage d'autre part. En ce sens, elle diffère de d'autres méthodes plus indirectes (marquage-recapture, marqueurs génétiques) qui permettent d'inférer le passage, mais sans détails sur les conditions qui prévalaient lors de celui-ci. Finalement, la méthode développée peut facilement s'adapter à d'autres espèces.

2. Comparaison des observations de terrain avec les prédictions de deux modèles de passage existants

Référence : Rapport de recherche publié dans la collection *Études et recherches en transports. Environnement* (Goerig *et al.*, 2014)é

Ce rapport peut être téléchargé grâce au lien suivant :

http://www.cubiq.ribg.gouv.qc.ca/in/faces/details.xhtml?id=p%3A%3Ausmarcdef_0001179352&highlight=omble+de+fontaine&posInPage=0&bookmark=4a579b93-6a70-4d78-b792-ecc0a7087efa&queryid=fa90d4fc-0693-4f72-9915-8428bd02f63f)

MÉTHODES

Les données brutes de mouvements pour chacun des ombles ont été importées dans le logiciel Access et organisées selon une structure hiérarchique composée des niveaux suivants : présence à une antenne, tentative et succès de passage. Un intervalle de plus de 1 s entre une série de détections pour le même individu était nécessaire pour incrémenter le nombre de présence à une antenne donnée. Une tentative était définie comme un mouvement vers l'amont débutant à l'antenne 1, située à l'extrémité aval du ponceau. Un intervalle de 30 secondes entre deux présences à l'antenne 1 était nécessaire pour qu'une nouvelle tentative soit considérée. Cette valeur a été définie de façon empirique en observant la distribution des intervalles entre les détections pour chaque individu, suivant la méthode décrite dans Castro-Santos *et al.*, (2013).

Des prédictions de succès de passage ont été effectuées avec le logiciel FishXing pour chaque individu testé dans les essais de passage. Les poissons n'ayant pas effectué de tentatives de passage n'ont pas été considérés dans cette analyse. Les prédictions ont été faites avec les paramètres standards du logiciel, sans utiliser de facteurs de correction de la vitesse moyenne de l'écoulement, et en utilisant les données de capacité de nage pour l'omble de fontaine provenant des travaux de Peake *et al.* (1997).

Des prédictions de passage ont également été produites en se basant sur l'approche de Castro-Santos (2005), qui assume que les poissons vont adopter une vitesse de nage visant à optimiser la distance parcourue lors de la traversée d'une zone caractérisée par de fortes vitesses d'écoulement. L'approche a utilisé les données de capacité de nage provenant de Peake et al (1997) et celles de (Castro-Santos *et al.*, 2013), obtenues respectivement dans un respiromètre et dans un canal ouvert de plus grandes dimensions.

Ces prédictions ont été comparées avec les observations de tentatives et de passage obtenues sur le terrain en utilisant des matrices de confusion évaluant la correspondance entre les prédictions et les observations.

RÉSULTATS

La performance des approches prédictives de passage est variable. Dans cette section, seule la performance globale est indiquée. Celle-ci varie toutefois en fonction du type de ponceau et est généralement meilleure pour les ponceaux lisses. Pour une description détaillée de cette analyse, il est conseillé de consulter le rapport de Goerig et Bergeron (2014). Il est également à noter que nous comparons ici l’issue d’une tentative de passage (succès ou échec) et non la distance maximale de remontée.

Le logiciel FishXing se révèle la moins performante des trois approches pour prédire le succès de passage, avec un taux de prédictions correctes de 40% (Tableau 1). Les prédictions incorrectes sont toutes des sous-estimations du succès de passage.

Tableau 1: Matrice de confusion pour l'ensemble des individus testés. Approche de FishXing.

PONCEAUX RUGUEUX ET LISSES
N = 344

	Observations		
Prédictions	Succès	Échec	Total
Succès	3	0	3
Échec	208	133	341
Total	211	133	344

Prédictions correctes:	40%		
Prédictions incorrectes:	60%	(sur-estimations):	0%
		(sous-estimations):	100%

Note : La modélisation a été effectuée avec les individus testés de 2009 à 2011. Des prédictions de passage n'ont par ailleurs pu être effectuées pour un ponceau à l'étude car le logiciel échouait à modéliser correctement les conditions hydrauliques pour ce site.

L'approche de Castro-Santos (2005) a un taux de classification correcte variant de 60 à 63%, selon les données de capacité de nage utilisées (Tableaux 2 et 3). Dans le cas des données de Peake et al (1997), les prédictions incorrectes sont à 75% des sous-estimations du succès de passage tandis qu'avec les données de Castro-Santos et al. (2013), elles sont à 64% des surestimations. Les données de capacité de nage obtenues pour l'omble de fontaine dans un canal expérimental révèlent une capacité de nage beaucoup plus élevée que celle décrite par les études précédentes. Toutefois, lors du passage d'un ponceau, certains ombles n'atteindront pas la limite supérieure de leur capacité et ce, pour des raisons comportementales. Par exemple, ils pourront échouer à optimiser leur vitesse de nage. Leur succès de passage peut donc être surestimé.

Tableau 2: Matrice de confusion pour l'ensemble des individus testés. Approche de Castro-Santos (2005), avec les données de capacité de nage de Peake et al., (1997)

PONCEAUX RUGUEUX ET LISSES

N = 532

	Observations		
Prédictions	Succès	Échec	Total
Succès	94	54	148
Échec	159	225	384
Total	253	279	532

Prédictions correctes:	60%		
Prédictions incorrectes:	40%	(sur-estimations):	25%
		(sous-estimations):	75%

Tableau 3: Matrice de confusion pour l'ensemble des individus testés. Approche de Castro-Santos (2005), avec les données de capacité de nage de Castro-Santos et al. (2013)

PONCEAUX RUGUEUX ET LISSES

N = **532**

	Observations		
Prédictions	Succès	Échec	Total
Succès	190	127	317
Échec	71	144	215
Total	261	271	532

Prédictions correctes:	63%		
Prédictions incorrectes:	37%	(sur-estimations):	64%
		(sous-estimations):	36%

DISCUSSION

Sur les trois approches évaluées, deux sont spécifiques et une est sensible. D'entrée de jeu, FishXing est très peu performant et sa présentation sous forme de logiciel peut rendre son utilisation difficile car l'utilisateur ne dispose pas de contrôle sur toutes les étapes de la modélisation. Il a toutefois l'avantage de permettre la modélisation des conditions hydrauliques lorsque le débit et les caractéristiques du ponceau sont disponibles. À la lumière des résultats précédents, son utilisation pour prédire la capacité de passage de l'omble de fontaine dans les ponceaux est discutable. Il serait toutefois intéressant de refaire la modélisation en utilisant les données de capacité de nage provenant des travaux de Castro-Santos et al (2013). Comme ces données sont susceptibles de mieux représenter la capacité de nage réelle de l'espèce, il est possible que la puissance prédictive de FishXing s'élève.

L'approche de Castro-Santos (2005) peut être utilisée avec les données de capacité de nage provenant des travaux de Peake et al. (1997) et de Castro-Santos et al. (2013) peuvent être utilisées, en gardant en mémoire leur propension respective à sous-estimer et surestimer la capacité de passage. Cela dépend des objectifs et du coût associé aux erreurs de prédiction. Ainsi, si l'objectif est de déterminer si une structure est impassable (par exemple afin de bloquer une espèce envahissante), le données de

Castro-Santos et al. (2013) sont préférables car elles produisent peu de cas «faux négatifs». Dans le cas où l'objectif est de déterminer si un ponceau est passable sous une gamme de conditions hydrauliques, les deux sont acceptables. Les données de Castro-Santos et al. (2013) offrent toutefois l'avantage de se baser sur des estimés de la capacité de nage provenant de conditions plus proche des conditions naturelles. Leur utilisation est également plus simple et ne nécessite pas de données sur la température de l'eau. Dans les deux cas, il est possible de modéliser, pour une gamme de longueurs d'ombles, des longueurs de ponceaux acceptables pour différentes vitesses d'écoulement.

Ces approches estiment la capacité physiologique de l'omble de fontaine à franchir une barrière de vitesse d'écoulement. L'approche utilisant la vitesse de nage optimale établit le seuil supérieur de performance pour l'omble de fontaine. Certaines barrières sont d'ordre physique, mais également comportemental. Il y aura donc toujours une proportion d'individus qui, bien qu'ayant la capacité physique requise, ne franchiront pas le ponceau. Cette proportion variera selon les populations, mais aussi en fonction de différents facteurs reliés au ponceau ou aux conditions environnementales.

3. Motivation des ombles à franchir les ponceaux

Référence : Partie 2, article 1

MÉTHODES

Les données sur les tentatives de passage recueillies avec les systèmes à transpondeurs passifs intégrés ont été analysées selon une approche statistique considérant le temps avant l'occurrence d'un événement (*time-to-event* ou *survival analysis*), décrite dans Allison (2014) et Castro-Santos *et al.* (2012). La fréquence des tentatives a été choisie pour représenter un index de la motivation des ombles à franchir le ponceau. Afin de pouvoir considérer les fluctuations dans le temps de certaines variables explicatives, seules les données comportant des mesures fréquentes du débit et de la température de l'eau ont été considérées.

Les données brutes ont été organisées de façon à identifier le début et la fin de chaque intervalle de temps avant une tentative de passage et ce, pour chaque valeur donnée des variables explicatives considérés dans l'analyse. Ainsi, si la température de l'eau variait trois fois durant l'intervalle avant la première tentative d'un individu, cet intervalle était divisé en trois parties comportant chacune un temps de début et de fin. Tous les ombles étaient considérés disponibles pour faire une tentative de passage dans l'analyse. Toutefois, ceux n'ayant pas effectué de tentative au terme de l'essai de passage étaient identifiés comme des données tronquées (*censored data*). L'effet de différentes variables (débit, température de l'eau, moment du jour, nombre de poissons dans la cage, longueur du poisson, période de reproduction) sur la fréquence des tentatives a été déterminé avec la régression de Cox, dans une approche mixte. Les effets fixes résidaient dans les variables explicatives (certaines statiques, d'autres fluctuant dans le temps) tandis que les effets aléatoires étaient constitués du cours d'eau d'origine ainsi que de l'individu. Ces effets aléatoires imbriqués ont permis de prendre en compte la dépendance statistique entre les observations d'ombles provenant du même cours d'eau et entre les événements étant le fait du même individu (ex. : tentatives multiples).

Le succès de passage des ombles a ensuite été modélisé avec une approche logistique mixte. La taille du poisson ainsi que la motivation de celui-ci ont été inclus comme effets fixes. Le degré individuel de motivation a été quantifié en utilisant les coefficients estimés pour les effets aléatoires reliés aux individus dans le modèle sur la fréquence des tentatives. Un effet aléatoire a par ailleurs été inclus sur l'essai de passage, afin de prendre en compte la variabilité dans la performance due aux conditions de l'essai ainsi qu'aux caractéristiques du ponceau.

La sélection du meilleur modèle parmi une gamme de modèles candidats a été effectuée dans les deux cas en minimisant le critère d'information d'Akaike (AIC).

RÉSULTATS

Un total de 447 ombles a été inclus dans cette analyse, dont 254 ont effectué au moins une tentative de passage.

Un modèle candidat a été sélectionné en tant que meilleur modèle, avec un poids d'Akaike de 0.71. Le poids d'Akaike peut être interprété comme la probabilité que ce modèle soit le meilleur, compte tenu des données (Burham *et al.*, 2002). Ce modèle inclut plusieurs variables explicatives, soit la proximité de la période de reproduction, le débit, la longueur du poisson, le nombre de poissons en aval du ponceau et le moment du jour. La proximité de la reproduction, le débit et la taille du poisson augmente la fréquence des tentatives de passage chez les ombles. À l'inverse, un nombre croissant de poisson en aval du ponceau diminue la fréquence des tentatives. Les tentatives sont par ailleurs plus fréquentes au crépuscule et diminuent durant le jour.

Les effets aléatoires inclus dans le modèle indiquent que la fréquence des tentatives varie selon le cours d'eau d'origine des ombles ainsi que selon chaque individu. La distribution des coefficients estimés pour l'effet aléatoire sur les individus indique que la motivation est variable selon les ombles, certain possédant une fréquence de tentative plus élevé que la moyenne alors que d'autres se situe en-dessous de celle-ci. Ces derniers inclut notamment les individus n'ayant pas effectué de tentative de passage.

DISCUSSION

La motivation à franchir les ponceaux se révèle être un phénomène complexe, variable dans le temps et entre les individus. Ses liens avec le succès de passage demeurent d'un grand intérêt. Dans le modèle de passage sélectionné, une fois les autres facteurs influençant la performance pris en compte, la motivation a un effet positif sur la probabilité de franchir avec succès le ponceau.

Une meilleure compréhension des facteurs qui affectent la motivation des ombles à franchir les ponceaux est essentielle pour la conception de nouvelles structures qui stimuleront la motivation, tout en assurant le passage.

4. Performance de passage des ombles dans les ponceaux

Référence : Partie 2, article 2

MÉTHODES

Les données de tentatives et de succès de passage recueillies en utilisant l'approche développée dans le premier objectif de la thèse ont été analysées avec une approche logistique. Une gamme de modèles candidats a été développée en se basant sur certains critères spécifiques afin de minimiser le nombre de modèles possibles. Ces modèles étaient composés de combinaisons raisonnables de variables explicatives susceptibles d'avoir un effet sur le succès de passage, telles que le rayon hydraulique, la pente et le type de ponceau, la vitesse moyenne de l'écoulement, la profondeur de la fosse en aval, la température de l'eau, la proximité de la période de reproduction et la longueur du poisson. La sélection du meilleur modèle s'est basée sur la minimisation du critère d'information d'Akaike.

La puissance prédictive du modèle sélectionné a été évaluée en effectuant une validation croisée utilisant les même données ayant servies à développer le modèle.

Elle a aussi été évaluée en utilisant des données de tentatives et succès de passage d'ombles relâchés librement en aval des ponceaux. Dans les deux cas, le degré de correspondance entre les probabilités de passage prédites par le modèle et les observations a été quantifié grâce au R^2 de Tjur et à la statistique *c*. Cette dernière est équivalente à l'aire sous la courbe ROC (*Receiver Operator Characteristic curve*), obtenue en considérant la spécificité et la sensibilité du modèle.

RÉSULTATS

Sur les 1090 ombles testés, 532 ont effectué au moins une tentative et ont été considérés dans l'analyse logistique.

Parmi les 208 modèles candidats, un modèle a été sélectionné comme ayant un bon ajustement aux données tout en étant parcimonieux. Ce modèle a un poids d'Akaike de 0.87 et une différence d'AIC de 3.9 avec son plus proche concurrent. Outre son ordonnée à l'origine, il est composé initialement de sept paramètres : la température de l'eau et son terme quadratique, le type de ponceau, la pente du ponceau, la vitesse moyenne de l'écoulement, la profondeur de la fosse en aval et la durée de l'essai. Un huitième paramètre a été ajouté a posteriori, soit une interaction entre la longueur du poisson et le type de ponceau. La probabilité de passage est plus élevée dans les ponceaux de tôle ondulée comparativement aux ponceaux lisses et ce, particulièrement pour les petits ombles. Elle est également plus élevée lorsque la température de l'eau s'élève durant les essais plus longs. Cette probabilité diminue avec une augmentation de la vitesse moyenne de l'écoulement, de la pente du ponceau et de la profondeur de la fosse en aval de celui-ci.

La puissance prédictive du modèle sélectionné est élevée, autant au terme de la validation croisée que lors de la validation avec les données provenant des poissons relâchés librement en aval du ponceau. La statistique *c* varient entre 0.87 et 0.94, ce qui signifie que la puissance prédictive du modèle est excellente (Hosmer *et al.*, 2013). Dans cette validation, le point de coupure pour passer d'une prédiction d'échec à une prédiction de succès se situait à une probabilité de 0.82. Cette valeur était celle optimisant simultanément la spécificité et la sensibilité du modèle (Allison, 2012).

Ce modèle, développé à partir de données provenant de plusieurs populations d'ombles de fontaine situées dans des bassin-versants distincts, possède la robustesse nécessaire pour être utilisé pour prédire la probabilité de passage de l'omble de fontaine dans les ponceaux.

5. Comportement et trajectoires de nage dans les ponceaux

Référence : Partie 2, article 3

MÉTHODES

Afin de caractériser le comportement et les trajectoires de nage des ombles de fontaine dans les ponceaux, des ombles ont été relâchés individuellement dans un ponceau de métal ondulé alors qu'une caméra installée hors de l'eau enregistrait leur tentatives de passage dans une zone d'environ 2 x 2 m.

La position de chaque omble dans le ponceau a ensuite été numérisée à une fréquence de 0.3 s, de façon à reconstituer leur trajectoire de nage. L'occurrence de périodes d'arrêt a également été enregistrée.

Les conditions hydrauliques dans la zone visible de la caméra ont été mesurées à plusieurs stations avec un courantomètre à hélice (Swoffer 3000). Les données de vitesses et de profondeurs d'écoulement ont ensuite été interpolées sur une grille de 1 cm, en utilisant le logiciel Tecplot.

Les trajectoires des ombles ont été superposées à la distribution des vitesses et des profondeurs d'écoulement, de façon à déterminer les conditions sélectionnées par les ombles durant leurs tentatives.

Un ratio entre la vitesse d'écoulement sélectionnée durant la remontée du ponceau et la vitesse moyenne de l'écoulement dans la structure a été calculé pour chaque omble. Le ratio de préférence d'écoulement a été analysé avec un modèle linéaire mixte. Ce modèle incluait la vitesse moyenne de l'écoulement, la profondeur moyenne de l'écoulement et la longueur du poisson comme effets fixes, ainsi que l'essai de passage comme effet aléatoire.

Le temps de transit dans la zone couverte par la caméra a également été calculé pour chaque omble.

RÉSULTATS

Cinq essais de passage ont été effectués, pour un total de 148 ombles testés. Plus de la moitié des individus ont effectué une tentative de passage, soit 84. Seize d'entre eux ont été observés pendant des périodes de repos dans le ponceau.

La vitesse moyenne de l'écoulement variait entre 0.3 et 0.65 m s^{-1} tandis que la profondeur moyenne variait de 0.05 à 0.20 m. La température est demeurée constante à 12 °C.

Durant leurs tentatives, les ombles ont majoritairement sélectionné des vitesses d'écoulement entre 0.25 et 0.5 m s^{-1} et des profondeurs entre 0.05 et 0.30 m. Pour tous les essais excepté un, les ombles ont choisi des vitesses d'écoulement plus élevées que la vitesse moyenne de l'eau dans le ponceau. Dans le troisième essai, toutefois, ils ont choisi des vitesses d'écoulement moindres, principalement localisées le long des parois du ponceau. Cet essai était celui ayant la plus forte vitesse moyenne de l'écoulement (0.63 m s^{-1}).

Un modèle a été sélectionné dans le cadre de l'analyse sur le ratio de préférence d'écoulement. Le modèle retenu inclut seulement la vitesse moyenne de l'écoulement comme variable explicative. Le ratio de préférence d'écoulement diminue lorsque la vitesse moyenne dans le ponceau augmente, ce qui indique que les ombles recherchent des zones de vitesses d'écoulement réduites durant leur tentative. La variance de l'effet aléatoire est faible, indiquant peu de variabilité entre les poissons testés dans des essais différents.

Enfin, le temps de transit est relativement similaire entre les essais, avec toutefois quelques individus ayant des temps de transit élevé. Ces observations correspondent aux ombles ayant effectué des arrêts dans le ponceau. Ce comportement n'est toutefois pas visible dans l'essai avec la plus forte vitesse d'écoulement.

5 CONCLUSION

Beaucoup d'études ont abordées la question du libre-passage des poissons dans les ponceaux, autant d'un point de vue hydraulique que biologique et ce, pour diverses espèces. Les salmonidés sont bien représentés dans ces études, dû à leur valeur économique et sociale, mais aussi parce qu'ils occupent souvent les cours d'eau à fort gradient, où les vitesses d'écoulement dans les ponceaux sont susceptibles de constituer une barrière à leurs mouvements.

La présente thèse avait pour objectif principal de mieux comprendre la capacité d'une seule espèce, l'omble de fontaine, à franchir les ponceaux. Son originalité repose en partie sur l'approche holistique utilisée, où la capacité de passage relève à la fois d'éléments comportementaux et physiologiques, tout en considérant l'effet de variables hydrauliques et environnementales sur ceux-ci. L'échelle de l'étude, comprenant plusieurs ponceaux et populations d'ombles de fontaine situés dans des bassins-versant distincts, est également peu courante dans la littérature. Cette échelle est un atout pour la robustesse des résultats de la thèse.

Le premier objectif de celle-ci visait à développer une méthode permettant de recueillir, en milieu naturel, des données sur la capacité de l'omble de fontaine à franchir les ponceaux. Cette méthode, inspirée de méthodes existantes et principalement basée sur la technologie des transpondeurs passifs intégrés, a été fructueuse et peut s'appliquer directement à d'autres espèces. L'utilisation d'une cage en aval du ponceau a par ailleurs permis de recueillir une quantité appréciable de données en peu de temps, ce qui a permis l'étude d'individus provenant de plus d'une population, sous une large gamme de conditions hydrauliques et environnementales.

La comparaison des données recueillies dans le cadre de la thèse avec les prédictions provenant de modèles de passage existants mène à deux conclusions : la capacité de passage est soit sous-estimée parce que les données de capacité de nage utilisées dans ces modèles sous-estiment la capacité de nage réelle de l'espèce, soit surestimée parce que l'approche utilisée assume que les poissons démontrent un comportement de nage optimal, ce qui n'est pas toujours le cas dans la réalité.

Différents éléments comportementaux peuvent entrer en ligne de compte et influencer le degré de motivation d'un omble à franchir un obstacle. Le troisième objectif, qui résidait dans la modélisation de la motivation à franchir les ponceaux, a révélé un phénomène complexe et dynamique dans le temps. La motivation est variable temporellement, en partie parce qu'elle est influencée par des facteurs qui varient eux-mêmes dans le temps (débit, reproduction, périodes circadiennes). Elle est également variable entre les poissons provenant de cours d'eau distincts et entre ceux d'un même cours d'eau. Le fait d'avoir pu quantifier l'effet des facteurs biologiques et environnementaux sur la fréquence des tentatives de passage des ombles constitue sans conteste une contribution majeure de la thèse.

Un degré de motivation plus élevé est garant d'une probabilité de succès plus élevée. Une fois entré dans le ponceau, d'autres facteurs influencent toutefois le succès de passage. Les analyses en lien avec le quatrième objectif de la thèse ont permis de quantifier l'effet de ces facteurs sur la probabilité de passage et donc de développer, à partir de données empiriques, un modèle prédictif de succès de passage de l'omble de fontaine dans les ponceaux. La puissance prédictive du modèle, lorsque validé avec les observations recueillies sur le terrain, s'est avéré excellente. Il pourra être utilisé lors de la conception de nouveaux ponceaux ou de la rénovation de structures existantes. Le développement de cet outil constitue une autre contribution d'importance de la thèse aux problématiques de connectivité des habitats fluviaux.

Un des éléments surprenant du modèle de passage développé est l'effet bénéfique des ponceaux de tôle ondulée sur le succès de passage, particulièrement pour les ombles de petite taille. Dans certaines circonstances, les poissons peuvent utiliser des stratégies d'économie d'énergie lors de leurs tentatives de passage, ce qui peut se traduire par une probabilité de passage élevée, même sous des conditions hydrauliques adverses. Le cinquième objectif de la thèse visait à documenter le comportement et les trajectoires de nage des ombles dans un ponceau de tôle ondulée. Bien que ces travaux aient été d'une ampleur moindre que ceux reliés aux autres objectifs, les résultats obtenus ont permis de déterminer que les ombles sélectionnent de façon préférentielle une certaine gamme de vitesses d'écoulement et qu'ils peuvent s'orienter rapidement dans le ponceau de façon à trouver ces conditions. Ce comportement ne semblait pas lié à la longueur des ombles. Certains individus, majoritairement d'une taille inférieure à 150 mm, ont toutefois utilisé les ondulations du ponceau pour effectuer des périodes d'arrêt lors de leurs tentatives de passage. La méthode développée pour recueillir ces données pourrait être utilisée, dans le futur, afin de documenter le comportement de nage d'un plus grand nombre d'individus et de raffiner les paramètres hydrauliques utilisés dans les modèles de passage.

Plusieurs avenues de recherche sont à considérer en ce qui concerne la capacité des poissons à franchir les ponceaux, notamment l'étude de la motivation et du succès de passage d'individus relâchés librement dans les cours d'eau, afin de supprimer l'éventuel biais induit par l'utilisation d'une cage de rétention. Par ailleurs, la variabilité individuelle dans la motivation des ombles à franchir les ponceaux est un élément à explorer. Cette variabilité, considérée en tant qu'effet aléatoire dans la thèse, peut éventuellement s'expliquer par différents facteurs tels l'histoire de vie ou les différences morphologiques entre les ombles. Ces facteurs, et leurs effets sur la motivation et le succès de passage, gagneraient à être quantifiés.

L'étude de ponceaux de longueurs supérieures à 45 m serait également une avenue à prendre en compte. La longueur du ponceau n'est pas incluse dans le modèle développé, mais vraisemblablement parce que les données recueillies se sont avérées insuffisantes pour détecter cet effet.

Le comportement de nage dans les ponceaux demeure un aspect incontournable des recherches futures. Une description détaillée de l'écoulement, des vitesses de progression et des trajectoires de nage dans les ponceaux apporterait les connaissances nécessaires pour quantifier les vitesses d'écoulement sélectionnées par les poissons et améliorer autant la puissance prédictive des modèles de passage que la conception des structures.

6 RÉFÉRENCES

Adams SB, Frissell CA & Rieman BE (2000) Movements of nonnative brook trout in relation to stream channel slope. *Transactions of the American Fisheries Society* 129(3):623-638.

Allison PD (2012) *Logistic Regression Using SAS: Theory and Application, Second Edition.* SAS Institute, SAS Institute Inc.

Allison PD (2014) *Event history and survival analysis.* SAGE, 2nd edition

Barber ME & Downs RC (1996) Investigation of culvert hydraulics related to juvenile fish passage.).

Bates K (2003) Design of Road Culverts for Fish Passage. Édit Wildlife WDOFA), p 1-53.

Behlke CE (1991) Power and energy implications of passage structures for fish. *American Fisheries Society Symposium* 10:289-298.

Behlke CE, Kane DL, McLean RF, Reynolds JB & Travis MD (1988) Spawning migration of Arctic grayling through Poplar Grove Creek culvert, Glennallen, Alaska, 1986.

Belford DA & Gould WR (1989) An Evaluation of Trout Passage through Six Highway Culverts in Montana. *North American Journal of Fisheries Management* 9(4):437-445.

Benton PD, Ensign WE & Freeman BJ (2008) The effect of road crossings on fish movements in small Etowah basin streams. *Southeastern Naturalist* 7(2):301-310.

Bjornn TC (1971) Trout and Salmon Movements in Two Idaho Streams as Related to Temperature, Food, Stream Flow, Cover, and Population Density.Transactions of the American Fisheries Society 100(3):423-438.

Blank M & Cahoon J (2009) Using three dimensional hydrodynamic modeling and fish swimming energetics to assess culverts as potential physical barriers to upstream fish movement. in *TRB Annual Meeting 09-2917*).

Blank MD (2008) *Advanced studies of fish passage through culverts: 1-d and 3-d hydraulic modeling of velocity, fish energy expenditure, and a new barrier assessment method.* MONTANA STATE UNIVERSITY,

Boubée J, Jowett I, Nichols S & Williams E (1999) Fish passage at culverts; A review, with possible solutions for New-Zealand indigenous species

Édit Department of Conservation W, New-Zealand (Manager,Science&Research unit, Science technology and Information Services, Department of Conservation).

Brett J (1964) The respiratory metabolism and swimming performance of young sockeye salmon. *Journal of the Fisheries Board of Canada* 21(5):1183-1226.

Burford DD, McMahon TE, Cahoon JE & Blank M (2009) Assessment of trout passage through culverts in a large Montana drainage during summer low flow. *North American Journal of Fisheries Management* 29:739-752.

Burham K & Anderson D (2002) Model Selection and Multivariate Inference: A Practical Information–Theoretical Approach. (Springer, New York).

Castro-Santos T (2004) Quantifying the combined effects of attempt rate and swimming capacity on passage through velocity barriers. *Canadian Journal of Fisheries and Aquatic Sciences* 61:1602-1615.

Castro-Santos T (2005) Optimal swim speeds for traversing velocity barriers: an analysis of volitional high-speed swimming behavior of migratory fishes. *J Exp Biol* 208(3):421-432.

Castro-Santos T, Haro A & Walk S (1996) A passive integrated transponder (PIT) tag system for monitoring fishways. *Fisheries Research* 28:253-261.

Castro-Santos T & Perry RW (2012) Time-to-Event Analysis as a Framework for Quantifying Fish Passage Performance. *Telemetry Techniques: a User Guide for Fisheries Research*, Adams NS, Beeman JW & Eiler JH (Édit.) American Fisheries Society, Bethesda, Maryland. p 427-452.

Castro-Santos T, Sanz-Ronda FJ & Ruiz-Legazpi J (2013) Breaking the speed limit comparative sprinting performance of brook trout (Salvelinus fontinalis) and brown trout (Salmo trutta). *Canadian Journal of Fisheries and Aquatic Sciences* 70(2):280-293.

Castro J (2003) Geomorphic impacts of culvert replacement and removal. Édit Office U-OFaWPortland, OR), p 19.

Chow VT (1959) *Open-channel hydraulics.* McGraw Hill Book Company,

Clark SP & Kehler N (2011) Turbulent flow characteristics in circular corrugated culverts at mild slopes. *Journal of Hydraulic Research* 49(5):676-684.

Coffman JS (2005) *Evaluation of a predictive model for upstream fish passage through culverts*. Master (James Madison University). 103 p(Consulté le May 2005)

Connolly PJ, Jezorek IG, Martens KD & Prentice EF (2008) Measuring the performance of two stationary interrogation systems for detecting downstream and upstream movement of PIT-tagged salmonids. *North American Journal of Fisheries Management* 28(2):402-417.

Curry RA, Allen S, Fox MG & Morgan GE (1993) Growth and food of young-of-the-year brook charr, Salvelinus fontinalis, in lake and creek environments. *Environmental Biology of Fishes* 37(2):131-138.

Erkinaro J & Gibson RJ (1997) Interhabitat migration of juvenile Atlantic salmon in a Newfoundland river system, Canada. *Journal of Fish Biology* 51(2):373-388.

Erkinaro J, Julkunen M & Niemelä E (1998) Migration of juvenile Atlantic salmon Salmo salar in small tributaries of the subarctic River Teno, northern Finland. *Aquaculture* 168(1-4):105-119.

Erkinaro J & Niemelä E (1995) Growth differences between the Atlantic salmon parr, Salmo salar, of nursery brooks and natal rivers in the River Teno watercourse in northern Finland. *Environmental Biology of Fishes* 42(3):277-287.

Fausch KD, Torgersen CE, Baxter CV & Li HW (2002) Landscapes to Riverscapes: Bridging the Gap between Research and Conservation of Stream Fishes. *BioScience* 52(6):483-498.

Fitch MG (1995) Nonanadromous Fish Passage in Highway Culverts. Édit Transportation VDO), p 1-18.

Forman RT & Alexander LE (1998) Roads and their major ecological effects. *Annual review of ecology and systematics*: 207-C202.

Furniss M, Love M, Firor S, Moynan K, Llanos A, Guntle J & Gubernick R (2008) FishXing, Version 3.0. US Forest Service, San Dimas Technology and Development Center, San Dimas, CA. *Also available at www. stream. fs. fed. us/fishxing*.

Gardner AN (2006) Fish passage through road culverts.

Gerking SD (1959) The restricted movement of fish populations. *Biological reviews* 34(2):221-242.

Gibson RJ, Haedrich RL & Wernerheim CM (2005) Loss of Fish Habitat as a Consequence of Inappropriately Constructed stream Crossings. *Fisheries* 30(1):10-17.

Goerig E & Bergeron NE (2014) Modélisation de la capacité de l’omble de fontaine (Salvelinus fontinalis) à franchir les ponceaux. . Édit Institut National De La Recherche Scientifique PLCDMDTDQQuébec), p 132 + annexes.

Goerig E, Castro-Santos T & Bergeron NÉ (2016) Brook trout passage performance through culverts. *Canadian Journal of Fisheries and Aquatic Sciences* 73(1):94-104.

Gowan C & Fausch KD (1996) Mobile brook trout in two high elevation Colorado streams: re-evaluating the concept of restricted movements. *Canadian Journal of Fisheries and Aquatic Sciences* 53:1370-1381.

Haro A, Castro-Santos T, Noreika J & Odeh M (2004) Swimming performance of upstream migrant fishes in open-channel flow: a new approach to predicting passage through velocity barriers. *Canadian Journal of Fisheries and Aquatic Sciences* 61:1590-1601.

Harper DJ & Quigley JT (2005) No net loss of fish habitat: a review and analysis of habitat compensation in Canada. *Environment Management* 36(3):343-355.

Hinch SG & Bratty J (2000) Effects of swim speed and activity pattern on success of adult sockeye salmon migration through an area of difficult passage. *Transactions of the American Fisheries Society* 129:598-606.

Hosmer DW, Lemeshow S & Sturdivant RX (2013) *Applied logistic regression.* John Wiley & Sons,

House MR, Pyles MR & White D (2005) Velocity distributions in streambed simulation culverts used for fish passage. *Journal of the American Water Resources Association* 41(1):209-217.

Hynes HBN & Hynes H (1970) *The ecology of running waters.* Liverpool University Press Liverpool,

Ice G & Peterson PN (2009) Assessing cutthroat passage through small culverts on steep slopes: phase 1- wild fish proof of concept. (Forest & Channel Metrics, Inc.), p 29.

Johnson GE, Pearson WH, Southard SL & Mueller RP (2012) Upstream Movement of Juvenile Coho Salmon in Relation to Environmental Conditions in a Culvert Test Bed. *Transactions of the American Fisheries Society* 141(6):1520-1531.

Kahler TH & Quinn TP (1998) Juvenile and resident salmonid Movement and Passage Through Calverts. Édit Washington State Department of Transportation and U.S DOT, Federal Highway Administration (Washington State Department of Transportation), p 1-46.

Kane DL, Behlke CE, Gieck RE & McLean RF (2000) Juvenile fish passage through culverts in Alaska: A field study.

Kemp PS, Gessel MH & Williams JG (2008) Response of downstream migrant juvenile Pacific salmonids to accelerating flow and overhead cover. *Hydrobiologia* 609:205-217.

Kondratieff MC & Myrick CA (2006) How High Can Brook Trout Jump? A Laboratory Evaluation of Brook Trout Jumping Performance. *Transactions of the American Fisheries Society* 135(2):361-370.

Langill DA & Zamora P (2002) An audit of small culvert installations in Nova Scotia: habitat loss and habitat fragmentation.

Larinier M (2002) Fish passage through culverts, rock weirs and estuarine obstructions. *Bulletin Français de la Pêche et de la Pisciculture* 364:119-134.

Letcher BH, Nislow KH, Coombs JA, O'Donnell MJ & Dubreuil TL (2007) Population Response to Habitat Fragmentation in a Stream-Dwelling Brook Trout Population. *PLoS ONE* 2(11):e1139.

Meyers LS, Thuemler TF & Kornely GW (1992) Seasonal movements of brown trout in northeast Wisconsin. *North American Journal of Fisheries Management* 12(3):433-441.

Morita K & Yamamoto S (2002) Effects of Habitat Fragmentation by Damming on the Persistence of Stream-Dwelling Charr Populations. *The Journal of the Society for Conservation Biology* 16(5):1318-1323.

Neary VS (2012) Binary Fish Passage Models for Uniform and Nonuniforms Flows. *River Research and Applications* 28(4):418-428.

Park D, Sullivan M, Bayne E & Scrimgeour G (2008) Landscape-level stream fragmentation caused by hanging culverts along roads in Alberta's boreal forest. *Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere* 38(3):566-575.

Peake S, McKinley RS & Scruton DA (1997) Swimming performance of various freshwater salmonids relative to habitat selection and fishway design. *Journal of Fish Biology* 51(3):710-723.

Peterson NP, Simmons RK, Cardoso T & Light JT (2013) A Probabilistic Model for Assessing Passage Performance of Coastal Cutthroat Trout through Corrugated Metal Culverts. *North American Journal of Fisheries Management* 33(1):192-199.

Powers PD, Bates K, Burns T, Gowen B & Whitney R (1997) Culvert hydraulics related to upstream juvenile salmon passage. Édit Wildlife WDOFA).

Prentice EF, Flagg TA, McCutcheon CS, Parker N, Giorgi A, Heidinger R, Jester Jr D, Prince E & Winans GA (1990) Feasibility of using implantable passive integrated transponder (PIT) tags in salmonids. *American Fisheries Society Symposium.* p 317-322.

Prévost L, Plamondon AP & Lévesque D (2002) Méthodologie pour évaluer l'effet de l'installation d'un ponceau sur le susbtrat des frayères de l'omble de fontaine (Salvelinus fontinalis). Édit Ministère Des Ressources Naturelles Du Québec, Société De La Faune Et Des Parcs Du Québec & Québec FDLFD), p 1-43.

Quinn GP & Keough MJ (2002) *Experimental design and data analysis for biologists.* Cambridge University Press, New York. 537 p

Richmond MC, Deng ZQ, Guensch GR, Tritico H & Pearson WH (2007) Mean flow and turbulence characteristics of a full-scale spiral corrugated culvert with implications for fish passage. *Ecological Engineering* 30(4):333-340.

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

Sanz-Ronda FJ, Ruiz-Legazpi J, Bravo-Córdoba FJ, Makrakis S & Castro-Santos T (2015) Sprinting performance of two Iberian fish: Luciobarbus bocagei and Pseudochondrostoma duriense in an open channel flume. *Ecological Engineering* 83:61-70.

Schlosser IJ (1991) Stream fish ecology: a landscape perspective. *Bioscience* 41(10):704-712.

Solcz AA (2007) *Assessment of culvert passage of Yellowstone cutthroat trout in a Yellowstone river tributary using a passive integrated transponder system*. Master (Montana State University, Bozeman). 63 p(Consulté le August 2007)

Thurman DR, Horner-Devine AR, Morrison RR & Hotchkiss RH (2007) Juvenile Salmon Passage in Sloped-Baffled Culverts.).

Torterotot J-B, Perrier C, Bergeron NE & Bernatchez L (2014) Influence of Forest Road Culverts and Waterfalls on the Fine-Scale Distribution of Brook Trout Genetic Diversity in a Boreal Watershed. *Transactions of the American Fisheries Society* 143(6):1577-1591.

Von Karman T (1931) *Mechanical similitude and turbulence*.

Warren ML & Pardew MG (1998) Road crossings as barriers to small-stream fish movement. *Transactions of the American Fisheries Society* 127(4):637-644.

Wofford JEB, Gresswell RE & Banks MA (2005) Influence of Barriers to Movement on Within-Watershed Genetic Variation of Coastal Cutthroat Trout. *Ecological Applications* 15(2):628-637.

Young MK (1998) Absence of autumnal changes in habitat use and location of adult Colorado River cutthroat trout in a small stream. *Transactions of the American Fisheries Society* 127(1):147-151.

Zwirn M (2002) Forest Road Contruction and Culvert Installations in Salmon Streams: Best Management Practices and Lessons for the Samarga Watershed. (The Wild Salmon Center), p 2-20.

PARTIE 2: ARTICLES

Article 1: Is motivation important for fish passage through culverts?

Titre en français : La motivation est-elle importante pour le passage des poissons dans les ponceaux?

La collecte de données et la rédaction de cet article ont été réalisées par Elsa Goerig. L'analyse et l'interprétation des résultats a été le fruit d'une étroite collaboration entre Elsa Goerig et Theodore Castro-Santos.

Elsa Goerig*[1] & Theodore Castro-Santos[2]
[1] INRS-Eau, Terre et Environnement, 490 rue de la Couronne, Québec, QC, GlK 9A9, Canada.
[2] USGS S.O. Conte Anadromous Fish Research Center. 1 Migratory way, Turners Falls (MA), 01376. USA
*Author to whom correspondence must be addressed
Present address :USGS S.O. Conte Anadromous Fish Research Center. 1 Migratory way, Turners Falls (MA), 01376. USA
Email: goerig.elsa@gmail.com

Accepté pour publication par *Canadian Journal of Aquatic and Fisheries Sciences (CJFAS)* le 22 septembre 2016

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.

Table 1: Study sites 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.

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 7). 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.

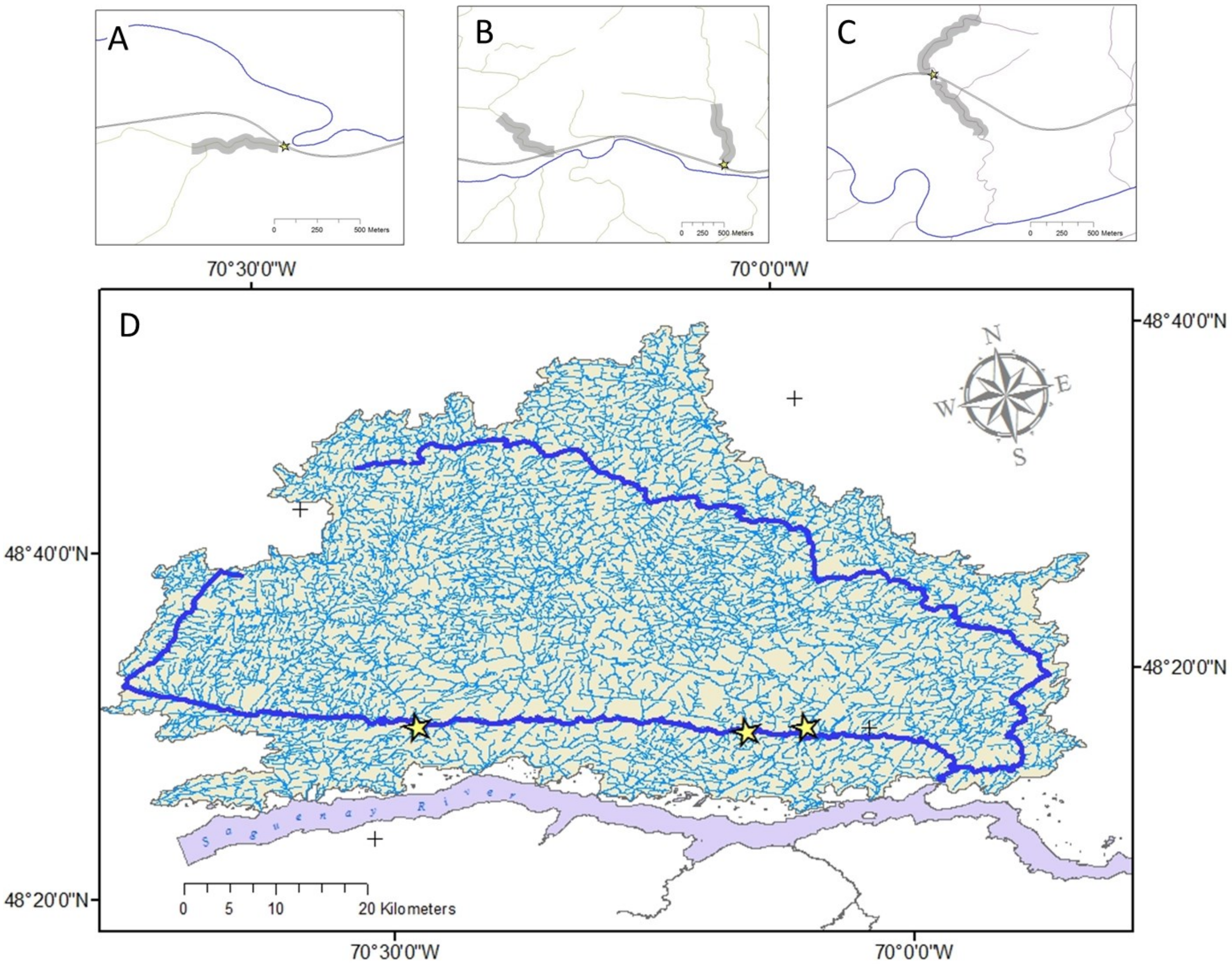

Figure 7: Study sites (stars) and their location within the Ste. Marguerite river watershed (Panel D). Details of studied culverts and collection locations (Tables 1 & 2) are shown in the upper panels (A: Résimond; B: Allaire; and C: Morin). Roads are shown as double-lines, and collection locations are 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.

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). The relationship between the discharge and the water level was strong for Résimond, Allaire and Morin stream, with coefficients of determination (R^2) of 0.86, 0.94 and 0.98, respectively. 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

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

$$b \sim G \ (0, \Sigma(\theta))$$

Where $\lambda_0 (t)$ 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 the b random effects G is modeled as Gaussian with a mean of 0 and a variance matrix Σ, 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:

$$(1)\quad AIC = -2\ log\ L + 2K$$

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).

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.

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 3). 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.

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.

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 8). 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.

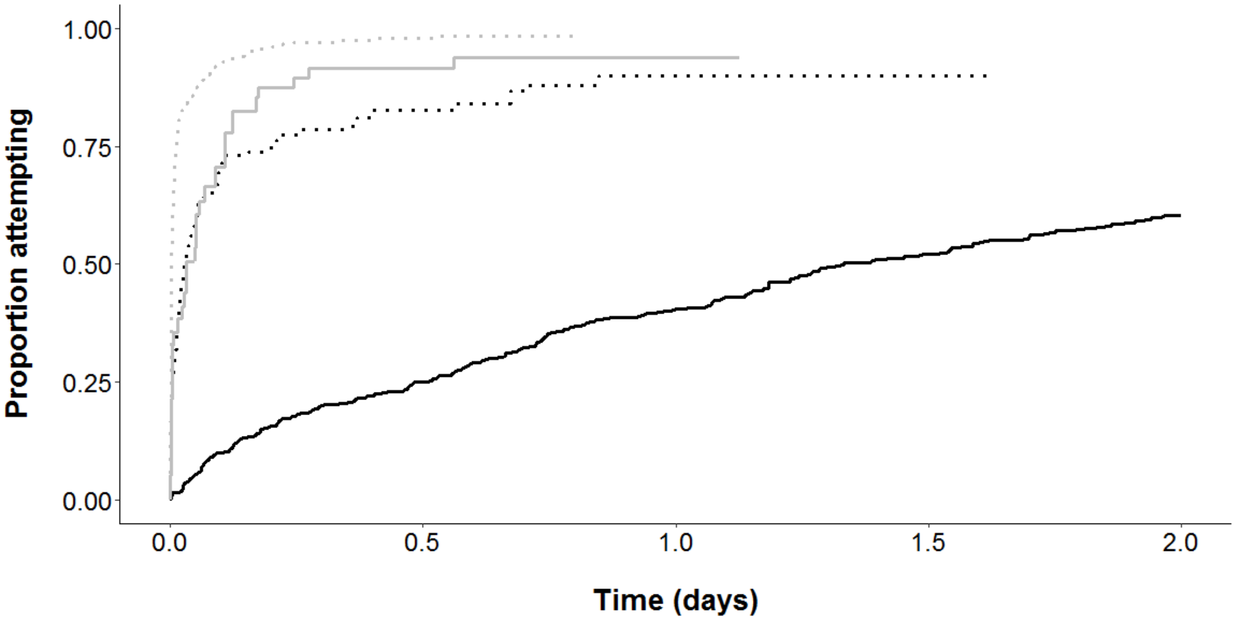

Figure 8: Cumulative incidence curves (1- empirical Kaplan-Meier curves) representing proportion of fish attempting to pass the culverts as a function of time. Data are stratified by attempts, the black curve representing the 1st attempts, the black dotted curve the attempts 2-5, the grey curve attempts 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.

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.

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 the data and w_i/w_j is the evidence ratio for model$_i$ versus model$_j$. Two models emerged from the model set as providing the best fit to the data. The first one, in bold, has an Akaike weight of 0.71. It is followed by a second model with a weigth of 0.26. The evidence ratio between these two models is 2.73, indicating evidence in favor of the first one (Burham and Anderson 2002).

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).

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.

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-^{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 9).

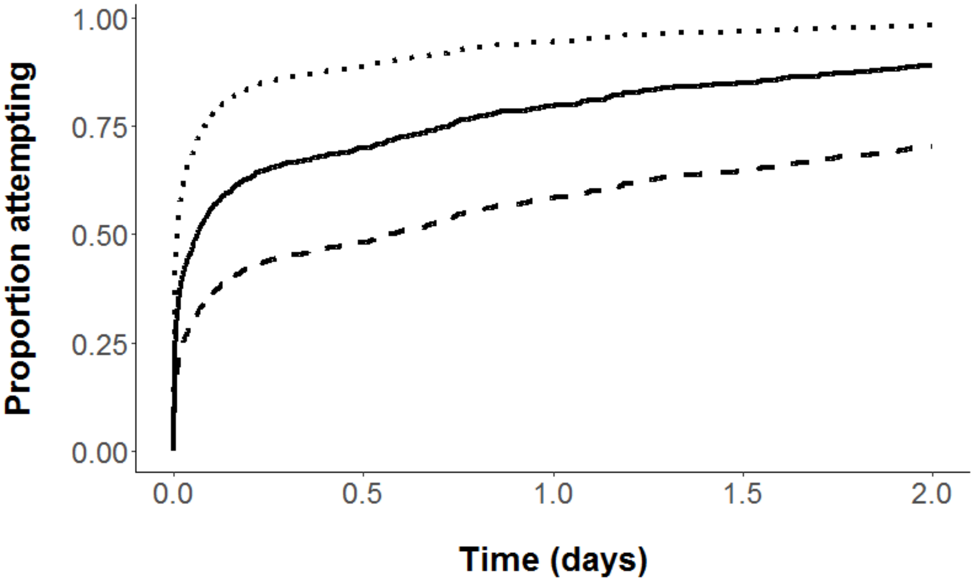

Figure 9: Proportion of fish attempting to pass the culvert as a function of time and flow discharge, modeled from the estimated Cox model. The attempt rate increases with higher values of discharge. Dashed line: 100 L s^{-1}; solid line: 300 L s^{-1} and dotted line: 500 L s^{-1}, which corresponds 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).

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, Table 5). 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 10).

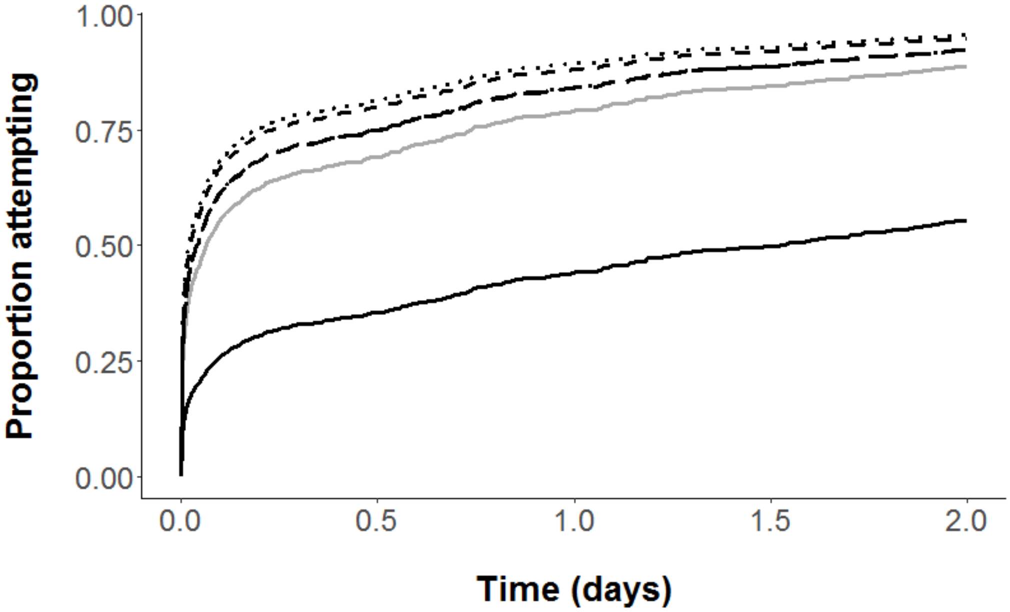

Figure 10: Proportion of fish attempting to pass the culvert as a function of time and stream of origin, modeled from the estimated Cox model. The curves represent the average attempt rate (solid grey line), fish from the stream Allaire (dotted line), Épinette (dashed line), Morin (dotdashed line), Morin 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.

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 11). 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).

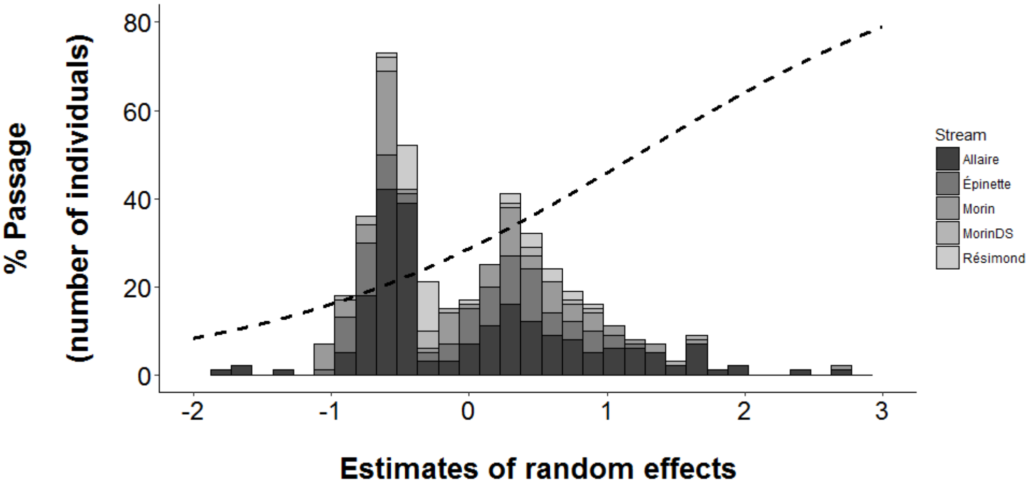

Figure 11: Estimates of random effect coefficients for individual fish in the Coxme model, as a function of stream of origin. The random effects coefficients are an index of the fish individual motivation. Each stream includes trout with low, average and high level of motivation. The dashed curve represents the predicted passage probability as a function of the fish motivation, as estimated by the logistic passage model.

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 6). 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 11). 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 mm increased the probability of success by ~ 1% (OR = 1.011, Table 6).

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 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.

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.

ACKNOWLEDGEMENTS

Support for this research was provided by INRS–Centre Eau, Terre et Environnement, the GRIL, the Ministère des Transports du Québec, and research scholarships to E.G. from Natural Sciences and Engineering Research Council of Canada and the Fonds de recherche Nature et Technologies du Québec. Any use of trade, product, or firm names is for descriptive purposes only and does not imply endorsement by the Canadian or US governments. We thank the research assistants who helped conduct the field work: A. Boivin, M.A. Pouliot, F. Bérubé, J.B. Torterotot and M. Fortin. We also extend special thanks to N. E. Bergeron for his input and guidance with the experimental design of the study, as well as to B.H. Letcher and R. W. Perry for their generous assistance with the analysis and the manuscript.

REFERENCES

Adams, S.B., Frissell, C.A., and Rieman, B.E. 2000. Movements of nonnative brook trout in relation to stream channel slope. Transactions of the American Fisheries Society **129**(3): 623-638.

Agostinho, C.S., Pereira, C.R., Oliveira, R.J.d., Freitas, I.S., and Marques, E.E. 2007. Movements through a fish ladder: temporal patterns and motivations to move upstream. Neotropical Ichthyology **5**: 161-167.Available from http://www.scielo.br/scielo.php?script=sci_arttext&pid=S1679-62252007000200010&nrm=iso.

Allison, P.D. 2014. Event history and survival analysis. SAGE.

Armstrong, J.D., and Herbert, N.A. 1997. Homing movements of displaced stream-dwelling brown trout. Journal of Fish Biology 50(2): 445-449. doi: 10.1111/j.1095-8649.1997.tb01372.x.

Barnard, C.J. 2004. Animal behavior: mechanism, development, function, and evolution. Pearson Education.

Barnard, C.J. 2012. Animal behaviour: ecology and evolution. Springer Science & Business Media.

Bunnell, D.B., Isely, J.J., Burrell, K.H., and Van Lear, D.H. 1998. Diel Movement of Brown Trout in a Southern Appalachian River. Transactions of the American Fisheries Society **127**(4): 630-636. doi: 10.1577/1548-8659(1998)127<0630:dmobti>2.0.co;2.

Burford, D.D., McMahon, T.E., Cahoon, J.E., and Blank, M. 2009. Assessment of trout passage through culverts in a large Montana drainage during summer low flow.

North American Journal of Fisheries Management **29**: 739-752. doi: 10.1577/M07-175.1.

Castro-Santos, T. 2004. Quantifying the combined effects of attempt rate and swimming capacity on passage through velocity barriers. Canadian Journal of Fisheries and Aquatic Sciences **61**: 1602-1615. doi: doi: 10.1139/F04-094.

Castro-Santos, T. 2005. Optimal swim speeds for traversing velocity barriers: an analysis of volitional high-speed swimming behavior of migratory fishes. J Exp Biol **208**(3): 421-432. doi: 10.1242/jeb.01380.

Castro-Santos, T., and Haro, A. 2003. Quantifying migratory delay: a new application of survival analysis methods. Canadian Journal of Fisheries and Aquatic Sciences **60**(8): 986-996. doi: 10.1139/f03-086.

Castro-Santos, T., and Perry, R.W. 2012. Time-to-Event Analysis as a Framework for Quantifying Fish Passage Performance. *In* Telemetry Techniques: a User Guide for Fisheries Research. *Edited by* N.S. Adams, J.W. Beeman and J.H. Eiler. American Fisheries Society, Bethesda, Maryland. pp. 427-452.

Castro-Santos, T., Sanz-Ronda, F.J., and Ruiz-Legazpi, J. 2013. Breaking the speed limit — comparative sprinting performance of brook trout (Salvelinus fontinalis) and brown trout (Salmo trutta). Canadian Journal of Fisheries and Aquatic Sciences **70**(2): 280-293. doi: doi:10.1139/cjfas-2012-0186.

Chow, V.T. 1959. Open-channel hydraulics. McGraw Hill Book Company.

Coffman, J.S. 2005. Evaluation of a predictive model for upstream fish passage through culverts. Thesis, Biology, James Madison University.

Cote, J., Clobert, J., Brodin, T., Fogarty, S., and Sih, A. 2010. Personality-dependent dispersal: characterization, ontogeny and consequences for spatially structured populations. Philosophical Transactions of the Royal Society B: Biological Sciences **365**(1560): 4065-4076. doi: 10.1098/rstb.2010.0176.

Dominy, C.L. 1973. Effect of Entrance-Pool Weir Elevation and Fish Density on Passage of Alewives (Alosa pseudoharengus) in a Pool and Weir Fishway. Transactions of the American Fisheries Society **102**(2): 398-404. doi: 10.1577/1548-8659(1973)102<398:eoewea>2.0.co;2.

Farwell, M., and McLaughlin, R.L. 2009. Alternative foraging tactics and risk taking in brook charr (Salvelinus fontinalis). Behavioral Ecology **20**(5): 913-921. doi: 10.1093/beheco/arp059.

Fausch, K.D., Torgersen, C.E., Baxter, C.V., and Li, H.W. 2002. Landscapes to Riverscapes: Bridging the Gap between Research and Conservation of Stream Fishes. BioScience **52**(6): 483-498. doi: 10.1641/0006-3568(2002)052[0483:ltrbtg]2.0.co;2.

Fox, J. 2002. Cox proportional-hazards regression for survival data. An R and S-PLUS companion to applied regression: 1-18.

Fraser, N.H.C., and Metcalfe, N.B. 1997. The costs of becoming nocturnal: feeding efficiency in relation to light intensity in juvenile Atlantic Salmon. Functional Ecology **11**(3): 385-391. doi: 10.1046/j.1365-2435.1997.00098.x.

Gibson, R.J., Haedrich, R.L., and Wernerheim, C.M. 2005. Loss of Fish Habitat as a Consequence of Inappropriately Constructed stream Crossings. Fisheries **30**(1): 10-17 [accessed 11 mai 2005.

Goerig, E., Castro-Santos, T., and Bergeron, N.É. 2016. Brook trout passage performance through culverts. Canadian Journal of Fisheries and Aquatic Sciences **73**(1): 94-104. doi: doi:10.1139/cjfas-2015-0089.

Gowan, C., and Fausch, K.D. 1996. Mobile brook trout in two high elevation Colorado streams: re-evaluating the concept of restricted movements. Canadian Journal of Fisheries and Aquatic Sciences **53**: 1370-1381.

Hasler, A.D., and Scholz, A.T. 2012. Olfactory imprinting and homing in salmon: Investigations into the mechanism of the imprinting process. Springer Science & Business Media.

Höjesjö, J., Johnsson, J.I., Petersson, E., and Järvi, T. 1998. The importance of being familiar: individual recognition and social behavior in sea trout (Salmo trutta). Behavioral Ecology **9**(5): 445-451.

Hosmer, D., Lemeshow, S., and May, S. 1999. Applied survival analysis: Regression modelling of time to event data. John Wiley & Sons. New York.

Hughes, N.F. 1992. Ranking of Feeding Positions by Drift-Feeding Arctic Grayling (Thymallus arcticus) in Dominance Hierarchies. Canadian Journal of Fisheries and Aquatic Sciences **49**(10): 1994-1998. doi: doi:10.1139/f92-222.

Jenkins Jr, T.M. 1969. Night Feeding of Brown and Rainbow Trout in an Experimental Stream Channel. Journal of the Fisheries Research Board of Canada **26**(12): 3275-3278. doi: 10.1139/f69-316.

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

Magurran, A.E. 1986. Individual Differences in Fish Behaviour. *In* The Behaviour of Teleost Fishes. *Edited by* T.J. Pitcher. Springer US, Boston, MA. pp. 338-365.

Mahlum, S., Cote, D., Wiersma, Y.F., Kehler, D., and Clarke, K.D. 2013. Evaluating the Barrier Assessment Technique Derived from FishXing Software and the Upstream Movement of Brook Trout through Road Culverts. Transactions of the American Fisheries Society **143**(1): 39-48. doi: 10.1080/00028487.2013.825641.

Marriam-Webster, d. 2006. The Merriam-Webster Dictionary. Merriam-Webster, Incorporated.

McFarland, D. 1999. Animal Behaviour: Psychobiology. Ethology and Evolution. Longman **3**.

Morita, K., and Yamamoto, S. 2002. Effects of Habitat Fragmentation by Damming on the Persistence of Stream-Dwelling Charr Populations. The Journal of the Society for Conservation Biology **16**(5): 1318-1323. doi: 10.1046/j.1523-1739.2002.01476.x.

Newman, M.A. 1956. Social Behavior and Interspecific Competition in Two Trout Species. Physiological Zoology **29**(1): 64-81.Available from http://www.jstor.org/stable/30152381.

NSERC. Sunrise/sunset calculator. National Research Council Canada.

O’Neal, J.S., Roni, P., Crawford, B., Ritchie, A., and Shelly, A. 2016. Comparing Stream Restoration Project Effectiveness Using a Programmatic Evaluation of Salmonid

Habitat and Fish Response. North American Journal of Fisheries Management **36**(3): 681-703. doi: 10.1080/02755947.2016.1165773.

Peake, S., McKinley, R.S., and Scruton, D.A. 1997. Swimming performance of various freshwater salmonids relative to habitat selection and fishway design. Journal of Fish Biology **51**(3): 710-723.

Peake, S.J. 2008. Behavior and passage performance of northern pike, walleyes, and white suckers in an experimental raceway. North American Journal of Fisheries Management **28**(1): 321-327. doi: 10.1577/m06-260.1.

Perkin, J.S., and Gido, K.B. 2012. Fragmentation alters stream fish community structure in dendritic ecological networks. Ecological Applications **22**(8): 2176-2187. doi: 10.1890/12-0318.1.

Peterson, N.P., Simmons, R.K., Cardoso, T., and Light, J.T. 2013. A Probabilistic Model for Assessing Passage Performance of Coastal Cutthroat Trout through Corrugated Metal Culverts. North American Journal of Fisheries Management **33**(1): 192-199. doi: 10.1080/02755947.2012.750633.

Poplar-Jeffers, I.O., Petty James, J.T., Anderson, T., Kite, S.J., Strager, M.P., and Fortney, R.H. 2009. Culvert Replacement and Stream Habitat Restoration: Implications from Brook Trout Management in an Appalachian Watershed, U.S.A. Restoration Ecology **17**(3): 404-413. doi: 10.1111/j.1526-100X.2008.00396.x.

R Core Team. 2015. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

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

Roy, M., Roy, A.G., Grant, J.W.A., and Bergeron, N.E. 2013. Individual variability of wild juvenile Atlantic salmon activity patterns: effect of flow stage, temperature, and habitat use. Canadian Journal of Fisheries and Aquatic Sciences **70**(7): 1082-1091. doi: doi:10.1139/cjfas-2012-0274.

Sanz-Ronda, F.J., Ruiz-Legazpi, J., Bravo-Córdoba, F.J., Makrakis, S., and Castro-Santos, T. 2015. Sprinting performance of two Iberian fish: Luciobarbus bocagei and Pseudochondrostoma duriense in an open channel flume. Ecological Engineering **83**: 61-70. doi: http://dx.doi.org/10.1016/j.ecoleng.2015.05.033.

Sundström, L.F., and Johnsson, J.I. 2001. Experience and social environment influence the ability of young brown trout to forage on live novel prey. Animal Behaviour **61**(1): 249-255. doi: http://dx.doi.org/10.1006/anbe.2000.1593.

Therneau, T.M. 2015a. Package 'coxme': Mixed effects Cox models. R.

Therneau, T.M. 2015b. Package 'survival' R.

Therneau, T.M., Grambsch, P.M., and Fleming, T.R. 1990. Martingale-based residuals for survival models. Biometrika **77**(1): 147-160.

Therneau, T.M., Grambsch, P.M., and Pankratz, V.S. 2003. Penalized Survival Models and Frailty. Journal of Computational and Graphical Statistics **12**(1): 156-175. doi: 10.1198/1061860031365.

Weaver, C.R. 1963. Influence of water velocity upon orientation and performance of adult migrating salmonids. Fisheries Bulletin **63**(1): 97-121.

Young, M.K. 1999. Summer diel activity and movement of adult brown trout in high-elevation streams in Wyoming, U.S.A. Journal of Fish Biology **54**(1): 181-189. doi: 10.1111/j.1095-8649.1999.tb00621.x.

Article 2: Brook trout passage performance through culverts

Titre en français : Performance de passage de l'omble de fontaine dans les ponceaux

Cet article a été rédigé par Elsa Goerig, sous la supervision de Theodore Castro-Santos. La conception expérimentale fut issue d'une collaboration étroite entre Elsa Goerig et Normand Bergeron. La collecte de données a été réalisée par Elsa Goerig, avec l'aide de plusieurs stagiaires et assistants de recherche. Le traitement et l'analyse des données, ainsi que l'interprétation des résultats, ont été effectués par Elsa Goerig, avec la collaboration de Theodore Castro-Santos et de Normand Bergeron.

Elsa Goerig*[1], Theodore Castro-Santos[2] & Normand E. Bergeron[1]
[1] INRS-Eau, Terre et Environnement, 490 rue de la Couronne, Québec, QC, GlK 9A9, Canada.
[2] USGS S.O. Conte Anadromous Fish Research Center. 1 Migratory way, Turners Falls (MA), 01376. USA
*Author to whom correspondence must be addressed
Present address : USGS S.O. Conte Anadromous Fish Research Center. 1 Migratory way, Turners Falls (MA), 01376. USA
Email: goerig.elsa@gmail.com

Référence pour citation :
Goerig, E., Castro-Santos, T., and Bergeron, N.E. 2015. Brook trout passage performance through culverts. Canadian Journal of Fisheries and Aquatic Sciences in press. doi: 10.1139/cjfas-2015-0089.

ABSTRACT

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

RÉSUMÉ

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

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, Pépino 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 7). 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.

Table 7: Study sites characteristics.

Site	Watershed	Latitude	Longitude	Material	Shape	Diameter	Length	Slope
Resimond	ainte-Marguerit	48°25'52"N	70°26'03"W	orrugated met	Circular	1600	44,6	0.92
MorinA	ainte-Marguerit	48°20'50"N	70°03'39"W	orrugated met	Circular	1500	33,2	1.38
MorinB	ainte-Marguerit	48°20'50"N	70°03'39"W	orrugated met	Circular	2200	32,3	1.38
MorinC	ainte-Marguerit	48°20'50"N	70°03'39"W	orrugated met	Circular	2200	33	1.38
MorinD	ainte-Marguerit	48°20'50"N	70°03'39"W	Polyethylene	Circular	2200	32,4	1.38
Allaire	ainte-Marguerit	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	orrugated met	Circular	2000	17,9	2.4
Adolphe	Saint-Louis	48°46'38"N	70°49'25"W	orrugated met	Circular	2000	14,3	1.6
Raquette	Saint-Louis	48°38'59"N	70°55'22"W	orrugated met	Circular	2700	8,6	1.8
Saumons	Saint-Louis	48°47'38"N	70°47'59"W	orrugated met	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

Note: Diameter is in mm, length in m and slope in %.

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 12). 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.

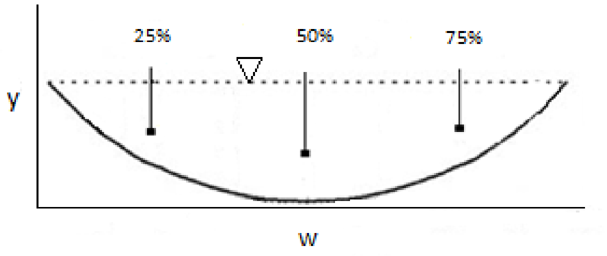

Figure 12 : : Schematic representation of culvert cross-section with dots representing the location of flow velocity measurements. At 25, 50 and 75% of flow width (w), flow depth (y) was measured, along with mean flow velocity.

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

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

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

where U is velocity (cm/s), y is mean flow depth (cm), v is kinematic viscosity (cm^2 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 Theta (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 13) 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. 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 13). 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.

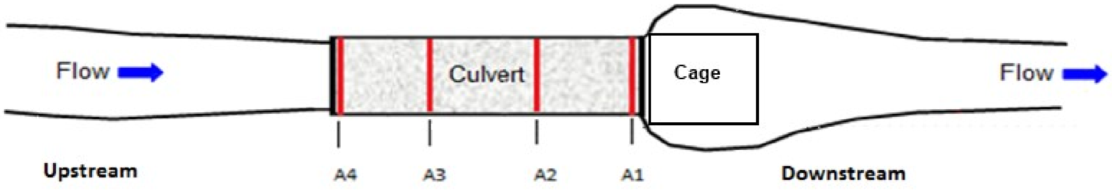

Figure 13: Schematic representation of the stationary PIT system installed in culverts, with the cage downstream and the 4 PIT antennas (A1-A4). Adapted from Cahoon et al. (2004)

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 8). 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.

Table 8 : Measured range of explanatory variables in their standard units and in body 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 dowstream pool	0.25-1 m or 1-11.5 BL	0.6 or 4.5
Trial duration or delay	24-48h	48

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

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

$$AIC = -2\log L + 2K \tag{9}$$

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

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

The predictive power of the selected model was assessed on two datasets: caged fish used to develop the model and a new dataset consisting of attempts and passage observations for uncaged fish released freely in the stream. In both datasets, a subsample comprising fish that reached at least the second antenna was also considered, in order to discriminate between truly motivated individuals and those showing only exploratory behaviors. A method derived from the *leave-one-out* principle (Proc logistic, Predprobs = X, SAS 9.3) was used to compute cross-validated individual probability of passage for the caged fish. Tjur's R^2 and *c* statistic, used to assess the predictive power of the model, are measures of predictive power based on the association between predicted probabilities and observed responses (Allison 2012, Hosmer et al. 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; ± 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; 5^{th}-95^{th} pctl range=54900-332600) than those in smooth culverts (median=55700; 5^{th}-95^{th} 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 unknow 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 9). 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

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

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

Table 9: 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+T2+P+D+Type	404.88	8	420.88	3.9	270.6	0.127
Uf+S+T+T^2+P+D+Type	**401.03**	**8**	**417.03**	**0.0**	**274.5**	**0.870**

Note: 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 weigth of 0.87.

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.

Table 10: Estimation of parameters for the selected model

		Variables in standard units			
	Parameters	***β**	**β**	**±SE**	**OR**
β0	Intercept		-4.563	4.411	
β1	Water temperature	2.744	1.436	0.722	
β2	Water temperature ^{2}	-2.022	-0.048	0.026	
β3	Culvert type (rough v/s smooth)	1.646	2.985	0.761	
β4	Culvert slope	-0.846	-1.304	0.363	0.270
β5	Mean flow velocity	-0.581	-2.985	0.625	0.050
β6	Depth of downstream pool	-0.845	-8.159	1.376	0.000
β7	Trial duration	0.395	0.078	0.022	1.080
β8	Culvert type * fish length	0.869	-0.012	0.005	

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

Standardized coefficients ($^{x}\beta$) measure the relative importance of the explanatory variables, regardless of the metrics in which the variables have been measured (Table 10). 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 14, panels A, B and C). Shorter fish performed better in rough culverts while in smooth culverts performance increased with the size of the fish.

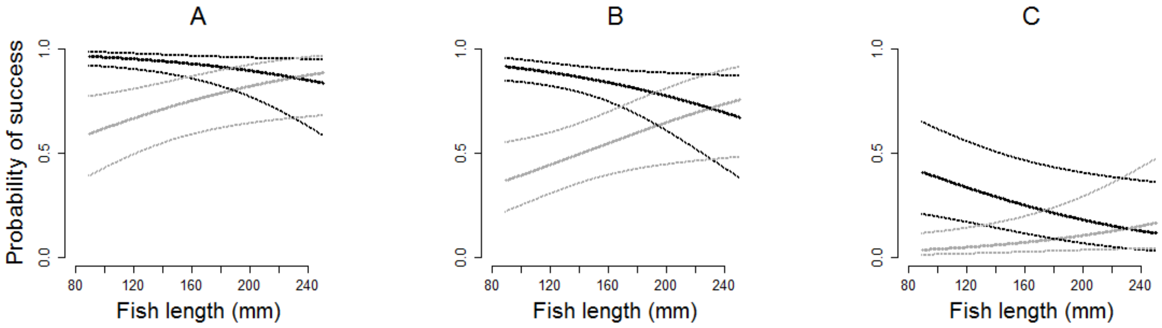

Figure 14 : Panels show the predicted probability and 95% confidence intervals of success in rough (black line) and smooth (grey line) culverts with regards to fish length for a mean flow velocity of 0.4 m/s (A), 0.8 m/s (B) and 1.7 m/s (C), which correspond to the 5th, 50th and 95th percentiles of tested flow velocities. In smooth culvert longer fish had superior passage success, but in rough culverts shorter fish performed better, regardless of the flow velocity

Slope had an evident negative impact on passage success (Figure 15, 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 10). 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.

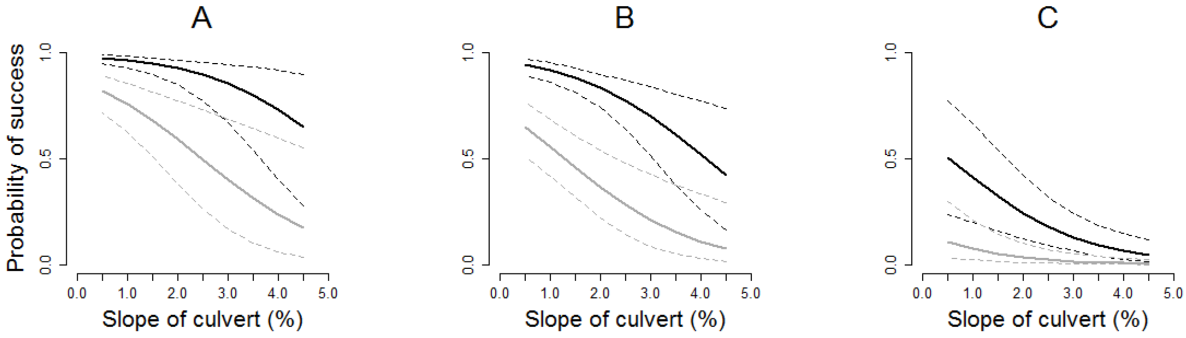

Figure 15: Panels show the predicted probability and 95% confidence intervals of success in rough (black line) and smooth (grey line) culverts with regards to culvert slope for a mean flow velocity of 0.4 m/s (A), 0.8 m/s (B) and 1.7 m/s (C), corresponding to the 5th, 50th and 95th percentiles of tested 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.

Depth of the staging area also affected $P_{success}$, with poorer success associated with deeper pools (Figure 16, panel A).

Passage success declined with increasing flow velocity, decreasing by 95% per m/s (odds ratio = 0.05, Table 10). Mean flow velocity had a negative effect on $P_{success}$ (Figure 16, 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 16, 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 10). This effect is however limited to 48h, which is the longest trial duration for caged fish.

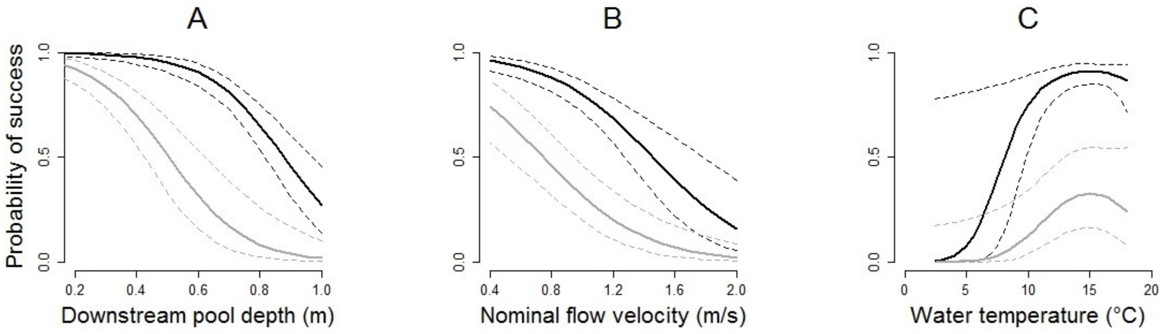

Figure 16: Predicted individual probabilities and 95% confidence intervals of success for fish ascending rough (black lines) and smooth (grey lines) culverts. Panels show the effect of depth of the downstream pool (A), mean flow velocity (B) and trial mean water temperature (C) on the probability of success for a fish of 126 mm, swimming in culverts of 9-45 m during a 48 h trial. 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 culvert slope=1.5%). For each parameter, the probability of success is higher in rough culverts. Passage performance of trout decreases with increasing depth of the downstream pool and flow velocity. Conversely, passage increases with water temperature to an optimum at 15°C. A limited number of fish (44) were tested at temperature below 7°C and panel C shows a large upper confidence interval for rough culvert. Caution should then be applied when predicting passage at low temperatures.

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 11). However, when only the fish that swam further than the first antenna were considered, the predictive power decreased in both datasets.

Table 11: Validation statistics for the selected model

		Variables in standard units		Variables normalized in BL	
Scored dataset	**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

Note: *C* and Tjur's R^2 statistics evaluating best model's predictive power for 4 datasets, in standards and body lengths units (BL): caged fish, caged fish that swam = > 2^{nd} antenna, uncaged fish and uncaged fish that swan = > 2^{nd} 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).

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 17). 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.

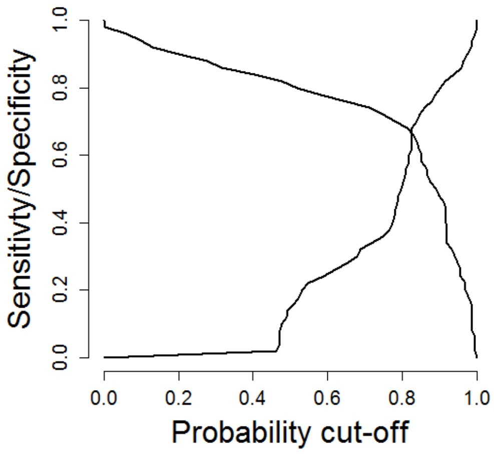

Figure 17 : Sensitivity and specificity under all possible cut-off points. When using the developed model to predict passage success of brook trout in culverts, sensitivity and specificity are both maximized at a probability cut-off of 0.82.

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 passage for a population. Ultimately it is both the rate of passage 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 ~ 15°C. Interestingly, 14-15°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 follows 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 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 13). 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 Uf < 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 7. Although extensive work remains to be done, this is a first step towards a more comprehensive approach to understand fish passage at road crossings.

ACKNOWLEDGEMENTS

Support for this research was provided by INRS-Centre Eau, Terre et Environnement, the GRIL, the Ministère des Transports du Québec, the Fonds de la recherche forestière du Saguenay-Lac Saint-Jean, and research scholarships to E.G from Natural Sciences and Engineering Research Council of Canada and the Fonds de recherche Nature et Technologies du Québec. Any use of trade, product, or firm names is for descriptive purposes only and does not imply endorsement by the Canadian or U.S. Governments**.** We would like to thank the research assistants who helped conducting the field work: M.A. Pouliot, F. Bérubé, J.N. Bujold, J.B. Torterotot, S. Dugdale, M. Fortin, C. Larouche, H. Bouchard, P. Marcotte, F. Pichon, J. Bédard and M. Tisserand. We also extend special thanks to P. Johnston, M. Lafrance and D Boula for their inputs and guidance throughout the study as well as to D. J. Alcott and B. H. Letcher for their generous assistance with the manuscript.

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

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

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

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

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

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

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

Castro-Santos, T. 2004. Quantifying the combined effects of attempt rate and swimming capacity on passage through velocity barriers. Can. J. Fish. Aquat. Sci. **61**: 1602-1615. doi: doi: 10.1139/F04-094.

Castro-Santos, T. 2005. Optimal swim speeds for traversing velocity barriers: an analysis of volitional high-speed swimming behavior of migratory fishes. J Exp Biol **208**(3): 421-432. doi: 10.1242/jeb.01380.

Castro-Santos, T. 2006. Modeling the effect of varying swim speeds on fish passage through velocity barriers. Trans. Am. Fish. Soc. **135**(5): 1230-1237. doi: 10.1577/t05-262.1.

Castro-Santos, T. 2012. Adaptive fishway design: a framework and rationale for effective evaluations. *In* Monitoring, Funktionskontrollen und Qualitätssicherung an Fischaufstiegsanlagen, 2. Kolloquium zur Herstellung der ökologischen Durchgängigkeit der Bundeswasserstraßen. Koblenz, Germany, pp. 76-89.

Castro-Santos, T., and Haro, A. 2006. Biomechanics and fisheries conservation. *In* Fish Physiology, volume 23: Fish Biomechanics. *Edited by* R.E. Shadwick and G.V. Lauder. Academic Press, New York. pp. 469-523.

Castro-Santos, T., Sanz-Ronda, F.J., and Ruiz-Legazpi, J. 2013. Breaking the speed limit — comparative sprinting performance of brook trout (Salvelinus fontinalis) and brown trout (Salmo trutta). Can. J. Fish. Aquat. Sci. **70**(2): 280-293. doi: doi:10.1139/cjfas-2012-0186.

Chow, V.T. 1959. Open-channel hydraulics. McGraw Hill Book Company.

Clausen, R.G. 1931. Orientation in Fresh Water Fishes. Ecology **12**(3): 541-546. doi: 10.2307/1928999.

Coffman, J.S. 2005. Evaluation of a predictive model for upstream fish passage through culverts, Biology, James Madison University.

Dominy, C.L. 1973. Effect of Entrance-Pool Weir Elevation and Fish Density on Passage of Alewives (Alosa pseudoharengus) in a Pool and Weir Fishway. Trans. Am. Fish. Soc. **102**(2): 398-404. doi: 10.1577/1548-8659(1973)102<398:eoewea>2.0.co;2.

Ead, S.A., Rajaratnam, N., Katopodis, C., and Ade, F. 2000. Turbulent open-channel flow in circular corrugated culverts. Journal of Hydraulic Engineering-Asce **126**(10): 750-757.Available from <Go to ISI>://000089579200004.

Farrell, A.P. 2007. Cardiorespiratory performance during prolonged swimming tests with salmonids: a perspective on temperature effects and potential analytical pitfalls. Philosophical Transactions of the Royal Society B: Biological Sciences **362**(1487): 2017-2030. doi: 10.1098/rstb.2007.2111.

Fausch, K.D., Torgersen, C.E., Baxter, C.V., and Li, H.W. 2002. Landscapes to Riverscapes: Bridging the Gap between Research and Conservation of Stream Fishes: A Continuous View of the River is Needed to Understand How Processes Interacting among Scales Set the Context for Stream Fishes and Their Habitat. BioScience **52**(6): 483-498. doi: 10.1641/0006-3568(2002)052[0483:ltrbtg]2.0.co;2.

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

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

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

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

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

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

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

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

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

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

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

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

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

MacPherson, L.M., Sullivan, M.G., Foote, A.L., and Stevens, C.E. 2012. Effects of Culverts on Stream Fish Assemblages in the Alberta Foothills. North American Journal of Fisheries Management **32**(3): 480-490. doi: 10.1080/02755947.2012.686004.

Mahlum, S., Cote, D., Wiersma, Y.F., Kehler, D., and Clarke, K.D. 2013. Evaluating the Barrier Assessment Technique Derived from FishXing Software and the Upstream Movement of Brook Trout through Road Culverts. Trans. Am. Fish. Soc. **143**(1): 39-48. doi: 10.1080/00028487.2013.825641.

Morita, K., and Yamamoto, S. 2002. Effects of Habitat Fragmentation by Damming on the Persistence of Stream-Dwelling Charr Populations. The Journal of the Society for Conservation Biology **16**(5): 1318-1323. doi: 10.1046/j.1523-1739.2002.01476.x.

Mueller, R.P., Southard, S.S., May, C.W., Pearson, W.H., and Cullinan, V.I. 2008. Juvenile coho salmon leaping ability and behavior in an experimental culvert test bed. Trans. Am. Fish. Soc. **137**(4): 941-950. doi: 10.1577/t06-244.1.

Neary, V.S. 2012. Binary Fish Passage Models for Uniform and Nonuniforms Flows. River Research and Applications **28**(4): 418-428. doi: 10.1002/rra.1564.

Neville, H.M., and Peterson, D.L. 2014. Genetic monitoring of trout movement after culvert remediation: family matters. Can. J. Fish. Aquat. Sci. **71**(11): 1680-1694. doi: doi:10.1139/cjfas-2014-0138.

Nislow, K.H., Hudy, M., Letcher, B.H., and Smith, E.P. 2011. Variation in local abundance and species richness of stream fishes in relation to dispersal barriers: implications for management and conservation. Freshwater Biol. **56**(10): 2135-2144. doi: 10.1111/j.1365-2427.2011.02634.x.

Normann, J.M., Houghtalen, R.J., and Johnston, W.J. 1985. Hydraulic design of highway culverts. *Edited by* U.D.o. Transportation. Federal Highway Administration, Washington, DC. p. 272.

Ombredane, D., Bagliniere, J., and Marchand, F. 1998. The effects of Passive Integrated Transponder tags on survival and growth of juvenile brown trout (<i>Salmo trutta L.) and their use for studying movement in a small river. Hydrobiologia **371-372**(0): 99-106. doi: 10.1023/a:1017022026937.

Park, D., Sullivan, M., Bayne, E., and Scrimgeour, G. 2008. Landscape-level stream fragmentation caused by hanging culverts along roads in Alberta's boreal forest. Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere **38**(3): 566-575. doi: 10.1139/x07-179.

Peake, S.J., and Farrell, A.P. 2006. Fatigue is a behavioural response in respirometer-confined smallmouth bass. J. Fish Biol. **68**(6): 1742-1755. doi: 10.1111/j.0022-1112.2006.01052.x.

Pépino, M., Rodríguez, M.A., and Magnan, P. 2012. Impacts of highway crossings on density of brook charr in streams. J. Appl. Ecol. **49**(2): 395-403. doi: 10.1111/j.1365-2664.2012.02108.x.

Perry, R.W., Plumb, J.M., Fielding, S.D., Adams, N.S., and Rondorf, D.W. 2013. Comparing Effects of Transmitters within and among Populations: Application to Swimming Performance of Juvenile Chinook Salmon. Transactions of the American Fisheries Society **142**(4): 901-911. doi: 10.1080/00028487.2013.788556.

Petty, J.T., Hansbarger, J.L., Huntsman, B.M., and Mazik, P.M. 2012. Brook Trout Movement in Response to Temperature, Flow, and Thermal Refugia within a Complex Appalachian Riverscape. Transactions of the American Fisheries Society **141**(4): 1060-1073. doi: 10.1080/00028487.2012.681102.

Peterson, N.P., Simmons, R.K., Cardoso, T., and Light, J.T. 2013. A Probabilistic Model for Assessing Passage Performance of Coastal Cutthroat Trout through Corrugated Metal Culverts. North American Journal of Fisheries Management **33**(1): 192-199. doi: 10.1080/02755947.2012.750633.

Poplar-Jeffers, I.O., Petty James, J.T., Anderson, T., Kite, S.J., Strager, M.P., and Fortney, R.H. 2009. Culvert Replacement and Stream Habitat Restoration: Implications from Brook Trout Management in an Appalachian Watershed, U.S.A. Restoration Ecology **17**(3): 404-413. doi: 10.1111/j.1526-100X.2008.00396.x.

Powers, P.D., and Orsborn, J.F. 1985. Analysis of Barriers to Upstream Migration: An Investigation of the Physical and Biological Conditions Affecting Fish Passage Success at Culverts and Waterfalls. Albrook Hydraulics Laboratory Washington State University, Pullman, WA.

Powers, P.D., Bates, K., Burns, T., Gowen, B., and Whitney, R. 1997. Culvert hydraulics related to upstream juvenile salmon passage. *Edited by* W.D.o.F.a. Wildlife.

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

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

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

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

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

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

Tudorache, C., O'Keefe, R.A., and Benfey, T.J. 2010. The effect of temperature and ammonia exposure on swimming performance of brook charr (Salvelinus fontinalis). Comp. Biochem. Physiol., Part A: Mol. Integr. Physiol.**156**(4): 523-528. doi: http://dx.doi.org/10.1016/j.cbpa.2010.04.010.

Videler, J.J. 1993. Fish swimming. Chapman & Hall, London.

Vogel, S. 1994. Life in Moving Fluids: The Physical Biology of Flow. Princeton University Press.

Von Karman, T. 1931. Mechanical similitude and turbulence.

Wagner, R.L., Makrakis, S., Castro-Santos, T., Makrakis, M.C., Dias, J.H.P., and Belmont, R.F. 2012. Passage performance of long-distance upstream migrants at a large dam on the Paraná River and the compounding effects of entry and ascent. Neotropical Ichthyology **10**: 785-795.Available from http://www.scielo.br/scielo.php?script=sci_arttext&pid=S1679-62252012000400011&nrm=iso.

Warren, M.L., and Pardew, M.G. 1998. Road crossings as barriers to small-stream fish movement. Trans. Am. Fish. Soc. **127**(4): 637-644.Available from <Go to ISI>://000075350600011.

Weaver, C.R. 1963. Influence of water velocity upon orientation and performance of adult migrating salmonids. Fisheries Bulletin **63**(1): 97-121.

Whiteley, A.R., Coombs, J.A., Hudy, M., Robinson, S.C., Colton, A.R., Nislow, K.H., and Letcher, B.H. 2013. Fragmentation and patch size shape genetic structure of brook trout populations. Can. J. Fish. Aquat. Sci. **70**(5): 678-688. doi: doi:10.1139/cjfas-2012-0493.

Whiteley, A.R., Coombs, J.A., Letcher, B.H., and Nislow, K.H. 2014. Simulation and empirical analysis of novel sibship-based genetic determination of fish passage. Can. J. Fish. Aquat. Sci. **71**(11): 1667-1679. doi: doi:10.1139/cjfas-2014-0137.

Wofford, J.E.B., Gresswell, R.E., and Banks, M.A. 2005. Influence of Barriers to Movement on Within-Watershed Genetic Variation of Coastal Cutthroat Trout. Ecological Applications **15**(2): 628-637.Available from http://www.jstor.org/stable/4543380.

Article 3: Swimming behavior and ascent paths of brook trout in a corrugated culvert

---

Titre en français : Comportement et trajectoires de nage de l'omble de fontaine dans un ponceau de tôle ondulée.

Cet article a été rédigé par Elsa Goerig. La conception expérimentale et la collecte de données ont été réalisées par Pascal Marcotte, étudiant stagiaire du laboratoire de Normand Bergeron, sous la supervision de Elsa Goerig. Le traitement et l'analyse des données ainsi que l'interprétation des résultats, ont été réalisés par Elsa Goerig, en collaboration avec Theodore Castro-Santos et Normand Bergeron. Dr. Castro-Santos a également fourni des ressources pour le traitement des données hydrauliques tandis que Dr. Normand Bergeron a fourni des ressources pour le développement du programme de numérisation des données spatiales.

Elsa Goerig*[1], Normand E. Bergeron[1] & Theodore Castro-Santos[2]
[1] INRS-Eau, Terre et Environnement, 490 rue de la Couronne, Québec, QC, GlK 9A9, Canada.
[2] USGS S.O. Conte Anadromous Fish Research Center. 1 Migratory way, Turners Falls (MA), 01376. USA
*Author to whom correspondence must be addressed
Present address :
USGS S.O. Conte Anadromous Fish Research Center. 1 Migratory way, Turners Falls (MA), 01376. USA
Email: goerig.elsa@gmail.com

Non soumis à ce jour

ABSTRACT

Culverts may restrict fish upstream movements under specific hydraulic conditions. Swimming capacity is a key element of fish passage success. However, fish behavior also plays an important role in the fish’s ability to overcome velocity barriers. Corrugated metal culverts are characterized by unsteady flow and existence of low velocity zones, which can sometimes improve passage success. Here we describe swimming behavior and ascent paths of 148 wild brook trout in a corrugated metal culvert under mean flow velocity ranging from 0.3 to 0.65 m s^{-1}. Fish were individually introduced in the culvert and their movements recorded with a camera located above the water. Lateral and longitudinal positions were recorded at a rate of three times per second in order to identify ascent paths. Results indicated that brook trout selected flow velocities from 0.25 to 0.5 m s^{-1} during their ascents. This behavior was consistent between individuals and resulted in the use of low-velocity zones at higher flows. Some fish used the corrugations as rest areas, although this behavior was marginal and did not occur at the highest flow.

RÉSUMÉ

Les ponceaux peuvent limiter les déplacements vers l’amont des espèces d’eau douce. La capacité de nage est un élément primordial du succès de passage. Toutefois, le comportement de nage joue également un rôle dans l’aptitude des poissons à franchir des obstacles. Les ponceaux de tôle ondulée sont caractérisés par un écoulement hétérogène et l’existence de zones où les vitesses de l’eau sont réduites, ce qui peut dans certains cas être bénéfique au passage du poisson. Dans la présente étude, nous décrivons le comportement et les trajectoires de nage de 148 ombles de fontaine dans un ponceau de tôle ondulée, sous des conditions d’écoulement de 0.3 à 0.65 m s^{-1}. Les ombles ont été introduits individuellement dans le ponceau et leurs mouvements enregistrés avec une caméra installée hors de l’eau. Les positions latérales et longitudinales des ombles ont été déterminées à un taux de trois fois par seconde, de façon à pouvoir reconstituer leurs trajectoires de nage. Les ombles ont

majoritairement sélectionné des vitesses d'écoulement entre 0.25 et 0.5 m s^{-1}, ce qui s'est traduit par l'utilisation de zones de vitesses réduites lorsque la vitesse moyenne de l'écoulement dans le ponceau s'élevait. Ce comportement était similaire entre les individus. Certains ombles ont également utilisé les ondulations du ponceau comme zones de repos, bien que ce comportement fut marginal et ne soit pas observé aux vitesses d'écoulement les plus élevées.

INTRODUCTION

When moving in their natural habitat, fish may encounter challenging environments. Culverts are ubiquitous structures that can often limit fish upstream movements due to outlet drops, shallow depths or excessive flow velocities with regards to the fish swimming capacity (Gibson *et al.*, 2005, Goerig *et al.*, 2016).

Passage success through culverts is a dynamic phenomenon influenced by variables that fluctuate over time, and thus is difficult to predict. Because each barrier is unique, relating the hydraulic conditions within the structure with the fish leaping and swimming capabilities (Castro-Santos 2005, Kondratieff and Myrick 2006, Neary 2012) seems essential in order to predict passage. However, behavior and motivation can also be key elements in the ability of a species to overcome a barrier. Under challenging conditions, fish may use various strategies to save energy and avoid relying exclusively on their anaerobic metabolism. They can either use roughness elements to rest or low velocity zones and vortices to achieve greater ascent distances under aerobic processes (Goerig et al. 2015, Liao 2004). Powers (Powers *et al.*, 1997) and Richmond (Richmond *et al.*, 2007) indeed suggested that ascending trout may use zones where local flow velocities are lower than the mean velocity of the culvert.

Predictive passage models (Furniss *et al.*, 2008, Goerig *et al.*, 2016) are usually based on the mean cross-sectional flow velocity inside the culvert. In the eventuality of fish selecting focal velocities lower than the mean cross-sectional velocity, passage success would be underestimated. Previous studies have attempted to define a correction factor to apply to the mean velocity for swimming performance assessment and passage predictions through velocity barriers (Behlke, 1991, Castro-Santos, 2005, Sanz-Ronda *et al.*, 2015). This requires to connect the fish's ascent paths with the distribution of flow velocities inside the structure. However, knowledge of actual ascent paths in culverts is surprisingly limited, with only a few studies made in an experimental culvert test bed (Johnson *et al.*, 2012, Peterson *et al.*, 2013, Thurman *et al.*, 2007) .

Here we describe swimming paths of wild brook trout ascending a section of a corrugated culvert and model the effects of hydraulic and biological factors on the extent to which fish exhibited energy-saving behaviors.

METHODS

Fish capture

Wild brook trout were caught by electrofishing 0-500 m upstream of the culvert and 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). Fish were then measured (total length, mm), and weighed (wet mass, gr).

Video recordings

A single video camera (Gopro HD Hero 2011) was used in a 9 m long and 2.7 m diameter steel culvert with helical corrugations (amplitude of 3 cm, wavelength of 15 cm, and right-handed pitch of 5°), located in Raquette stream, in Québec. The camera was mounted 4 m from the downstream extremity of the culvert, at a right angle above the water surface, in order to record individual ascent paths and swimming behavior in an area where the flow was fully developed. It monitored a zone of 200 cm x 200 cm, which encompassed the full flow width and a comparable length.

Trout were individually tested in passage trials. Each fish was introduced 2.5 m inside the culvert by means of a bucket filled with water and gently immersed in the culvert centerline, facing upstream. Total recording time was three minutes per individual. After this period, if a fish had not ascended the culvert or returned downstream, it was removed from the trial to allow the testing of a new individual.

Hydraulic data

Flow velocity was measured with a propeller-type velocimeter (Swoffer, model 3000) for each trial at three transects inside the culvert: one meter downstream of the camera location, under the camera and one meter upstream of the camera. At each transect, flow depth and mean flow velocity were measured at 15%, 30%, 45%, 60%, and 75% of the flow cross-section width. Depth was measured from the surface to the crest of the corrugations, and the corrugation's amplitude was considered as the boundary roughness height. Velocity at each location was calculated by averaging instantaneous velocities measured over a 30 s 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). Additional points were interpolated using linear regression in order to obtain a more complete distribution of flow depth and mean velocity in the cross-sections. Mean flow depth and velocity for the culvert were computed by averaging the mean values for each transect. Flow depth and flow velocity distributions in the area covered by the camera were integrated from the measured points on a 1 cm grid using kriging interpolation with the octant method (Tecplot 360 2015 R1).

Video analysis

Ascent paths of fish were assessed by using a custom automated digitizing program written in Matlab (R2014a). As the fish was ascending the culvert, a point corresponding to its approximate center of mass was digitized at every 10 frames or 0.33 second. The center of mass of fish varies by species and is located between 25 % and 45 % of total body length (Xiong and Lauder, 2014) . For brook trout, it corresponds to 37 ± 1.5 % of total body length (Goerig et al, unpublished data). Pixel values were extracted, corresponding respectively to the longitudinal (x) and lateral (y) position of the fish in the culvert. The field of view of the camera was calibrated with known landmarks and the fish positions were translated to x-y spatial coordinates in cm by using a spatial transformation (Matlab R2014a, image processing toolbox, cpt2form function). For each trial, we used as landmarks the extremities and center of the wet width at each crest of the corrugations, whose spacing was 15 cm. By applying an inverse spatial transformation, we were able to infer pixels values for the landmarks and estimate the error inherent to the method.

Individual ascent paths were superimposed to the distribution of depths and velocities in the culvert. For each fish x-y position, we associated a value of flow depth and mean flow velocity on the vertical profile. The ratios between the flow velocities selected by the fish and the actual mean flow velocity in the culvert were computed and averaged for the ascent path of each fish. From now on, we will refer to these as velocity preference ratios.

Transit time, expressed as the amount of time spent in the zone covered by the camera, was also recorded for each fish.

Behavior of fish was also characterized as 1) continuous swimming or 2) alternating continuous swimming with rest periods.

Statistical analysis

Ascent paths and swimming behavior were then analyzed to determine the extent to which fish selected reduced flow velocities while ascending the culvert. We used a mixed linear model (R 3.2.0, package Lme4, function lmer) to assess the effect of mean flow depth, mean flow velocity, and fish length on the velocity preference ratio. This model included a random effect on trial in order to account for any statistical dependence between the fish tested in the same trial (Quinn *et al.*, 2002). Flow depth and flow velocity were correlated together (R = -0.32). An interaction term was added when they were used together in the same model.

RESULTS

A total of 148 brook trout of total length 70-190 mm (mean = 114 mm, SD = 27mm) were tested in five trials conducted in mid-August. The mean velocity conditions ranged from 0.30 to 0.63 m s^{-1} and the depth from 0.13 to 0.19 m (Table 12). Flow was always faster in the middle of the culvert cross-section and slower close to the walls. The reduced velocity zone was more pronounced along the right wall when looking upstream due to the angle of the corrugations. This is similar with observations from previous hydraulic studies in corrugated culverts (Barber *et al.*, 1996, Richmond *et al.*, 2007). However, this also depends of the substrate configuration at the inlet. Thus, in the first trial, the reduced velocity zone was located more along the left wall. The water temperature remained constant at 12 °C, which corresponds to the average temperature of the stream for August.

Table 12: Trials conditions

ID	Date	Velocity (m s^{-1})	Depth (m)	n
1	8/17/2011	0.30	0.19	22
2	8/18/2011	0.33	0.17	36
3	8/23/2011	0.63	0.13	23
4	8/24/2011	0.45	0.22	32
5	8/25/2011	0.38	0.19	35

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

Among all fish tested, 84 trout ascended the zone covered by the camera. Of these 84, 67 were characterized as swimming continuously and 16 as alternating steady swimming with rest periods involving minimal body motions. The average positioning error in the culvert varied among trials, but was < 1 cm on both the x and y axis. Given the fact that flow depths and velocities were integrated on a 1 cm grid, the risk of assigning a wrong depth or velocity to a fish was therefore negligible. The ascent path pattern differed by individual (Figure 18). Fish consistently selected a median flow velocity located of 0.4 m s^{-1}, regardless of the trial, with an interquartile range from 0.38 to 0.48 m s^{-1}. In response to the distribution of flow velocities during the trials, trout thus exploited different spatial locations (Figure 19, panel A). Their preferred depths were more widely distributed (Figure 19, panel B), ranging from 5 to 30 cm. Fish however selected shallower depths in the third trial, which corresponded to locations with slower velocities, along the walls of the culvert.

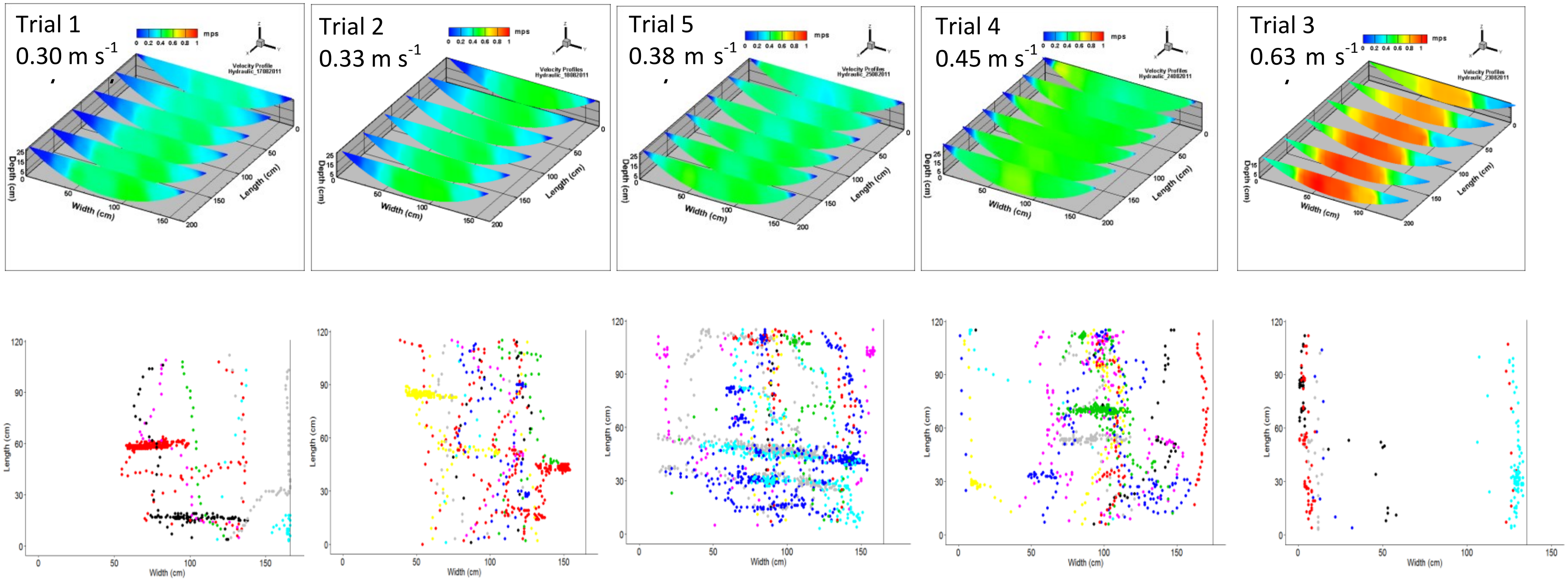

Figure 18: Distribution of flow velocities (upper panels) and fish ascent paths (lower panels) in the zone covered by the camera (1 cm grid), for the five trials ordered by increasing mean flow velocity. Colors in the upper panels go from blue (0-0.4 m s^{-1}) to red (0.8-1.0 m s^{-1}). Colors in the lower panels identify ascent path of individual fish. In trials 1 and 2, fish occupied only a portion of the flow cross-section, where flow velocities were between 0.25 and 0.5 m s^{-1}. In trials 4 and 5, trout ascent paths were more laterally distributed and also corresponded to flow velocities of 0.25 to 0.5 m s^{-1}. In trial 3, where the flow velocities were the highest, trout were ascending the culvert by swimming close to the walls, against flow velocities of 0.3 to 0.5 m s^{-1}.

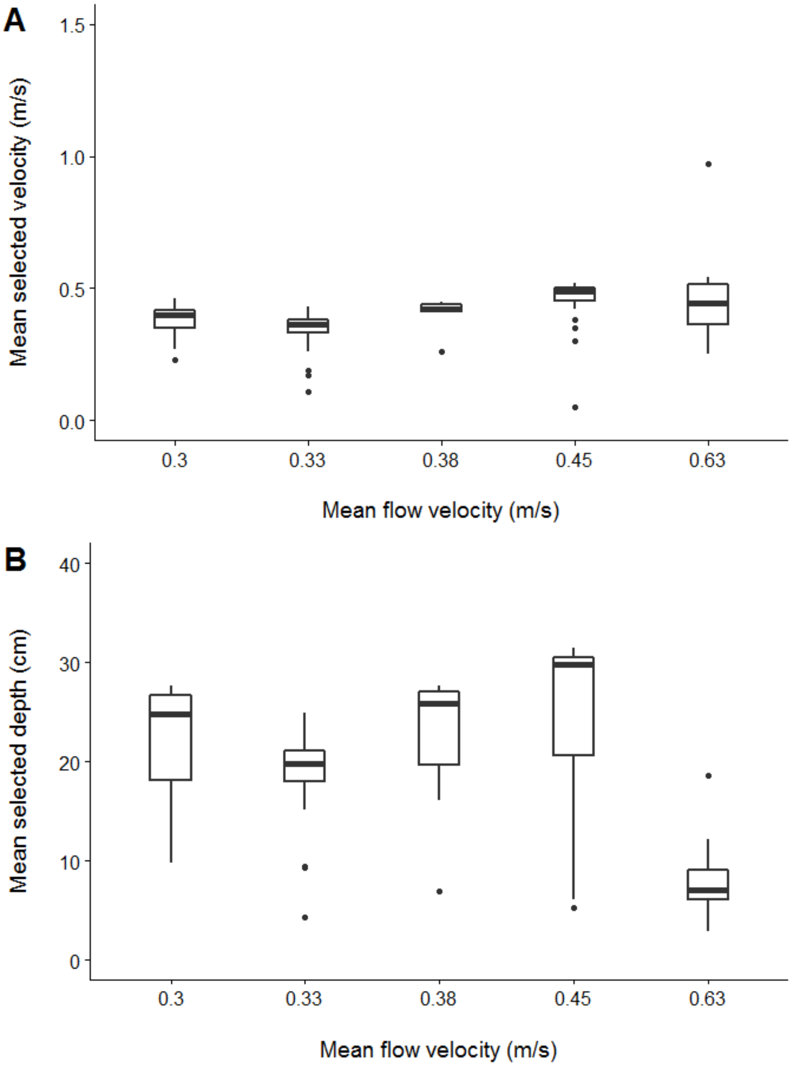

Figure 19: Distribution of mean selected flow velocity (panel A) and flow depth (panel B) during culvert ascents. Trials are ordered by increasing mean flow velocity. Trout mostly selected locations with flow velocities between 0.25 and 0.5 m s^{-1} and flow depths between 5 and 30 cm

Fish selected flow velocities equal to or higher than the mean cross-sectional flow velocity in the culvert for all trials, except the third (Figure 20). In this trial, they selected focal velocities ~ 40% lower than the mean cross-sectional velocity (mean velocity preference ratio = 0.6).

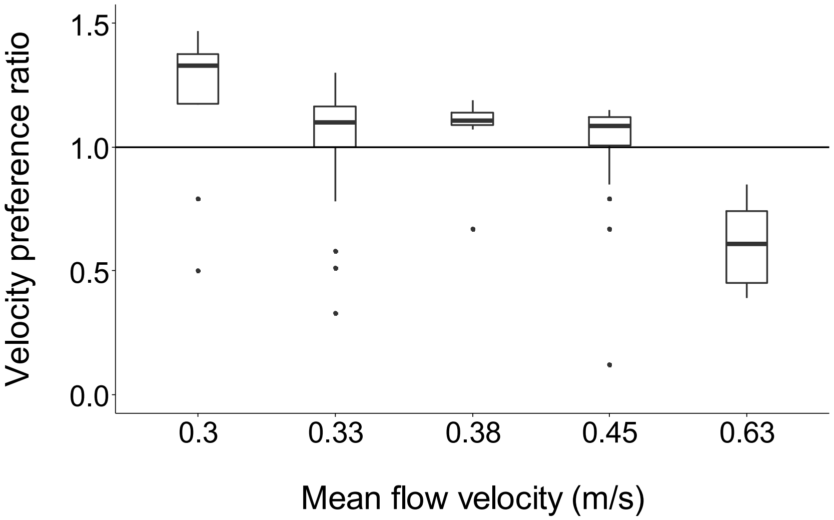

Figure 20: Velocity preference ratio in function of mean flow velocity in the culvert. The ratios are calculated as the mean velocity selected by the fish during an ascent, divided by the mean velocity in the culvert. Trout selected velocities higher or equal to the mean velocity in the culvert. At the highest mean velocity (0.63 m s^{-1}), however, they selected paths corresponding to velocities ~ 40% lower than the mean one.

Among the nine models tested for the velocity preference ratio, only one emerged as providing a good fit to the data (Table 13). This best-fitting model included only mean flow velocity as a covariate, as well as a random effect on trial. The velocity preference ratio decreased when the mean water velocity was increasing (Table 14). This means that fish were more incline to select lower velocities when the mean velocity in the culvert was higher.

Table 13: Model selection based on the Akaike information criterion (AIC)

Velocity preference ratio

Model $_i$	**RE**	**-2 log (L)**	**K**	**AIC $_i$**	**Δ $_i$ AIC**	**w $_i$**
Flow velocity	**(1 |Trial)**	**-1,643**	**4**	**11,2800**	**0,00**	**1,00**
Flow velocity + flow depth + flow velocity*flow depth	(1 |Trial)	-3.615	6	19,23	7,95	0,00
Flow depth	(1 |Trial)	-6,862	4	21,71	10,43	0,00
Flow velocity +fish length	(1 |Trial)	-7,565	5	25,13	13,85	0,00
Fish length	(1 |Trial)	-11,146	4	30,29	19,01	0,00
Null	(1 |Trial)	-12,528	2	29,06	17,77	0,00

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

Table 14: Parameters' estimates for the best-fitting model

Velocity preference ratio

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

Note: Estimates (β) and standard errors (± SE) of parameters for the best-fitting model for the mean velocity preference ratio of all fish tested in the five trials (n = 84). The best-fitting model includes only the mean flow velocity as a predictor. The mean preference velocity ratio decreases at higher flow velocity. The variance of the random effect on trial was very small, indicating little unobserved variability between trials.

Transit time was similar across trials, with median values ranging from 10 to 20 s (Figure 21). The distribution was skewed to the left, with most individuals having short transit times and a few ones having long transit times, up to 150 s. These individuals were present in every trial, except the third one, and they correspond to trout alternating continuous swimming with rest periods.

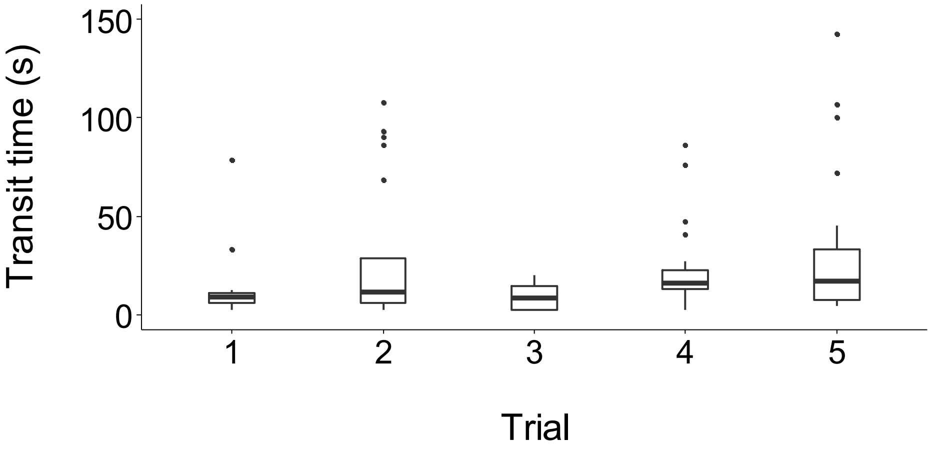

Figure 21 : Transit times for each trial. The amount of time spent in the zone covered by the camera was similar among trials and corresponded to a median value of ~ 12 seconds. Some trout had longer transit times, due to rest periods during their ascents. This behavior was however not observed in the third trial.

DISCUSSION

This study describes wild fish ascent paths in a culvert located in their natural environment. Other studies have however made visual observations of juvenile fish swimming in culverts (Behlke *et al.*, 1988, Matthew David Blank, 2008, Kane *et al.*, 2000). Despite the limited range of tested flow velocities, we believe the present results bring an interesting insight on fish ascent behavior in culverts.

In the current study, trout exhibited preference for a median flow velocity of 0.4 m s^{-1} and were able to quickly orient to find them in the culvert. Locations with flow velocities slower than 0.25 and higher than 0.5 m s^{-1} were rarely selected during the ascents. This may be due to distinct causes. At low flow conditions, velocities > 0.25 m s^{-1} may be more attractive to trout and increase their motivation to swim upstream. During the trials with mean flow velocities < 0.5 m s^{-1}, fish occupied a larger area of the flow cross-sectional area. Groundspeeds, or transit times, were consistent among trials, despite a twofold range of mean flow velocity.

Some individuals however used the lee of the corrugations, either to swim in parallel of those or to hold positions, with their body oriented perpendicular to the flow. Similar behavior was also observed in the study from Kane and al. (2000). Interestingly, all of the fish exhibiting periods with minimal body motions had a total body length < 150 mm. The spacing between the corrugations was also 150 mm, suggesting a mechanistic influence on behavior.

At the highest flow, fish selected locations with velocities slower than the mean velocity in the culvert, which could indicate that the level of challenge was increasing. Movement was also more directed, with no period of reduced activity in the corrugations. Paths were located close to the walls, in shallow depths. For brook trout, the transition from sustained to prolonged swimming mode, and thus from the aerobic to the anaerobic metabolism, occurs when the flow velocity is located between 2.5 to 4 bodylengths (Peake 2008). The mean fish length being 115 mm in the current study, this transition should occur at ~ 0.45 m s^{-1}.The behavior observed in the trial with the mean velocity of 0.65 m s^{-1} may correspond to fish selecting locations with slower velocities to try to avoid the transition to the anaerobic metabolism.

This behavior was also observed in studies performed in an experimental culvert, where most fish ascended the culvert by swimming close to the walls at higher discharge (Powers *et al.*, 1997, Thurman *et al.*, 2007) or exit the culvert on the right side of inlet (Johnson *et al.*, 2012), as well as in field culverts (Behlke *et al.*, 1988, Kane *et al.*, 2000). The current results however differed of the ones from Castro-Santos (2013), where trout swam mostly halfway between the center and the walls of a smooth open flume, at velocities close to mean cross-sectional channel velocity. That study was performed under high flow velocities (1.6 to 2.5 m s^{-1}), where fish used the prolonged or sprint mode, and results are therefore hard to compare with those of the current study. A previous study (Goerig *et al.*, 2016) indicated that passage success of brook trout through culverts was higher in corrugated culverts (~ 75-90%) than in smooth ones (~30-50%) at flow velocity of 1 m s^{-1}. This could be explained by the higher hydraulic complexity in corrugated culverts and the existence of reduced velocity zones which fish could use during their ascents. The level and structure of turbulence may also be higher in corrugated culverts (Richmond *et al.*, 2007), and it will be important to understand better how this affect both swimming capacity and behavior.

When modelling the effect of hydraulic or biological factors on the velocity preference ratio, only the mean flow velocity in the culvert was retained as an explanatory variable. Surprisingly, the fish body length was not retained as a predictor, large trout being as likely to select reduced flow velocities as small ones.

The current study shows that trout had a strong preference for velocities between 0.25 and 0.5 m s-1 and that they used velocities ~ 40% slower than the mean velocity in the culvert when flow increased. This is similar to the 0.4 to 0.6 correction factor for the mean velocity developed by Behlke (1991). The current study has limitations because it monitored only a small area in the culvert over a limited range of hydraulic conditions. However, the methods used can easily be applied to a larger study, with an emphasis on testing a wider range of velocities, characterizing turbulences and fish ascent paths along the entire culvert. This would allow to further develop correction factors for use in predictive fish passage models.

ACKNOWLEDGEMENTS

Support for this research was provided by INRS–Centre Eau, Terre et Environnement, the Ministère des Transports du Québec, the Fonds de la Recherche forestière du Saguenay-Lac-Saint-Jean and research scholarships from the Natural Sciences and Engineering Research Council of Canada and the Fonds de recherche Nature et Technologies du Québec. Any use of trade, product, or firm names is for descriptive purposes only and does not imply endorsement by the Canadian or US governments. We thank the research assistants who helped conduct the field work: H. Bouchard, F. Pichon and C. Larouche. We also extend special thanks to P. Marcotte for his hard work with the experimental design and implementation of the study, F. Bérubé and S. Dugdale for the development of a custom digitizing program, as well as to J. Noreika for his generous assistance with the hydraulic data processing.

REFERENCES

Barber, M.E., and Downs, R.C. 1996. Investigation of culvert hydraulics related to juvenile fish passage.

Behlke, C.E., Kane, D.L., McLean, R.F., Reynolds, J.B., and Travis, M.D. 1988. Spawning migration of Arctic grayling through Poplar Grove Creek culvert, Glennallen, Alaska, 1986.

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

Castro-Santos, T. 2005. Optimal swim speeds for traversing velocity barriers: an analysis of volitional high-speed swimming behavior of migratory fishes. J Exp Biol **208**(3): 421-432. doi: 10.1242/jeb.01380.

Chow, V.T. 1959. Open-channel hydraulics. McGraw Hill Book Company.

Furniss, M., Love, M., Firor, S., Moynan, K., Llanos, A., Guntle, J., and Gubernick, R. 2008. FishXing, Version 3.0. US Forest Service, San Dimas Technology and Development Center, San Dimas, CA. Also available at www. stream. fs. fed. us/fishxing.

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

Goerig, E., Castro-Santos, T., and Bergeron, N.É. 2016. Brook trout passage performance through culverts. Canadian Journal of Fisheries and Aquatic Sciences **73**(1): 94-104. doi: doi:10.1139/cjfas-2015-0089.

Johnson, G.E., Pearson, W.H., Southard, S.L., and Mueller, R.P. 2012. Upstream Movement of Juvenile Coho Salmon in Relation to Environmental Conditions in a Culvert Test Bed. Transactions of the American Fisheries Society **141**(6): 1520-1531. doi: 10.1080/00028487.2012.699013.

Kane, D.L., Behlke, C.E., Gieck, R.E., and McLean, R.F. 2000. Juvenile fish passage through culverts in Alaska: A field study.

Liao, J.C. 2004. Neuromuscular control of trout swimming in a vortex street: implications for energy economy during the Kármán gait. Journal of Experimental Biology **207**(20): 3495-3506. doi: 10.1242/jeb.01125.

Peterson, N.P., Simmons, R.K., Cardoso, T., and Light, J.T. 2013. A Probabilistic Model for Assessing Passage Performance of Coastal Cutthroat Trout through Corrugated Metal Culverts. North American Journal of Fisheries Management **33**(1): 192-199. doi: 10.1080/02755947.2012.750633.

Powers, P.D., Bates, K., Burns, T., Gowen, B., and Whitney, R. 1997. Culvert hydraulics related to upstream juvenile salmon passage. *Edited by* W.D.o.F.a. Wildlife.

Quinn, G.P., and Keough, M.J. 2002. Experimental design and data analysis for biologists. Cambridge University Press, New York. p. 537.

R Core Team. 2015. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

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

Sanz-Ronda, F.J., Ruiz-Legazpi, J., Bravo-Córdoba, F.J., Makrakis, S., and Castro-Santos, T. 2015. Sprinting performance of two Iberian fish: Luciobarbus bocagei and Pseudochondrostoma duriense in an open channel flume. Ecological Engineering **83**: 61-70. doi: http://dx.doi.org/10.1016/j.ecoleng.2015.05.033.

Thurman, D.R., Horner-Devine, A.R., Morrison, R.R., and Hotchkiss, R.H. 2007. Juvenile Salmon Passage in Sloped-Baffled Culverts.

Von Karman, T. 1931. Mechanical similitude and turbulence.

Xiong, G., and Lauder, G.V. 2014. Center of mass motion in swimming fish: effects of speed and locomotor mode during undulatory propulsion. Zoology **117**(4): 269-281.