Université du Québec

INRS Institut national de la recherche scientifique

Centre Eau, Terre et Environnement

MOUVEMENTS ET UTILISATION DE L'HABITAT PAR LE SAUMON ATLANTIQUE (SALMO SALAR) LORS DE LA COLONISATION D'UN NOUVEL HABITAT

Investigating the drivers of Atlantic salmon movements and habitat use during colonization of a novel habitat

Par

Danielle M. Frechette

Thèse présentée pour l'obtention
du grade de Philosophiae Doctor (Ph.D.)
en sciences de l'eau

Jury d'évaluation

Président du jury et examinateur interne	Valérie Langlois INRS-ETE
Examinateur externe	Katrine Turgeon Université du Québec en Outaouais
Examinateur externe	William Ardren US Fish & Wildlife Service
Directeur de recherche	Normand E. Bergeron INRS-ETE
Codirecteur de recherche	Julian Dodson Université Laval

REMERCIEMENTS

Research funding for this work was provided by the *Programme de mise en valeur des habitats du saumon de la Côte-Nord*, the *Atlantic Salmon Conservation Foundation* and an *NSERC Discovery grant* to Normand Bergeron. Funding for my studies in Quebec was provided by the *Fonds de recherche du Québec - Nature et technologies (FRQNT) Merit Scholarship Program for Foreign Students*.

The work presented in this thesis would not have been possible without the help and support of a large number of people.

First and foremost, I want to thank Normand, Julian, and Mélanie Dionne, who all independently welcomed me to Quebec during a whirlwind trip in 2011, long before this project even began to take shape, long before we knew that we would all be working together. Normand, thank you for your support throughout this process, for always having my back, and for pushing me to think as much about the habitat as I thought about the fish – through this you have helped me to become a more holistic biologist. I have truly enjoyed my time in your lab. Julian, I am honored that you chose to come out of retirement to serve as my co-director for this project. Thank you for encouraging me to think more analytically about fish movement patterns: your insights have been invaluable in shaping the thermal refuge and movement chapters. Mélanie, thank you for your encouragement throughout this process, and for reminding me to consider how the impacts of the translocation on the genetics of the salmon population.

The Ministère de la Faune, des Forêts, et des Parcs du Québec was an invaluable research partner during the course of this work, and provided support in the form of equipment, field assistance, and logistics, without which this work would not have been possible. Serge Gravel and Marc Valentine surveyed the river for hazards and helped in the creation and first deployment of the telemetry array. Vanessa Cauchon helped me assemble field equipment, trained me to surgically tag the salmon, and helped me to get organized when I did not speak French. Julien April and Karine Gagnon provided staff and logistical support. Mathieu Roberge, Mathieu McCann and O. Flamand provided much needed help and fun in the field.

I would also like to thank the Association de la Rivière Sainte-Marguerite and the Corporation de Pêche Ste-Marguerite for their vital collaboration and support of this research, especially the members of the ARSM board, Claude Poirier, Martin Murdock, Pierre Rousseau, Réjean Gagnon. Valérie Maltais – thank you for everything you did during the course of this project: your insights about the fish, your help in the field, but most importantly for your friendship – I could not have accomplished this without you!

Thanks also to the members of Labo Bergeron and CIRSA that participated in this work along the way, especially: JB Torterotot for helping me navigate my first field season when I spoke no French; Elsa Goerig and Steve Dugdale for becoming collaborators; Joanie Carrier, for being the third member of Team Filles; Sébastien Ouellet-Proulx for brainstorming and translation; François Caron for sharing his extensive knowledge of salmon in Québec; Jérémie Isabelle, Marie-Camille St-Amour and Ian Bergeron for helping to tag salmon; Joannie Beaupré for electro-fishing help. Et enfin, un gros merci à mon professeur de français André Boivin. Merci de m'avoir appris à naviguer en canoë sur la rivière et pour toute ton aide sur le terrain!

Thank you to André St-Hilaire, Gaétan Daigle, Ted Castro-Santos and Jon Lefcheck for providing statistical advice and to Mathilde Renaud, Orion Zydlewski, Nicola Mayot, and Sébastien Ouellet-Proulx for help with translation.

Thank you to my family – especially to my dad for piquing my interest in the outdoors, and my mom for not getting too mad when I came home all muddy from playing in the woods. Thank you to my international Québec family for fun, support, and lots of good food and laughs. And of course, thank you to Thew: my partner, my lobster, the whole reason I moved to Québec – without you I never would have found this project, the people, and the place that I love and am happy to have called home.

Finally, this thesis is dedicated to Gayle Skye. May there always be salmon in the rivers for you to enjoy.

RÉSUMÉ

La capture et le transport des salmonidés est une pratique commune qui permet aux adultes en migration vers l'amont et aux smolts en phase de dévalaison de contourner les barrières anthropiques à la migration, telles que les barrages hydroélectriques. Le transfert de saumons reproducteurs dans un habitat inutilisé est de plus en plus envisagée comme moyen d'accroître la population par les programmes de rétablissement des salmonidés. Une compréhension approfondie de la manière dont le saumon adulte utilise l'espace lors de la colonisation est cependant essentielle afin de garantir que ces programmes atteignent les résultats souhaités en matière de conservation. Cette thèse vise à améliorer notre compréhension des schémas de migration et d'utilisation de l'habitat par le saumon atlantique adulte (*Salmo salar*) après un transfert, en relation avec les conditions environnementales et les caractéristiques intrinsèques du poisson.

Ce travail a été fait au cours d'un programme de colonisation mis en œuvre sur la Rivière Sainte-Marguerite Nord-Est (Québec) de 2014 à 2016. Le programme de colonisation impliquait de transporter des adultes dans un nouvel habitat en amont d'une paire de chutes infranchissables, dans le but de réduire les effets de la densité sur la croissance et la survie des juvéniles. Tous les saumons transportés ont été marqués avec des émetteurs acoustiques et suivis à l'aide d'une série de récepteurs acoustiques afin d'examiner leurs déplacements et l'utilisation de l'habitat. Au total, 68 saumons atlantiques ont été transportés et marqués pendant les trois années de l'étude.

La majorité des saumons transportés sont restés dans le nouvel habitat [58% en 2014 (7 sur 12); 72% en 2015 (18 sur 25); 68% en 2016 (21 sur 31)]. Les résultats d'une analyse de survie effectuée à l'aide d'un modèle de risques proportionnels de Cox ont montré que la longueur à la fourche était l'unique facteur influençant de façon positive le retour vers l'aval suite au transport. Ni les conditions du transport ni les conditions environnementales dans la rivière après le transport ne semblaient affecter significativement le taux de retour vers l'aval. Enfin, le taux de retour vers l'aval est très peu variable en fonction des années.

L'utilisation d'une combinaison de techniques incluant la télémétrie acoustique, l'imagerie infrarouge thermique et la surveillance de la température des rivières, a montré que, bien que la température du chenal principal de la rivière Sainte-Marguerite Nord-Est est demeuré relativement fraîche (< 23 °C) pendant l'étude, certaines fosses ont été utilisées par les saumons adultes comme refuges frais au cours de la période la plus chaude de l'été. Les résultats indiquent que cette thermorégulation comportementale s'est produite à une température moins chaude qu'anticipée par des études précédentes sur l'utilisation de ces refuges thermiques par les saumons atlantiques juvéniles et adultes. Ces résultats soulignent l'importance 1) d'associer les méthodes aériennes et terrestres afin d'identifier les refuges thermiques appropriés pour le saumon adulte et 2) de considérer la présence/absence de refuges thermiques lors de la sélection de tronçons pour les programmes de colonisation.

La mesure en simultané de la température de l'eau et du débit de la rivière, combinée à des positionnements à haute résolution spatiale et temporelle des saumons obtenus à l'aide de la télémétrie acoustique (de la remise en liberté dans le nouvel habitat jusqu'au début de la fraie) ont servi à montrer que le sexe du poisson, les conditions environnementales et la morphologie de la rivière influençaient le déplacement et l'utilisation de l'habitat par les individus restés dans l'habitat colonisé. Les saumons ont démontré deux types de schémas de déplacement : le type « sédentaire » effectuant peu de déplacements sur de courtes distances et le type « explorateur » effectuant beaucoup de déplacements et sur de longues distances. Les résultats indiquent que les femelles avaient plus tendance à être sédentaires indépendamment de la température ou du débit, comparativement aux mâles qui étaient plus souvent sédentaires lors de fortes températures et lorsque le débit était élevés. De toutes les caractéristiques physiques mesurées, la taille de la fosse était la variable de l'habitat la plus importante pour déterminer si une fosse de rétention était adéquate, les fosses les plus grandes et les plus profondes étant fréquentées plus souvent.

Cette étude a permis d'obtenir une image détaillée, avec une haute résolution spatiale et temporelle, des schémas de déplacements et d'utilisation de l'habitat par le saumon atlantique adulte lors de la colonisation d'une rivière naturelle non régulée en lien avec les variables biotiques et abiotiques. Une compréhension approfondie de la manière dont les saumons colonisent un nouvel habitat sera un atout précieux pour optimiser de futurs programmes de réintroduction et de colonisation.

Mots-clés : *Salmo salar,* télémétrie, refuges thermiques, télédetection, migration, retour vers l'aval, température

ABSTRACT

Translocation of salmonids is a common practice to enable upstream migrating adults or downstream migrating smolts to bypass anthropogenic barriers to migration, such as hydroelectric dams or adverse habitats. Translocation of breeding adult salmon into vacant habitat as a means of population enhancement is increasingly being considered as part of salmonid recovery programs. Thorough understanding of how adult salmon use space during colonization is essential to ensuring that such programs achieve desired conservation outcomes. This thesis therefore aims to improve our understanding of migration patterns and habitat use by adult Atlantic salmon (*Salmo salar*) in relation to environmental conditions and intrinsic fish characteristics following transport and release into novel habitat.

This work was conducted in conjunction with a colonization program that operated in the Rivière Sainte-Marguerite Nord-Est (Quebec) from 2014-2016. The colonization program entailed trapping a subset of returning adults for transport into novel habitat upstream of a pair impassible waterfalls, with the goal of reducing density-dependent effects on juvenile growth and survival. All salmon released into the novel habitat were tagged with acoustic transmitters and tracked using an array of acoustic receivers to examine movement patterns and habitat use. A total of 68 adult Atlantic salmon were transported and tagged during the three years of the study.

The majority of transported salmon remained in the novel habitat [58% in 2014 (7 of 12); 72% in 2015 (18 of 25); 68% in 2016 (21 of 31)]. Post-transport fallback (movement out of the novel habitat) occurred within seven days of release. Application of time-to-event analysis using Cox proportional hazards regression indicated that larger fish had a greater propensity to fallback. Neither conditions experienced during transport nor environmental conditions experienced in-river after transport appeared to significantly affect the fallback rate, and there was no apparent variability in fallback rate among years.

A novel combination of acoustic telemetry, thermal infrared remote sensing, and river temperature monitoring indicated that although mainstem river temperature in the Nord-Est was relatively cool and did not exceed 23°C, adult salmon used large mainstem pools as cool refuges during the warmest period of the summer at substantially cooler ambient river temperatures than expected from previous studies that described thermal refuge use by juvenile and adult Atlantic salmon. These findings highlight the importance of 1) combining aerial and ground-based methods to identify suitable thermal refuges and 2) prioritizing river basins or reaches that contain adequate thermal refuges to support adult salmon when selecting habitat for colonization programs.

Simultaneous measurement of river temperature and discharge, combined with discrete positions of salmon at high spatial and temporal resolution obtained using acoustic telemetry indicated that fish sex, environmental conditions, and river morphology influenced movement patterns and habitat use by individuals that remained in colonization habitat. Salmon exhibited two primary movement patterns: an exploratory pattern characterized by many long-distance movements, and a sedentary movement pattern characterized by fewer, short-distance movements. Sex and river temperature had the greatest influence on the type of movement pattern exhibited by a given individual on a given day. Females were more likely to be sedentary regardless of the river temperature or discharge and males were more likely to be sedentary at high temperature and high discharge. Of the physical features measured, pool size was the most important habitat feature defining suitable holding pools, with larger and deeper pools being used more often.

This study provided a detailed picture of the movement patterns and habitat use by adult Atlantic salmon during the colonization of a pristine, unregulated river in relation to biotic and abiotic variables at a high spatial and temporal resolution. Thorough understanding of how salmon colonize novel habitat will be a direct asset for optimizing future reintroduction and colonization programs.

Keywords : *Salmo salar*, telemetry, remote sensing, migration, fallback, temperature

SOMMAIRE RÉCAPITULATIF

Introduction

Le saumon atlantique (*Salmo salar*) est un membre de la famille des salmonidés que l'on retrouve dans les bassins versants tempérés et subarctiques qui drainent vers l'océan Atlantique (Thorstad et al. 2011). Le saumon atlantique est un poisson anadrome; il pond ses oeufs en eau douce où il séjourne d'une à plusieurs années avant de subir des changements physiologiques qui lui permettent de migrer vers l'océan. La croissance en milieu marin permet aux saumons de tirer profit des ressources abondantes pour atteindre de plus grandes tailles et une meilleure fécondité que les poissons qui sont strictement limités aux habitats d'eau douce (Fleming 1998). Après un séjour en mer qui dure entre un et quatre ans, les saumons atlantiques adultes reviennent frayer en eau douce dans les rivières où ils sont nés (Thorstad et al 2011). Les saumons atlantiques sont itéropares, ce qui signifie qu'ils peuvent se reproduire plus d'une fois, à la différence de la plupart des saumons du Pacifique qui sont sémelpares et meurent après la reproduction. Donc, si un saumon atlantique survit à sa première reproduction, il retourne à l'océan et peut par la suite revenir frayer en eau douce plusieurs fois au cours de sa vie (Fleming 1998).

La répartition historique de l'espèce s'étendait des bassins versants du sud de la Nouvelle-Angleterre en passant par les Maritimes jusqu'à la baie d'Ungava dans le nord et en Eurasie du Portugal jusqu'en Russie (Figure S1). Les impacts de l'activité humaine sur les écosystèmes marins et d'eau douce ont causé une réduction des populations de saumon atlantique (*Salmo salar*) dans la majeure partie de leur aire de répartition mondiale et plusieurs sous-populations sont aujourd'hui disparues ou en voie de l'être (Thorstad et al 2011). Dans l'Est du Canada, certaines populations sont classées en voie de disparition, menacées, ou dont le statut est préoccupant par le Comité sur la situation des espèces en péril au Canada (COSEPAC). Le déclin des populations est attribuable à la perte d'habitats d'eau douce et à une réduction de la survie en mer liée aux changements dans l'écosystème (COSEWIC 2010).

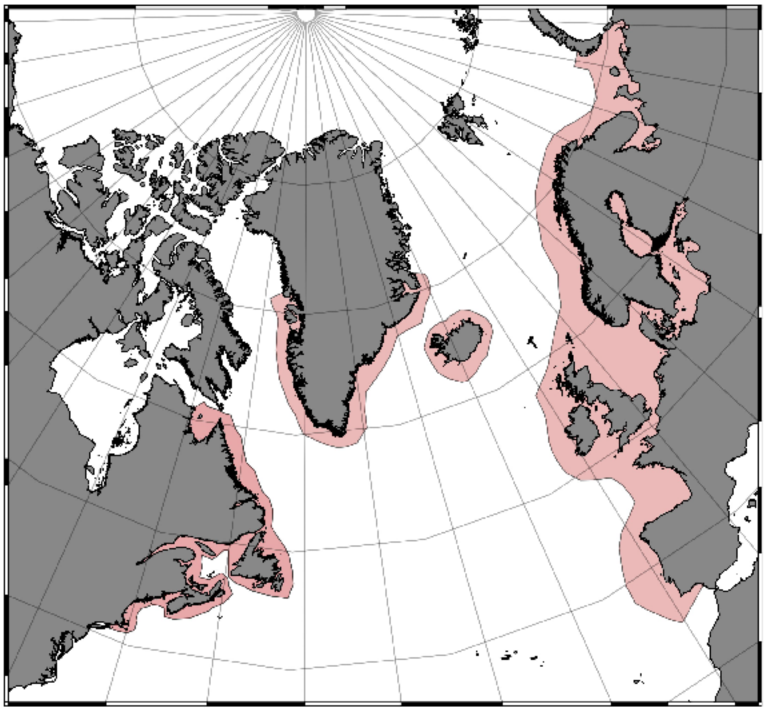


Figure S1. Atlantic Salmon Range

Carte de l'aire de répartition mondiale de l'étendue historique du saumon atlantique. Adapté de Thorstad et al 2011 en utilisant la version 2.18 de QGIS.

En dépit du statut précaire des populations, la pêche au saumon atlantique a une grande valeur économique, en particulier dans le secteur de la pêche récréative. La pêche au saumon atlantique dont la valeur dans l'économie canadienne était estimée en 2011 à plus de 250 millions de dollars par année supporte l'équivalent de 3 872 emplois à temps plein (ASF 2011). La conservation des populations de saumon dans l'est du Canada est donc importante sur le plan écologique et économique. De plus en plus d'attention est portée au rôle de la réduction de la survie en mer comme facteur limitant des populations de saumon atlantique. Cependant, à l'exception d'une diminution des prises en mer, la plupart des actions posées en vue de conserver et augmenter les populations de saumon le sont en eau douce, avec un accent sur la restauration de l'habitat, l'amélioration du calcul des limites de pêche et la mise en valeur des stocks (DFO 2015).

Une des méthodes les plus utilisées pour la mise en valeur des stocks de salmonidés est la production de saumons juvéniles dans des stations piscicoles pour ensuite les relâcher dans des écosystèmes naturels. Ces stations piscicoles sont utilisées depuis plus d'un siècle pour améliorer le succès des pêches récréative et commerciale ou pour atténuer les réductions dans les populations sauvages causées par la perte ou la dégradation d'habitats (Fisch et al. 2015, Kostow 2009). Ces stations permettent de produire et de relâcher dans la nature des saumons juvéniles aux différents stades de développement : oeuf, alevin, tacon et smolt. La relâche en milieu naturel de saumons à un certain stade de développement permet d'éviter le risque de mortalité associé aux stades précédents et ainsi accroît leur survie jusqu'à l'âge adulte.

La production de saumons en stations piscicoles est cependant associée à un ensemble de risques génétiques et écologiques. La fraie artificielle et le nombre généralement restreint de géniteurs utilisés dans les programmes d'introduction réduisent la taille efficace et la diversité génétique de la population et augmentent la consanguinité (Christie et al. 2012, Ryman et Laikre 1991). Une telle perte de diversité génétique peut rendre les populations plus vulnérables aux perturbations environnementales (Schindler et al. 2010, Carlson et Satterthwaite 2011). Les individus produits en écloseries ont souvent une moins bonne croissance, une survie réduite et un moins bon succès reproducteur que leurs congénères d'origine naturelle (Araki et Schmid 2010). Par exemple, les smolts élevés dans des stations piscicoles peuvent avoir plus tendance à demeurer près de la surface que les smolts sauvages, ce qui augmente leur susceptibilité à la prédation (Collis et al. 2001). De plus, lorsque des poissons produits en écloseries sont introduits en milieu naturel aux stades d'oeuf, d'alevin ou de tacon, ils peuvent faire compétition aux individus d'origine naturelle ou être des vecteurs de maladies (Naish et al. 2008, Kostow 2009, Anderson et al. 2014). Les préoccupations croissantes à propos des impacts négatifs de la production de salmonidés en stations piscicoles ont mené à la recommandation de mettre fin aux programmes qui ne répondent pas à un « besoin social ou biologique démontré » (Fisch et al. 2015, Kostow 2009).

La prise de conscience des risques liés à la propagation d'individus provenant des stations piscicoles a mené à un ensemble de solutions de rechange basées sur le processus naturel de reproduction de l'espèce en améliorant la fraie en rivière (Fraser 2008). Permettre à des saumons adultes de se reproduire en milieu naturel au lieu d'ensemencer avec des juvéniles produits en écloseries peut réduire les impacts évolutifs sur la population grâce à l'action de la sélection sexuelle, absente des programmes de fraie en stations piscicoles, mais présente en milieu naturel (Anderson et al. 2010). À la différence des juvéniles ensemencés, les jeunes d'origine naturelle auront été exposés aux prédateurs et se seront nourris par eux-mêmes, permettant ainsi à la sélection naturelle d'agir. De plus, ces jeunes d'origine naturelle auront été exposés à l'environnement biotique et abiotique local durant tout leur cycle de vie, ce qui peut faciliter l'adaptation locale (Taylor 1991, Anderson et al. 2014). L'adaptation au milieu local engendre des différences adaptatives entre les populations et est considérée comme extrêmement importante pour la persistance des stocks de salmonidés, particulièrement pour leur permettre de faire face aux perturbations environnementales (Hilborn et al. 2003, Carlson et Satterthwaite 2011, O'Toole et al. 2015).

Les programmes conçus pour augmenter la reproduction en milieu naturel requièrent divers niveaux d'intervention humaine. Dans les programmes de réintroduction, on permet à des adultes reproducteurs d'accéder à des habitats situés à l'intérieur de leur aire de répartition historique dans lesquels leurs populations ont été extrêmement réduites ou sont même disparues. Par exemple, les habitats en amont de barrages ou d'autres infrastructures qui bloquent l'accès aux aires de fraie et d'élevage en amont (Anderson et al. 2014). Dans les programmes de colonisation, on permet à des saumons d'accéder à des parties de rivières qui possèdent des habitats de fraie et d'élevage adéquats, mais qui sont inaccessibles aux adultes en montaison en raison de barrières naturelles à la migration comme de hautes chutes d'eau (Bryant et al. 1999). Les programmes de réintroduction et de colonisation peuvent utiliser des individus élevés en rivière de façon naturelle ou dont les parents ont frayé dans des stations piscicoles. Dans certains cas, la réintroduction ou la colonisation peut se baser sur des programmes d'élevage en captivité dans lesquels des juvéniles sauvages sont capturés pour ensuite être élevés jusqu'à maturité dans des bassins d'eau douce ou salée ou dans des cages en mer (Fraser 2008, O'Reilly et Kozfkay 2014, Kozfkay 2015).

Les deux approches les plus utilisées dans les programmes de réintroduction ou de colonisation sont le passage volontaire et le transport d'individus par camion, barge, ou dans certains cas, par hélicoptère. Dans le cas du passage volontaire, une barrière à la migration (par exemple un barrage dans le cas de réintroduction ou une chute d'eau dans le cas de colonisation) est retirée ou modifiée (par exemple en installant une passe migratoire) de manière à permettre aux saumons en montaison d'atteindre l'habitat de fraie par leurs propres moyens. Dans des programmes de capture-transport, des saumons en montaison sont capturés à une barrière de migration et transportés en amont dans un aquarium (Anderson et al. 2014). Cette approche est nommée ci-après « translocation ».

Sans une compréhension approfondie de la manière dont les saumons exploitent l'espace une fois introduit dans le « nouvel » habitat, il est difficile de déterminer si les programmes de réintroduction et de colonisation atteindront le résultat escompté qui est d'augmenter la productivité de la population par l'établissement (ou le rétablissement) d'une population. Les patrons de migration, l'utilisation de l'habitat et les déplacements des saumons adultes sont influencés par un ensemble de facteurs extrinsèques et intrinsèques. L'hydrologie et la géomorphologie de la rivière façonnent l'habitat du poisson et influencent la migration de fraie en modifiant la difficulté de la montaison, ce qui détermine le temps et l'énergie nécessaire pour atteindre les frayères (Milner et al. 2012). Ces facteurs peuvent également limiter la disponibilité des fosses de rétention adéquates où les saumons se reposent avant de poursuivre leur migration (Bardonnet et Bagliniere 2000, Milner et al. 2012). Le métabolisme des saumons augmentant avec la température, les individus dépensent plus d'énergie à la nage lorsque la température de la rivière est élevée (Martin et al. 2015). Les coûts énergétiques accrus durant la migration peuvent réduire la valeur adaptative de la reproduction, soit par une réduction de la quantité d'énergie pouvant être allouée à l'activité de fraie et/ou au développement des gonades, soit par une augmentation de la mortalité suite à la fraie, ce qui affecte négativement la reproduction les années suivantes chez les espèces itéropares (Thorstad et al. 2008). Le sexe, la taille et la proximité avec la période de fraie peuvent également influencer le patron de migration d'un individu (Baglinière et al. 1990, Baglinière et al. 1991, Dahl et al. 2004, Thorstad et al. 2008, Richard et al. 2014). Le stress lié à la manipulation peut faire en sorte que les individus quittent l'habitat choisi pour la colonisation ou la réintroduction, réduisant ainsi le nombre de parents disponibles pour la fraie et les gains potentiels dans la productivité de la population. Caractériser les patrons de migration et d'utilisation de l'habitat des individus relâchés et examiner comment ces patrons sont influencés par les facteurs biotiques et abiotiques aidera les gestionnaires à choisir les habitats et les individus pour la réintroduction et à s'assurer que le transport est fait dans des conditions optimales pour le succès de l'établissement d'une population de fraie. De telles informations sont donc essentielles au succès des programmes de réintroduction et de migration assistée qui visent à augmenter et à protéger les populations de salmonidés (Thorstad et al. 2008).

Bien que les programmes de réintroduction de salmonidés soient de plus en plus utilisés comme stratégie pour conserver et augmenter les populations (Anderson et al. 2014, O'Reilly et Kozfkay 2014, Askling 2015, Izzo et al. 2016), les programmes de colonisation sont quant à eux assez rares en raison des risques qu'ils posent pour les espèces aquatiques résidentes (MFFP 2016). Les effets négatifs décrits précédemment liés à l'introduction de salmonidés provenant d'écloseries ont fait que cette approche est beaucoup moins utilisée qu'auparavant au Québec pour augmenter les populations de saumons atlantiques. Son utilisation est limitée aux rivières qui n'ont pas atteint un seuil déterminé de conservation et font face à de graves problèmes d'abondance (MFFP 2016). Ainsi, dans certaines conditions, la colonisation en tout ou en partie de plans d'eau dans lesquels les saumons étaient absents est une stratégie maintenant acceptée pour augmenter les populations et est évaluée au cas par cas. Le raisonnement derrière cette stratégie repose sur l'hypothèse que la production de smolts est limitée par la densité de tacons, donc en augmentant la quantité d'habitats disponibles pour la fraie, on réduit les effets de la densité sur la survie des tacons ce qui augmentera la production de smolts et se traduira par un nombre accru d'adultes qui reviendront à la rivière (Bley et Moring 1988, MFFP 2016).

Site d'étude

Entre 2014 et 2016, un programme de translocation a été mise en oeuvre sur la branche Nord-Est de la rivière Sainte-Marguerite au Québec. Ce programme a fourni une occasion unique d'examiner les patrons de déplacement et l'utilisation de l'habitat par les saumons atlantiques adultes durant la colonisation d'un nouvel habitat. Le bassin versant de la rivière Sainte-Marguerite Nord-Est couvre une superficie d'environ 1000 km^2. La branche Nord-Est rejoint la rivière Sainte-Marguerite à 5 km en amont de la confluence avec le fjord de Saguenay (Figure 1.1). Une passe migratoire a été installée sur la rivière Sainte-Marguerite Nord-Est en 1981 pour permettre aux poissons de franchir la chute Blanche au point kilométrique 7. Avant que cette passe ne soit installée, les saumons adultes pouvaient accéder à seulement

7 km de la rivière. La passe migratoire a ouvert 18 km de rivière supplémentaire pour la fraie et l'élevage des jeunes. Plus en amont, le passage des poissons est bloqué par une paire de chutes infranchissables aux points kilométriques 33,7 (chute du 16 miles) et 36,2 (chute du 18 miles). En 2014, un programme de translocation a été initié pour capturer un sous-groupe d'adultes revenant à la passe migratoire de la chute Blanche et les transporter en amont de la chute du 18. Les saumons adultes transportés pouvaient alors accéder à entre 13 et 25 km de la rivière selon si la chute André était franchissable ou non (Figure S.2).

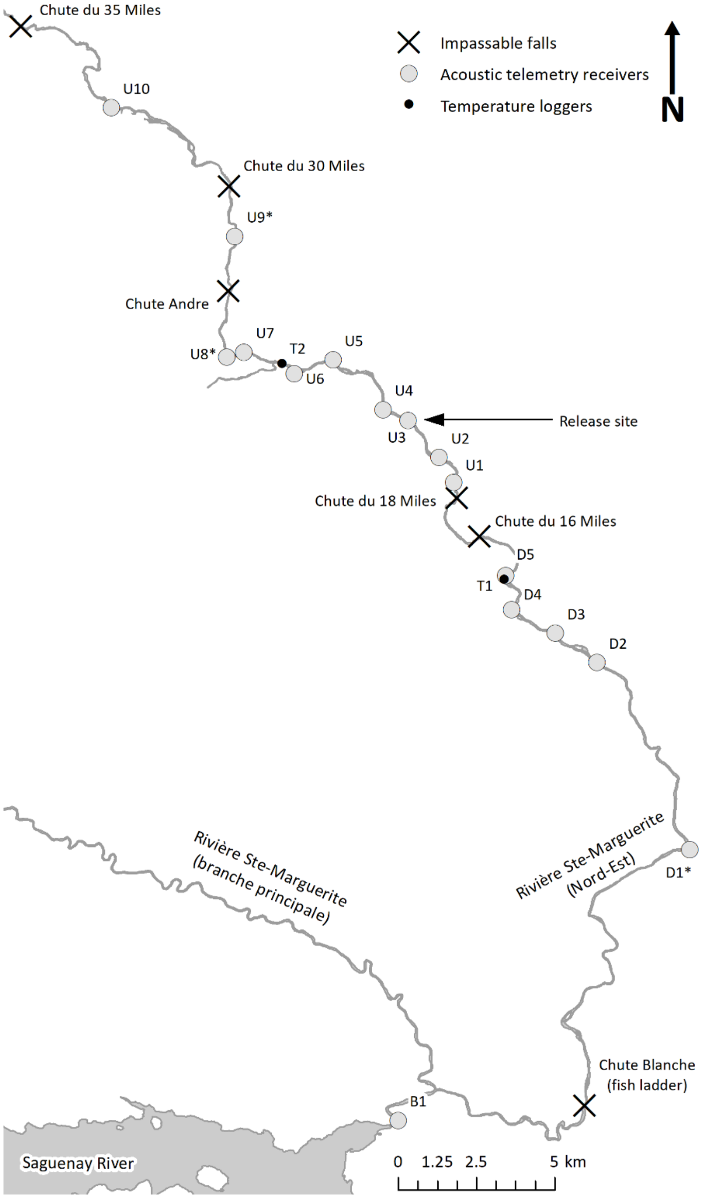


Figure S.2: Carte de l'aire d'étude

Carte de l'aire d'étude indiquant les positions des chutes d'eau infranchissables, de la passe migratoire, du site de relâche en amont, des émetteurs acoustiques et des enregistreurs de température. Les émetteurs acoustiques identifiés par un astérisque n'ont pas été fonctionnels pour les trois années de l'étude : D1 a été fonctionnel en 2016 seulement, U8 en 2015 et 2016, et U9 en 2015 seulement.

Objectifs

L'objectif global de cette thèse était d'examiner les patrons de migration et l'utilisation de l’habitat par le saumon atlantique (*Salmo salar*) à la suite du transport d’individus adultes dans un nouvel habitat en amont de la chute du 18 dans la rivière Sainte-Marguerite Nord-Est. La thèse comprend trois chapitres rapportant des recherches effectuées en vue d’atteindre cet objectif.

L'objectif du premier chapitre était de déterminer les facteurs qui influencent la rétention des saumons adultes dans le nouvel habitat suite au transport. Un des principaux facteurs déterminants du succès d'un programme de translocation de saumons reproducteurs, indépendamment de l'objectif du programme, est si les saumons demeurent et fraient dans l'habitat où ils ont été relâchés. Quelques individus meurent suite au transport alors que d'autres retournent vers l’aval (Frank et al. 2009, Keefer et al. 2010). Si lors de ce retour, les poissons franchissent les obstacles vers l’aval, ces individus ne pourront plus frayer dans le nouvel habitat (Keefer et al. 2010, Hagelin et al. 2015, 2016). Puisque le retour vers l’aval réduit le nombre de reproducteurs dans la population de fraie par rapport au nombre d'individus transportés, il peut avoir d’importantes conséquences pour le succès d'un programme de translocation. La capacité de prédire le taux de retour des saumons vers l’aval à partir de caractéristiques intrinsèques aux poissons et des conditions environnementales au moment du transport permettrait donc d’améliorer considérablement le succès d’un programme.

L'objectif du deuxième chapitre était d'examiner l'utilisation de refuges thermiques par les saumons adultes transportés à l'été 2016. Le saumon atlantique est une espèce d'eau froide dont la tolérance à la température se situe dans une fourchette étroite. Toutefois, dans une bonne partie de leur aire de répartition, les saumons atlantiques sont exposés à des températures estivales qui dépassent souvent la limite supérieure de leur fourchette de tolérance. Les saumons survivent aux épisodes de chaleur élevée en adoptant des comportements de thermorégulation dans des zones d'eau plus fraîche que l’on nomme « refuges thermiques ». Bien que de nombreuses recherches se soient penchées sur l'utilisation de refuges thermiques par les saumons atlantiques juvéniles, relativement peu d'information existe sur l'utilisation de ces refuges par les adultes. C’est étonnant puisque les adultes reviennent à leur rivière natale durant l'été, plusieurs mois avant le début de la fraie et nécessitent l'accès à des refuges thermiques afin de réduire la mortalité et maintenir une quantité suffisante d'énergie pour la fraie. Améliorer la compréhension de l’utilisation des refuges thermiques par les saumons atlantiques adultes durant la période précédant la fraie peut devenir essentiel afin de développer des stratégies d’atténuation des effets des changements climatiques sur les saumons durant la montaison en rivière. Cette meilleure compréhension pourra également aider les gestionnaires à déterminer si l'habitat visé par un programme de colonisation ou de réintroduction comprend suffisamment d’habitats de refuge thermique pour permettre aux saumons adultes de survivre jusqu’à la fraie avec des ressources suffisantes pour assurer le succès de la reproduction.

L'objectif du troisième chapitre était de relier les patrons de déplacement et l'utilisation de l'habitat des saumons atlantiques aux caractéristiques intrinsèques des poissons et aux conditions environnementales extrinsèques durant la colonisation dans une rivière à écoulement naturel. Même s'il existe de nombreuses études sur la montaison des saumons adultes, aucun modèle général n’a été développé pour prédire la réponse migratrice des saumons aux variables environnementales (Thorstad et al. 2008, Bendall et al. 2012). Les liens entre les patrons de migration et les variables environnementales sont probablement spécifiques à chaque rivière et contexte. De plus, les liens entre les variables environnementales sont complexes et ces dernières sont souvent corrélées entre elles (Jonsson 1991, Bendall et al. 2012, Martin et al. 2015). Les différences de méthodologie (par exemple, décompte aux passes migratoires vs télémétrie) utilisées pour examiner les effets des variables environnementales sur la migration rendent difficile la comparaison entre les études. De plus, les études effectuées dans des rivières dont le débit est régulé ne sont pas nécessairement représentatives des conditions expérimentées par les saumons dans des écosystèmes fluviaux naturels (Thorstad et al. 2008, Bendall et al. 2012).

Par ailleurs, les saumons adultes utilisent des empreintes olfactives produites par la composition chimique de l'eau de leur rivière natale et la présence de congénères (juvéniles ou adultes) pour se diriger durant leur migration en eau douce (Hasler et al. 1978, Quinn et al. 1983, Bett et Hinch 2015). Ainsi, l'absence de telles empreintes dans le nouvel habitat peut également influencer comment les saumons utilisent l'habitat lors d’une réintroduction et d’une colonisation. Un effort de recherche concerté est donc nécessaire pour comprendre comment les individus utilisent l'habitat durant la colonisation dans le but d’optimiser la conception de nouveaux programmes. Dans ce chapitre, nous avons d’abord examiné comment les patrons de déplacement des saumons varient en fonction des conditions environnementales (température de l’eau, débit de la rivière, saison, cycle diurne) et des caractéristiques des poissons (sexe et taille) pendant la colonisation. Nous avons en second lieu cherché à déterminer les caractéristiques physiques des fosses (par exemple, superficie et profondeur) qui constituent des habitats adéquats pour la rétention de saumons adultes durant leur résidence en rivière et nous avons examiné si l'utilisation de ces fosses variait en fonction de facteurs environnementaux (par exemple, la température de l’eau et le débit de la rivière).

Méthodologie

La télémétrie acoustique a été utilisée pour répondre aux objectifs des trois chapitres de la thèse et la méthodologie générale est décrite dans la présente section. Des saumons adultes en montaison ont été capturés à la passe migratoire de la chute Blanche et transportés jusqu'à un site 3 km en amont de la chute du 18. Un émetteur acoustique de 69 kHz à code unique a été implanté dans la cavité intrapéritonéale de chaque saumon capturé. L'incision a été refermée à l'aide de trois ou quatre sutures et l'ensemble du procédé chirurgical a été réalisé sous asepsie. La longueur du poisson et du maxillaire, la masse et le sexe ont été mesurés et la présence de blessures notée. La longueur du maxillaire a servi à confirmer la détermination visuelle du sexe faite sur le terrain. Un échantillon d'écailles a été collecté en vue d'une analyse de l'âge et un petit échantillon de la nageoire adipeuse (2014) ou caudale (2015 et 2016) a été récolté pour des analyses génétiques qui ne font pas partie de cette thèse. Après la chirurgie, les saumons ont été transférés dans une cage de rétablissement dans la rivière. Une fois que les poissons étaient revenus à l'équilibre, la cage a été ouverte sous l'eau. La plupart des saumons sont sortis dans un délai d'une heure après la chirurgie. Les saumons qui étaient encore dans la cage après une heure ont été libérés manuellement.

Les saumons marqués ont été détectés après avoir été relâchés à l'aide d'une série de récepteurs acoustiques (Figure S.2). Bien que le nombre de récepteurs ait augmenté chaque année de l'étude, un groupe de 8 récepteurs a été déployé annuellement aux mêmes endroits, ce qui a favorisé une détection similaire des saumons entre les années. Des tests de distance de détection effectués en 2014 ont indiqué que 95 % des émetteurs acoustiques étaient détectés à une distance de 40 m et 80 % à 200 m en conditions calmes. La distance de détection était réduite lorsque le débit de la rivière dépassait 60 m^3s^{-1} et lors d'événements pluvieux en raison d'une augmentation du bruit ambiant. Néanmoins, la redondance produite par la combinaison d'une fréquence élevée de transmission du signal (chaque 30 à 90 sec) et un monitorage à long terme à des endroits fixes a permis de suivre avec succès les déplacements des saumons, même au plus fort débit d'eau enregistré pendant l'étude (167 m^3s^{-1}). Les récepteurs étaient installés en juin avant le premier transport de poissons et étaient récupérés pendant la fraie en automne avant que la rivière ne gèle.

La température de la rivière et son débit ont été enregistrés en continu (à intervalles de 15 min) au cours de cette étude (2014-2016). Les mesures de température des enregistreurs déployés dans des secteurs peu profonds et bien mélangés du chenal principal de la rivière ont été obtenues à partir du réseau RivTemp (Boyer et al. 2016) ou d'enregistreurs installés spécifiquement pour cette étude. Le débit de la rivière a été obtenu du gouvernement du Québec (station 062803; 48,267962 N, -69,908823 O).

Résultats généraux

La cible annuelle de transport de saumons était de 30 adultes : 15 mâles et 15 femelles. En 2014, des restrictions de permis interdisaient le transport avant que 75 saumons aient accédé à la passe migratoire. Ainsi, le premier saumon a été transporté que le 22 juillet. Après cette date, peu de poissons sont entrés dans la passe migratoire lorsque la température de la rivière était assez fraîche (< 20 °C) pour permettre leur transport. Bien que la passe migratoire soit restée ouverte jusqu'à la mi-septembre, les derniers individus y sont entrés le 5 septembre et un total de 12 saumons (3F, 9M) ont été transportés et marqués en 2014. En 2015, le transport a pu commencer dès que les premiers poissons sont entrés dans la passe migratoire et 25 saumons (12F, 13M) ont été transportés et marqués. En 2016, c'est 33 saumons (15F, 16M) qui ont été transportés et marqués. Au total, 68 saumons avec émetteurs acoustiques ont été relâchés dans le nouvel habitat de 2014 à 2016 et ont été inclus dans l'analyse du retour vers l'aval (Chapitre 1). En 2016, 16 saumons avec des émetteurs et sondes de température sont restés dans l'habitat d'étude et ont été inclus dans l'analyse de l'utilisation des refuges thermiques (Chapitre 2). Quarante-six saumons dont les émetteurs acoustiques sont demeurés fonctionnels durant les trois années de l'étude sont restés dans le nouvel habitat et ont été inclus dans l'analyse des patrons de déplacement (Chapitre 3).

Résumés des chapitres

Chapitre 1 : Facteurs influençant le retour vers l'aval des saumons atlantiques adultes suite à leur transport dans un nouvel habitat

L'objectif du chapitre 1 était d'examiner les facteurs qui influencent le retour vers l'aval après le transport, en particulier pour déterminer si : 1) les caractéristiques individuelles des saumons peuvent les prédisposer à ce comportement, ou 2) les conditions environnementales ou les conditions du transport influencent la propension des saumons à retourner vers l'aval après le transport. Pour atteindre cet objectif, une analyse de survie (durée jusqu'à un événement) a été effectuée à l'aide du modèle de risques proportionnels de Cox. Les variables explicatives supposées influencer le retour vers l'aval étaient la longueur à la fourche, le sexe, les blessures (variable catégorielle définissant la sévérité de la blessure), la durée du transport, la température dans la passe migratoire lors de la capture, la différence de température de l'eau entre la passe migratoire et la rivière au site de relâche en amont au moment de la remise en liberté, la température de l'eau et le débit de la rivière enregistrés en continu, et l'année. L'analyse a été limitée aux retours vers l'aval qui se sont produits au cours de sept premiers jours après le transport, parce qu'une régression de type « moving point » a indiqué que les effets du transport et de la manipulation des poissons semblaient influencer le retour vers l'aval surtout dans la première semaine après le transport.

Au total, 19 saumons sont retournés vers l'aval dans les sept jours qui ont suivi leur transport. Trois autres saumons ont fait de même durant la période estivale précédant la fraie, ils ont donc été retirés de la population de fraie en amont de la chute du 18, mais ils n'ont pas été inclus dans l'analyse de survie. Une seconde vague de retour vers l'aval s'est produite après le début du creusement des nids de fraie à la mi-octobre et représente probablement l'avalaison normale suivant la fraie.

Deux types de retours vers l'aval suite au transport des saumons ont été observés. Dix individus ont effectué un retour complet en franchissant vers l'aval les chutes du 18 et du 16. Douze autres individus ont effectué un retour partiel en franchissant vers l'aval la chute du 18, mais en demeurent en amont de la chute du 16. Il n'a pas été possible de déterminer si les saumons qui ont fait un retour partiel vers l'aval sont morts en franchissant la chute du 18 ou s'ils ont frayé dans l'habitat entre les deux chutes. En 2016, un des mâles qui a fait un retour partiel vers l'aval quatre jours après avoir été transportés a été détecté en aval de la chute du 16 vers la fin de la période de fraie. Trois femelles et un autre mâle étaient également présents dans l'habitat entre les deux chutes et on suppose que certains des saumons qui ont fait un retour partiel vers l'aval ont frayé.

Les résultats de la régression de Cox ont montré que la longueur à la fourche était l'unique facteur influençant de façon positive le retour vers l'aval suite au transport. Plus spécifiquement, les saumons de plus grande taille (pluribermarins) étaient plus à risques de retourner vers l'aval, et ce, plus rapidement que les individus de petite taille (madeleineaux). Les plus grands saumons (975 mm, longueur à la fourche [LF]) ont eu un taux de retour 9,7 fois plus rapide que les plus petits saumons (520 mm LF), alors que les saumons pluribermarins moyens (792 mm) ont eu des taux de retour 3,1 fois plus rapides que les madeleineaux moyens (568 mm). Sept jours après le transport, près de 30 % des saumons de taille médiane (750 mm LF) étaient retournés vers l'aval, tandis qu'un peu plus de 10 % des saumons dont la taille se situait dans le 25^e^ percentile (580 mm LF) avaient effectué un tel retour. Sept jours après le transport, la proportion d'individus de grande taille (75^e^ percentile = 780 mm LF) ayant effectué un retour vers l'aval avait augmenté d'environ 5 % par rapport aux saumons de taille médiane. La divergence dans les taux de retour entre les saumons médianes et grands est apparue environ deux jours après le transport (Figure 3.4).

Ni les conditions du transport ni les conditions environnementales dans la rivière après le transport ne semblaient affecter significativement le taux de retour vers l'aval. Il n'y avait pas non plus de variabilité apparente entre les années dans le taux de retour. La direction initiale vers laquelle un poisson se déplaçait après avoir été relâché dans le nouvel habitat, quoique non incluse dans l'analyse de survie, pourrait être un bon indicateur de la propension à retourner vers l'aval. En effet, la majorité des saumons qui sont retournés vers l’aval se sont d’abord déplacés dans cette direction après avoir été relâchés, alors que 70 % des saumons qui se sont d’abord déplacés vers l’amont ont poursuivi leurs déplacements dans cette direction.

Sept jours après leur transport, 40 % des femelles (12 de 30) et 21 % des mâles (8 de 38) étaient retournés vers l’aval, mais la variable sexe n’est pas ressortie dans l’analyse de survie comme un facteur prédictif significatif du risque de retour. Dix des 68 saumons marqués ont été retenus dans une cage durant la nuit à la passe migratoire. Bien qu'il n'ait pas été possible de tester l'effet de ce séjour nocturne en cage en raison de la trop faible taille de l’échantillon, huit des dix saumons retenus dans la cage sont retournés vers l’aval et les deux autres comptent parmi les quatre saumons qui ont soit perdu leur marqueur ou qui sont morts au cours des trois années de l'étude. Par ailleurs, deux saumons se sont échappés de la cage en sautant par-dessus la barrière durant la nuit. Il s'avère probable que la nuit en cage a induit une réponse de stress chez les saumons transportés, cependant, plus de données seront nécessaires avant que des recommandations puissent être faites à ce sujet aux gestionnaires.

Le nombre de poissons qui sont retournés vers l’aval après le transport était relativement faible (20 individus), ce qui a limité le nombre de degrés de liberté et restreint à quatre le nombre de covariables qui ont pu être incluses dans les modèles retenus pour l'analyse de survie. De plus, la faible taille d'échantillon pour certaines des variables d'intérêt (par exemple, retenue en cage durant la nuit, type de remise en liberté, saturation en oxygène) a empêché qu’elles soient incluses dans les modèles retenus. Cependant, dans la rivière Sainte-Marguerite Nord-Est, la longueur du poisson semble être un élément important pour le retour vers l’aval après transport. En effet, le transport de saumons de petite ou de moyenne taille engendrerait moins de retours vers l’aval que le transport de saumons de grande taille (> 780 mm). De plus, l’estimé obtenu de 30 % des saumons de taille médiane qui retournent vers l’aval à l’intérieur de sept jours après le transport suggère que pour atteindre la cible du programme de colonisation du nouvel habitat sur la Sainte-Marguerite Nord-Est, il sera peut être nécessaire d'augmenter de 30 % le nombre d'individus transportés. Les résultats de cette étude sont de première importance pour les gestionnaires locaux, mais ils ont également des implications plus vastes, car ils peuvent être utiles pour déterminer des cibles initiales de transport lors de la mise en oeuvre de programmes similaires dans d'autres rivières à écoulement libre.

Chapitre 2 : Évaluation de l’utilisation estivale des refuges thermiques par les saumons atlantiques adultes à l’aide de la télédétection, du suivi de la température en rivière et de la télémétrie acoustique

L'objectif du chapitre 2 était d'examiner l'utilisation des refuges thermiques par les saumons atlantiques adultes durant la période de résidence en rivière précédant la fraie. Une combinaison novatrice d’imagerie aérienne infrarouge thermique (IRT), de suivi de la température en rivière et de télémétrie acoustique a permis de tester l'hypothèse voulant que les adultes utilisent des zones d'eau plus fraîche lorsque la température de l’eau atteindrait la zone que l’on croit être stressante chez les saumons atlantiques adultes (c.-à-d., 20° à 23° C, Shepard 1995, Wilke et al. 1995, Breau 2013). On s’attendait également à ce que les patrons de thermorégulation comportementale des saumons adultes suivent le cycle journalier de la température et que les individus fréquentent les refuges frais pendant les heures les plus chaudes de la journée (Ebersole et al. 2001).

Les images aériennes infrarouges thermiques (IRT) obtenues en août 2014 ont d’abord servi à identifier les refuges thermiques potentiels (Figure 4.1). L'utilisation des refuges potentiels a été évaluée durant l'été 2016 en installant des récepteurs acoustiques à l’intérieur et à l’extérieur des zones d’eau fraîche identifiées à partir des images IRT et dont la profondeur était d’au moins 0,5 m qui est la profondeur minimale requise pour installer ces récepteurs dans la Sainte-Marguerite Nord-Est. Les refuges moins profonds ne semblent pas être utiles aux saumons adultes pour la thermorégulation comportementale à long terme. Tous les refuges potentiels répondant à ces critères étaient situés soit dans des fosses, soit dans des panaches aux confluents avec des tributaires. La température corporelle des saumons a été mesurée à l’aide de sondes de température équipées d’émetteurs acoustiques (N=20). La température de l’eau du chenal principal de la rivière a été mesurée à l’aide de thermographes enregistrant les données. La température corporelle des saumons était enregistrée chaque fois que ceux-ci se trouvaient à proximité d'un récepteur, c.-à-d., lorsqu’ils étaient dans des panaches ou des fosses où se trouvaient ces récepteurs.

La différence de température instantanée (ΔT_I) entre la température corporelle des saumons (T_B) enregistrée par les récepteurs acoustiques et la température de l’eau du chenal principal de la rivière (T_R) mesurée par les enregistreurs de température a été calculée et a servi à déterminer quand et où les saumons ont utilisé les refuges thermiques. Un seuil de différence de 1 °C a servi à déterminer le lieu et le moment de la fréquentation des refuges. Les saumons ont été classés comme utilisant des refuges frais lorsque $\Delta T_I \leq -1$ °C. À l’opposé, des valeurs de $\Delta T_I \geq 1$ °C indiquaient que les poissons se trouvaient dans une zone d’eau plus chaude que la température ambiante du chenal principal de la rivière (Figure 4.2).

Les tendances dans la thermorégulation comportementale au cours de l'été ont été examinées à l’aide de la différence (ΔT_H) entre la moyenne horaire de la température corporelle des poissons (T_{BH}) et la moyenne horaire de la température de l'eau du chenal principal de la rivière (T_{RH}). Les moyennes horaires ont été utilisées puisque la température de l'eau de la rivière variait très peu au cours d'une heure. Pour déterminer si les saumons avaient recours à la thermorégulation comportementale, une régression de T_{BH} vs T_{RH} a été réalisée pour chaque individu (Figure 4.3). Un rapport de 1:1 entre T_{BH} et T_{RH} indiquerait l'absence de thermorégulation comportementale, tandis qu'une différence significative du ratio 1:1 indiquerait que les poissons présentent ce comportement (Berman et Quinn 1991, Hillyard et Keeley 2012).

Pour déterminer à quelles températures de l'eau de la rivière les saumons avaient recours à la thermorégulation comportementale, les températures de l'eau ont été regroupées en sous-ensembles de 1 ˚C pour la gamme des températures ambiantes observées dans le chenal principal (Figure 4.4). Des histogrammes de fréquence ont été construits pour les valeurs de ΔT_H de chaque groupement de 1 ˚C de température de la rivière et la valeur médiane de ΔT_H pour chaque groupement (et les intervalles de confiance [IC] à 95 % associés) a été calculée. Si l'IC à 95 % ne chevauchait pas zéro, alors ΔT_H médian (ci-après ΔT_{Hmed}) était considéré comme significativement différent de zéro. Une valeur négative de ΔT_{Hmed} indiquait que pour une température de l'eau donnée, les saumons étaient détectés principalement dans des zones fraîches (c.-à-d., qu'ils se trouvaient dans des zones où l'eau était plus froide que la température ambiante du chenal principal de la rivière), tandis qu'un ΔT_{Hmed} positif indiquait que les saumons étaient détectés principalement dans des zones chaudes. Lorsque ΔT_{Hmed} ne différait pas significativement de zéro, cela indiquait que les saumons n'utilisaient pas de façon préférentielle des zones plus fraîches ou plus chaudes pour une température donnée.

Durant l'été 2016, des 20 saumons portant des sondes de température avec émetteurs acoustiques, 15 individus ont été systématiquement détectés en juillet et août qui étaient les seuls mois au cours de la période d'étude de 2016 (juin-octobre) pour lesquels la température a dépassé 20 ˚C. Tous les saumons atlantiques adultes avec émetteurs de température ont eu recours à la thermorégulation comportementale (Figure 4.3) et toutes les périodes où ils ont fréquenté des zones fraîches ont eu lieu en août (Figure 4.2). Ce dernier mois est le seul pour lequel la température mesurée dans le chenal principal de la rivière est demeurée dans la fourchette de températures considérées comme stressantes pour les saumons atlantiques adultes (20-23 ˚C, Breau 2013) pour plus de quelques heures à la fois.

Bien que la température du chenal principal de la Sainte-Marguerite Nord-Est est relativement fraîche et n'a pas dépassé 23 ˚C, les fosses ont été utilisées par les saumons adultes comme refuges frais au cours de la période la plus chaude de l'été. Les panaches d'eau fraîche au confluent des tributaires n'ont pas été utilisés comme refuges thermiques, probablement parce qu'ils n'étaient pas assez profonds pour servir aux fins de thermorégulation comportementale à long terme pour les saumons atlantiques adultes. Les fosses profondes quant à elles constituent des refuges thermiques stables qui permettent aux individus de se thermoréguler en dépensant relativement peu d'énergie (Berman et Quinn 1991). Les saumons adultes dans les grandes fosses peuvent maintenir une température corporelle stable en changeant de position dans la fosse ou en demeurant dans ce refuge thermique stable pendant que la température de l'eau ambiante autour du refuge varie au cours de la journée, ce qui les protège des fluctuations journalières importantes de la température. Le débit de la rivière, la proximité aux sites de fraie, la saison et la densité des congénères peuvent également influencer le choix de l'habitat de rétention. Par exemple, les grandes fosses servent probablement également de refuges hydrauliques dans lesquels les adultes se tiennent en attendant un débit d'eau adéquat pour une migration efficace (Gendron 2013). De telles fosses sont susceptibles d'être particulièrement importantes dans les rivières peu profondes à lit de gravier comme la Sainte-Marguerite Nord-Est dont le débit a tendance à être faible au cours des périodes les plus chaudes de l'été.

Les individus ont eu recours à la thermorégulation comportementale à des températures ambiantes de l'eau sensiblement plus fraîches (17 ˚C dans l'habitat entre la chute Blanche et la chute du 16 et 19 ˚C dans l'habitat en amont de la chute du 18) qu'attendu selon les études précédentes sur l'utilisation de refuges thermiques par les saumons atlantiques juvéniles et adultes (Gibson 1966, Shepard 1995, Cunjak et al. 2005, Dugdale et al. 2016). Ces résultats supportent les conclusions de Breau (2013) que les températures au-dessus de 20 ˚C sont stressantes pour les saumons atlantiques adultes. Ceux-ci ont utilisé les refuges frais surtout l'après-midi lorsque les températures de l'eau les plus chaudes ont été enregistrées. Dans les refuges, les températures corporelles des saumons pouvaient atteindre 5 ˚C de moins que la température de l'eau du chenal principal de la rivière.

Un fait intéressant que nous avons observé est que les saumons atlantiques adultes ont également fréquenté des zones plus chaudes lorsque la température de l'eau de la rivière était sous 17 ˚C (Figure 4.4). Sur une période d'un mois, on a retrouvé les poissons dans des zones fraîches en fin d'après-midi et dans des zones chaudes au début de la matinée suivant le cycle journalier de la température de l'eau de la rivière. Une telle utilisation de zones d'eau plus chaude par les saumons adultes en migration durant l'été n'avait pas été précédemment rapportée dans la littérature, elle pourrait permettre aux adultes de demeurer à l'intérieur d'une gamme de températures ambiantes optimales pour atteindre un équilibre entre la conservation d'énergie et la maturation des gamètes (Berman et Quinn 1991, Newell et Quin 2005, Hasler et al. 2012). La fréquentation de zones fraîches et chaudes dans la Sainte-Marguerite Nord-Est suggère que les adultes auraient une fourchette étroite de températures ambiantes optimales similiaire à celle précédemment décrite pour l'optimisation de la croissance chez les saumons atlantiques juvéniles, c.-à-d. environ 16-20 ˚C (Elliott 1991; Jonsson et Jonsson 2009).

La cartographie à l'aide d'images IRT a seulement permis de détecter des refuges frais de petite taille identifiables en surface qui, malgré leur abondance, n'ont pas été utilisés par les saumons adultes pour la thermorégulation. Nos résultats soulignent l'importance de combiner les méthodes aériennes et au sol pour détecter les refuges thermiques adéquats. Le maintien de l'accès à de tels grands refuges stables peut être crucial pour la persistance des saumons atlantiques dans leur aire de répartition nord-américaine étant donné les scénarios actuels de changements climatiques qui prévoient des étés plus chauds et plus secs.

Chapitre 3 : Les patrons de déplacement et l’utilisation de l'habitat des saumons atlantiques lors de la colonisation d’un nouvel habitat sont modulés par l'évolution et l'environnement

L'objectif du chapitre 3 était de relier les patrons de déplacement et l'utilisation de l'habitat des saumons atlantiques à leurs caractéristiques intrinsèques et aux conditions environnementales extrinsèques expérimentées lors de la colonisation d’une rivière à écoulement libre. La mesure en simultané de la température de l’eau et du débit de la rivière, combinée à des positionnements des saumons à haute résolution spatiale et temporelle obtenus à l’aide de la télémétrie acoustique (de la remise en liberté dans le nouvel habitat jusqu'au début de la fraie) ont servi à aborder deux questions de recherche. En premier lieu, nous avons examiné comment les patrons de déplacement des saumons varient en réponse aux conditions environnementales (température de l’eau, débit de la rivière, saison, cycle diurne) et aux caractéristiques des poissons (sexe et taille) lors de la colonisation. En second lieu, nous avons déterminé les caractéristiques physiques (par exemple, superficie et profondeur) qui rendent une fosse adéquate pour les saumons adultes durant leur période de résidence dans la rivière, et évalué si la fréquentation des fosses change en fonction des facteurs environnementaux (par exemple, la température de l’eau et le débit de la rivière). Une modélisation linéaire généralisée mixte et l’apprentissage automatique ont été utilisés afin d’identifier les variables clés affectant les déplacements des saumons dans le nouvel habitat et d’obtenir une image détaillée de la façon dont les saumons atlantiques adultes utilisent l'habitat lors de la colonisation.

Les déplacements des saumons se sont surtout produits à l’aube et au crépuscule. Le nombre de déplacements initiés à l’aube et au crépuscule était plus élevé qu’attendu alors que le nombre de déplacements initiés durant la journée était moins élevé qu’attendu pour les mâles ($X^2 = 479$, ddl = 3, p = 0,01) et les femelles ($X^2 = 536$, ddl = 3, p = 0,01).

La probabilité de déplacement pour un jour donné, par opposition à rester dans une fosse, a été évaluée à l’aide d’un modèle linéaire généralisé mixte avec une distribution binomiale. Le modèle retenu incluait la saison, le débit, la température et les interactions entre le sexe et la température et entre le sexe et le débit en tant que variables explicatives. La pente négative significative pour l'effet de la saison indiquait que les saumons étaient moins enclins à se déplacer en été, c.-à-d. jusqu’au 10 septembre. L’interaction significative entre le sexe et le débit indiquait que même si les femelles avaient plus tendance à se déplacer lors de forts débits, la probabilité de se déplacer pour les mâles n’était pas affectée par le débit.

La pente non significative pour la température indiquait que cette variable n'affectait pas la probabilité qu'une femelle se déplace, toutefois l'interaction significative entre le sexe et la température indiquait que les mâles étaient moins enclins à se déplacer lors de températures élevées.

Un ensemble d'indicateurs des déplacements quotidiens a été extrait à partir des données de télémétrie et a servi à examiner comment les saumons se déplaçaient (*sensu* Roy et al 2013). Ces indicateurs étaient le nombre de déplacements, le nombre de sites visités, la distance totale parcourue par jour, ainsi que la distance entre les deux récepteurs les plus éloignés (nommée « étendue ») couverte en une journée donnée. En combinant le regroupement par la méthode des k-moyennes et l'analyse en composantes principales, deux principaux types de déplacements sont ressortis. Les saumons ayant un patron de déplacement de type « sédentaire » effectuaient peu de déplacements ($\bar{x}$ = 1,4), sur de courtes distances ($\bar{x}$ = 1,52 km) et visitaient environ 2 sites. L'étendue spatiale de rivière couverte quotidiennement était faible ($\bar{x}$ = 1,18 km). Les saumons ayant un patron de déplacement de type « exploratoire » effectuaient beaucoup plus de déplacements ($\bar{x}$ = 4,31), visitant en moyenne 3,74 sites. La distance parcourue ($\bar{x}$ = 5, 58 km) et l'étendue spatiale couverte ($\bar{x}$ = 3,98 km) étaient également beaucoup plus grandes en mode exploratoire que sédentaire.

La probabilité de présenter un patron de déplacements donné (sédentaire ou exploratoire) a été évaluée à l'aide d'un modèle linéaire généralisé mixte avec une distribution binomiale. Les covariables retenues dans le modèle choisi étaient la température, le débit et les interactions entre le sexe et la température et entre le sexe et le débit. Ni la température ni le débit n'influençaient la probabilité qu'une femelle soit sédentaire. En effet, les femelles avaient plus tendance à être sédentaires indépendamment de la température ou du débit. Les interactions significatives entre le sexe et la température et entre le sexe et le débit indiquaient que les mâles étaient plus souvent sédentaires aux températures et débits élevés. La variance due aux effets aléatoires des individus était très faible (0,39).

Une approche de forêt aléatoire d'arbres de décision a été employée pour déterminer l'importance des caractéristiques physiques des fosses et des conditions environnementales pour la fréquentation des fosses par les saumons adultes. Les caractéristiques physiques des fosses incluses dans l'analyse consistaient en trois mesures de leur taille (profondeur maximale, superficie et facteur d'expansion), la présence ou l'absence de refuge thermique frais et la distance moyenne à tous les secteurs de fraie connus. Le facteur d'expansion était le rapport de la largeur maximale de la fosse à la largeur du chenal en amont, où la largeur du chenal était calculée comme la moyenne de trois mesures de largeur de la rivière d'une rive à l'autre. Les conditions environnementales incluses étaient la température journalière moyenne de l'eau et le débit journalier moyen de la rivière. Le jour de l'année a été inclus pour évaluer comment l'utilisation des fosses variait dans le temps. De toutes les caractéristiques physiques mesurées, la taille de la fosse était la variable de l’habitat la plus importante pour déterminer si une fosse de rétention était adéquate, les fosses plus grandes et plus profondes étant fréquentées plus souvent. La fréquentation des fosses variait avec la température, le débit et le moment au cours de la période précédant la fraie. Spécifiquement, l'utilisation des fosses augmentait au cours de l'été avec le nombre de saumons dans la population de colonisation, atteignait un pic à la mi-septembre, et déclinait légèrement lorsque la fraie approchait et que les saumons devenaient plus actifs. Les fosses étaient plus fréquentées lors de faibles débits (< 10 m^{3}s^{-1}) et lorsque la température était élevée (≥ 20 °C), ce qui se produisait en été. Une seule fosse a été systématiquement utilisée pour la rétention à long terme au cours des trois années de l’étude, suggérant que les fosses de rétention adéquates sont probablement rares sur la Sainte-Marguerite Nord-Est.

Cette étude a permis d’obtenir une image détaillée des patrons de déplacements et d'utilisation de l’habitat de saumons atlantiques adultes lors de la colonisation d'une rivière naturelle non régulée en lien avec les variables biotiques et abiotiques à haute résolution spatiale et temporelle. La compréhension approfondie obtenue sur la manière dont les saumons colonisent un nouvel habitat sera un atout précieux pour optimiser de futurs programmes de réintroduction et de colonisation. Les résultats de cette étude soulignent également l'importance des fosses où les saumons peuvent se reposer durant la montaison (Økland et al. 2001, Finstad et al. 2005, Richard et al. 2014). Les modèles comportementaux observés pourraient refléter les différentes stratégies évolutives adoptées par les mâles et les femelles pour maximiser leur valeur adaptative. Les saumons atlantiques mâles maximisent leur succès reproducteur en frayant avec plusieurs femelles (Fleming 1996). L'incidence plus grande du comportement exploratoire chez les mâles peut être expliquée par un effort visant à augmenter leur succès reproducteur en recherchant activement des femelles, cette hypothèse étant supportée par l'augmentation observée des déplacements exploratoires à partir de la mi-septembre lorsque la température de la rivière a baissé et que la fraie approche. L'incidence plus grande du comportement sédentaire chez les femelles pourrait refléter la nécessité de conserver des réserves d'énergie suffisantes pour le développement des oeufs, le creusement des nids et la ponte afin de maximiser leur succès reproducteur (Fleming 1996, 1998). Étant donné que le comportement de fraie est fortement conservé chez les saumons pour que la fraie doit se produise au meilleur moment afin de maximiser la survie des jeunes (Fleming 1998), les patrons observés sur la Sainte-Marguerite Nord-Est peuvent être en grande partie applicables à divers écosystèmes et ainsi servir à prédire comment les saumons vont réagir dans un nouvel habitat lors d’une réintroduction, d’une migration assistée, ou d’une expansion de l’aire de répartition.

Conclusions générales

Les trois chapitres de cette thèse fournissent dans leur ensemble une description détaillée de la façon dont les saumons utilisent l'habitat lors du processus de colonisation d'un nouvel habitat. La forte propension des saumons à rester dans le nouvel habitat confirme que la translocation d'adultes est une stratégie viable pour restaurer ou réintroduire des populations de saumons atlantiques. La fréquentation des refuges thermiques pour la thermorégulation comportementale à des températures plus faibles que ce qui avait été précédemment rapporté pour l'espèce, combinée au fait que les individus étaient moins actifs lors de températures élevées et de faibles débits, met l'accent sur l'importance de l'habitat de refuge thermique pour les saumons adultes lors de leur résidence estivale en rivière, et ce, en particulier dans les rivières où de faibles débits et des températures élevées coexistent. En conséquence, lors de la sélection des bassins ou segments de rivière pour une colonisation par des saumons adultes, la priorité devrait être mise sur ceux qui comprennent un nombre suffisant de fosses profondes en fonction du nombre d'adultes à introduire. Si l'habitat de refuge thermique est insuffisant, le transport des adultes pourrait être fait plus tard dans la saison, lorsque le risque d'exposition à des épisodes de chaleur est réduit, mais avant que les températures ne baissent trop ce qui pourrait limiter la capacité des saumons à franchir des obstacles. Le choix du moment pour le transport devrait également tenir compte du régime local de débit, puisqu'un débit trop faible pourrait empêcher les saumons d'avoir accès aux refuges thermiques ou aux sites de fraie.

Bibliographie

Anderson JH, Pess GR, Carmichael RW, Ford MJ, Cooney TD, Baldwin CM, McClure MM (2014) Planning Pacific salmon and steelhead reintroductions aimed at long-term viability and recovery. *North American Journal of Fisheries Management.* 34:72-93.

Araki H, Schmid C. (2010) Is hatchery stocking a help or harm? *Aquaculture.* 308:S2-S11.

ASF (2011) Economic value of wild Atlantic Salmon. *Atlantic Salmon Federation.* http://www.asf.ca/.

Askling O (2015) A telemetry study for reintroducing wild Atlantic salmon (*Salmo salar* L.) in the Daugava and Ogre Rivers, Latvia. Master's Thesis. Karlstads University.

Baglinière J-L, Maisse G, Nihouarn A (1990) Migratory and reproductive behaviour of female adult Atlantic salmon, Salmo salar L., in a spawning stream. *Journal of Fish Biology.* 36:511-520.

Baglinière J-L, Maisse G, and Nihouarn A (1991). Radio-tracking of male adult Atlantic salmon, *Salmo salar* L., during the last phase of spawning migration in a spawning stream (Brittany, France). *Aquatic Living Resources.* 4:161–167.

Bardonnet A, Baglinière JL, (2000) Freshwater habitat of Atlantic Salmon (*Salmo salar*). *Canadian Journal of Fisheries and Aquatic Sciences.* 57:497-506.

Bendall B, Moore A, Maxwell D, Davison P, Edmonds N, Archer D, Solomon D, Greest V, Wyatt R, Broad K (2012) Modelling the migratory behaviour of salmonids in relation to environmental and physiological parameters using telemetry data. *Fisheries Management and Ecology.* 19:475-483.

Berman CH, Quinn TP (1991) Behavioural thermoregulation and homing by spring chinook salmon, *Oncorhynchus tshawytscha* (Walbaum), in the Yakima River. *Journal of Fish Biology* 39: 301-312.

Bett NN, Hinch, SG (2015) Attraction of migrating adult sockeye salmon to conspecifics in the absence of natal chemical cues. *Behavioral Ecology.* 26:1180-1187.

Breau C (2013) Knowledge of fish physiology used to set water temperature thresholds for in- season closures of Atlantic salmon (*Salmo salar*) recreational fisheries. Canadian Science Advisory Secretariat, Research Document 2012/163, *Department of Fisheries and Oceans*, Moncton, N.B.

Bryant MD, Frenette BJ, McCurdy SJ (1999) Colonization of a watershed by anadromous salmonids following the installation of a fish ladder in Margaret Creek, Southeast Alaska. *North American Journal of Fisheries Management.* 19:1129-1136.

Carlson SM, Satterthwaite, WH (2011) Weakened portfolio effect in a collapsed salmon population complex. *Canadian Journal of Fisheries and Aquatic Sciences.* 68:1579–1589.

Christie MR, Marine ML, French RA, Waples RS, Blouin MS (2012) Effective size of a wild salmonid population is greatly reduced by hatchery supplementation. *Heredity*. 109:254-260.

COSEWIC (2010) COSEWIC assessment and status report on the Atlantic Salmon **Salmo salar** (Nunavik population, Labrador population, Northeast Newfoundland population, South Newfoundland population, Southwest Newfoundland population, Northwest Newfoundland population, Quebec Eastern North Shore population, Quebec Western North Shore population, Anticosti Island population, Inner St. Lawrence population, Lake Ontario population, Gaspé-Southern Gulf of St. Lawrence population, Eastern Cape Breton population, Nova Scotia Southern Upland population, Inner Bay of Fundy population, Outer Bay of Fundy population) in Canada. Committee on the Status of Endangered Wildlife in Canada. Ottawa. xlvii + 136 pp.

Cunjak RA, Roussel JM, Gray MA, Dietrich JP, Cartwright DF, Munkittrick KR, Jardine TD (2005) Using stable isotope analysis with telemetry or mark-recapture data to identify fish movement and foraging. *Oecologia*. 144: 636–646. doi:10.1007/s00442-005-0101-9.

Dahl J, Dannewitz J, Karlsson L, Petersson E, Löf A, Ragnarsson B (2004) The timing of spawning migration: implications of environmental variation, life history, and sex. *Canadian Journal of Zoology.* 82:1864-1870.

DFO (2015) Special Report on Atlantic Salmon. Prepared by the Minister's Advisory Committee on Atlantic Salmon. *Department of Fisheries and Oceans Canada*. July 2015. 65 p.

Dugdale SJ, Franssen J, Corey E, Bergeron NE, Lapointe M, and Cunjak RA (2016) Main stem movement of Atlantic salmon parr in response to high river temperature. *Ecology of Freshwater Fish*. 25(3): 429–445. doi:10.1111/eff.12224.

Elliott JM (1991) Tolerance and resitance to thermal stress in juvenile Atlantic salmon, *Salmo salar*. *Freshwater Biology*. 25: 61–70.

Fleming, IA (1996) Reproductive strategies of Atlantic salmon: ecology and evolution. *Reviews in Fish Biology and Fisheries* 6:379-416.

Fleming, IA (1998) Pattern and variability in the breeding system of Atlantic salmon (Salmo salar), with comparisons to other salmonids. *Canadian Journal of Fisheries and Aquatic Sciences* 55:59–76.

Fisch KM, Kozfkay CC, Ivy JA, Ryder OA, Waples RS (2015) Fish hatchery genetic management techniques: integrating theory with implementation. *North American Journal of Aquaculture.* 77:343-357.

Fraser DJ (2008) How well can captive breeding programs conserve biodiversity? A review of salmonids. *Evolutionary Applications*. 1: 535-86.

Finstad, AG, Okland F, Thorstad EB, Heggberget TG (2005) Comparing upriver spawning migration of Atlantic salmon *Salmo salar* and sea trout *Salmo trutta*. *Journal of Fish Biology* 67:919-930.

Gibson,RJ (1966) Some factors influencing the distributions of brook trout and Atlantic salmon. *Journal of the Fisheries Research Board of Canada*. 23: 1977–1980.

Hagelin A, Calles O, Greenberg L, Nyqvist D, Bergman E (2016) The migratory behaviour and fallback rate of landlocked Atlantic salmon (*Salmo salar*) in a regulated river: does timing tatter? *River Research and Applications*. 32(6), 1402-1409.

Hagelin, A, Calles O, Greenberg L, Piccolo J, Bergman E. (2016) Spawning migration of wild and supplementary stocked landlocked Atlantic salmon (*Salmo salar*). *River Research and Applications.* 32(3), 383-389.

Hasler AD, Scholz AT, Horrall RM (1978). Olfactory Imprinting and Homing in Salmon: Recent experiments in which salmon have been artificially imprinted to a synthetic chemical verify the olfactory hypothesis for salmon homing. *American Scientist*. 66, 347-355.

Hasler, CT, Cooke SJ, Hinch SG, Guimond E, Donaldson MR, Mossop B, Patterson DA (2012) Thermal biology and bioenergetics of different upriver migration strategies in a stock of summer-run Chinook salmon. J. Therm. Biol. 37: 265–272. doi:10.1016/j.jtherbio.2011.02.003.

Hilborn R, Quinn TP, Schindler DE, Rogers DE (2003). Biocomplexity and fisheries sustainability. *Proceedings of the National Academy of Sciences.* 100:6564-6568.

Hillyard RW, and Keeley ER (2012) Temperature-related changes in habitat quality and use by Bonneville cutthroat trout in regulated and unregulated river segments. Trans. Am. Fish. Soc. 141: 1649–1663. doi:10.1080/00028487.2012.717517.

Izzo LK, Maynard GA, Zydlewski J. (2016). Upstream Movements of Atlantic Salmon in the Lower Penobscot River, Maine Following Two Dam Removals and Fish Passage Modifications. Marine and Coastal Fisheries 8:448-461.

Jonsson N (1991) Influence of water flow, water temperature and light on fish migration in rivers. *Nordic Journal of Freshwater Research*. 66:20-35.

Jonsson B, Jonsson N (2009) A review of the likely effects of climate change on anadromous Atlantic salmon Salmo salar and brown trout Salmo trutta, with particular reference to water temperature and flow. *Journal of Fish Biology* 75: 2381–2447.

Keefer ML, Taylor GA, Garletts DF, Gauthier GA, Pierce TM, Caudill CC (2010) Prespawn mortality in adult spring Chinook salmon outplanted above barrier dams. *Ecology of Freshwater Fish*. 19:361-372.

Kostow K. (2009). Factors that contribute to the ecological risks of salmon and steelhead hatchery programs and some mitigating strategies. *Reviews in Fish Biology and Fisheries.* 19:9-31.

Martin BT, Nisbet RM, Pike A, Michel CJ, Danner EM (2015) Sport science for salmon and other species: ecological consequences of metabolic power constraints. *Ecology Letters*. 18:535-544.

Milner NJ, Solomon DJ, Smith GW (2012) The role of river flow in the migration of adult Atlantic salmon, *Salmo salar*, through estuaries and rivers. *Fisheries Management and Ecology*. 19:537-547.

Naish KA, Taylor III JA, Levin PS, Quinn TP, Winton JR, Huppert D, Hilborn R (2008) An evaluation of the effects of conservation and fishery enhancement hatcheries on wild populations of salmon. *Advances in Marine Biology*. 53:61–194.

Newell JC, Quinn TP (2005) Behavioral thermoregulation by maturing adult sockeye salmon (*Oncorhynchus nerka*) in a stratified lake prior to spawning. *Canadian Journal of Zoology* 83: 1232-1239.

MFFP (2016) Plan de gestion du saumon atlantique 2016–2026, ministère des Forêts, de la Faune et des Parcs, Direction générale de l'expertise sur la faune et ses habitats, Direction de la faune aquatique, Québec, 40 p.

Økland F, Erkinaro J, Moen K, Niemelä E, Fiske P, McKinley RS, Thorstad EB (2001) Return migration of Atlantic salmon in the River Tana: phases of migratory behaviour. *Journal of Fish Biology* 59:862-874.

O'Reilly PT, Kozfkay C (2014) Use of microsatellite data and pedigree information in the genetic management of two long-term salmon conservation programs. *Reviews in Fish Biology and Fisheries*. 24(3):819-848.

O'Toole CL, Reed TE, Bailie D, Bradley C, Cotter D, Coughlan J, Cross T, Dillane E, McEvoy S, NO Maoiléidigh, Prodohl P, Rogan G, McGinnity P (2015) The signature of fine scale local adaptation in Atlantic salmon revealed from common garden experiments in nature. *Evolutionary Applications*. 8:881-900.

Quinn TP, Brannon EL, Whitman RP (1983) Pheromones and the water source preferences of adult coho salmon Oncorhynchus kisutch Walbaum. *Journal of Fish Biology.* 22:677–684

Ryman N, Laikre L (1991) Effects of Supportive Breeding on the Genetically Effective Population Size. *Conservation Biology*. 5:325-329.

Thorstad EB, Økland F, Aarestrup K, Heggberget TG (2008) Factors affecting the within-river spawning migration of Atlantic salmon, with emphasis on human impacts. *Reviews in Fish Biology and Fisheries* 18:345-371.

Richard A, Bernatchez L, Valiquette E, Dionne M, Jonsson B (2014) Telemetry reveals how catch and release affects prespawning migration in Atlantic salmon (Salmo salar). Canadian Journal of Fisheries and Aquatic Sciences 71:1730-1739.

Thorstad EB, Whoriskey F, Rikardsen AH, Aarestrup, K (2011) Aquatic Nomads: The Life and Migrations of the Atlantic Salmon. Page 467 *in* Ø. Aas, S. Einum, A. Klemetsen, and J. Skurdal, editors. Atlantic Salmon Ecology. John Wiley & Sons Ltd, Chichester, West Sussex, PO19 8SQ, United Kingdom.

TABLE DES MATIÈRES

LISTE DES FIGURES

LISTE DES TABLEAUX

1 INTRODUCTION

The Atlantic salmon (*Salmo salar*) is a member of the family Salmonidae that occurs in temperate and subarctic watersheds that drain into the Atlantic Ocean (Thorstad et al. 2011). As an anadromous fish, Atlantic salmon hatch from eggs in freshwater where they remain for one to several years before undergoing physiological changes that enable them to migrate to the ocean. Ocean rearing enables salmon to take advantage of enhanced growth opportunities to reach larger sizes and attain greater fecundity than would be possible for a strictly river-dwelling individual (Fleming 1998). After spending one to four years at sea, adult Atlantic salmon return to freshwater to spawn in the rivers where they were hatched (Thorstad et al. 2011). Atlantic salmon are iteroparous, which means that they can reproduce more than once, unlike most Pacific salmon, which are semelparous and die after reproducing. Thus, if an Atlantic salmon survives its first spawning attempt, it is capable of returning to the ocean post-spawning, and may make multiple spawning trips during its lifetime (Fleming 1998).

Historically, the species was distributed in North American watersheds ranging from southern New England through Atlantic Canada to Ungava Bay in the north and Eurasian watersheds ranging from Portugal to Russia. Anthropogenic impacts in freshwater and at sea have caused decreases in populations of Atlantic salmon (*Salmo salar*) throughout much of their global range and many stocks are currently endangered or extirpated (Thorstad et al. 2011). In eastern Canada, populations in some rivers are listed as endangered, threatened, or of concern by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC), with population declines attributed to loss of freshwater habitat and decreased survival at sea related to changes in the marine ecosystem (COSEWIC 2010).

Despite the depleted status of these populations, Atlantic salmon fisheries are economically valuable, especially in the recreational fishing sector. The value of Atlantic salmon to the Canadian economy was estimated in 2011 to exceed $250 million annually, supporting the equivalent of 3 872 full-time jobs (ASF 2011). Preservation of salmon populations in eastern Canada is therefore of ecological and economic value. Increasing attention is being placed on the role of reduced marine survival in limiting Atlantic salmon populations. With the exception of reducing at-sea harvest, however, most actions designed to conserve and augment salmon populations are focused on rivers, with an emphasis on habitat restoration, refining catch limits, and stock enhancement

(DFO 2015).

Perhaps the most well-known method of stock enhancement for salmonid species is the use of hatcheries to rear juvenile salmonids in captivity for subsequent release into natural systems. Hatcheries have been employed for more than a century to increase recreational and commercial fishing opportunities or mitigate reductions in natural production caused by habitat loss or degradation (Fisch et al. 2015, Kostow 2009). Hatchery enhancement has been accomplished via releases of juveniles at the egg, fry, parr, or smolt stage. Releasing individuals at a given life history stage enables them to bypass the natural mortality that occurs during previous life stages and can lead to increased survival to the adult stage.

Hatchery propagation, however, is associated with a suite of genetic and ecological risks. The artificial mating and the generally low number of broodstock used in hatchery supplementation programs reduce the effective population size and genetic diversity of the population and increases inbreeding (Christie et al. 2012, Ryman and Laikre 1991). Such loss of genetic diversity can make populations more susceptible to environmental perturbations (Schindler et al. 2010, Carlson and Satterthwaite 2011). Hatchery-produced individuals also often have decreased growth, survival, and reproductive success relative to natural-origin conspecifics (Araki and Schmid 2010). For example, hatchery produced smolts may be more surface oriented than wild smolts, increasing their susceptibility to predation (Collis et al. 2001). Additionally, when hatchery-reared fish are introduced in river as eggs, fry, or parr, they may compete with wild-spawned individuals or serve as a disease vector (Naish et al. 2008, Kostow 2009, Anderson et al. 2014). Increasing concern over the negative impacts of hatchery production of salmonids has led to recommendations to terminate programs that do not serve a “clear social or biological need” (Fisch et al. 2015, Kostow 2009).

The increasing awareness of the risks associated with hatchery propagation has led to a suite of alternatives that are based on allowing natural mating systems to operate by increasing spawning in rivers (Fraser 2008). Allowing adults to spawn in the wild instead of out-planting hatchery juveniles can reduce evolutionary impacts on the population because sexual selection, which is absent in hatchery mating programs, can occur during reproduction (Anderson et al. 2010). Unlike out-planted hatchery juveniles, naturally spawned offspring will have been exposed to predators and engage in self-feeding, allowing natural selection to act on progeny. Further, these naturally spawned offspring will have been exposed to the local biotic and abiotic environment throughout their entire life cycle, which can facilitate local adaptation (Taylor 1991, Anderson et al. 2014). Local adaptation leads to adaptive differences among populations, and is considered extremely important to persistence of salmonid stocks, especially in the face of environmental perturbation (Hilborn et al. 2003, Carlson and Satterthwaite 2011, O'Toole et al. 2015).

Programs designed to increase natural spawning require varying degrees of human intervention. In reintroduction programs, reproductive adults are allowed to access habitat within their historic range from which their populations are severely depleted or extirpated, for example, habitat upstream of dams or other anthropogenic features that block access to upstream spawning and rearing areas (Anderson et al. 2014). In colonization programs, salmon are given access to portions of rivers that have appropriate spawning and rearing habitat, but are historically inaccessible to upstream migrating adults because of natural barriers to migration, e.g. large waterfalls (Bryant et al. 1999). Reintroduction and colonization programs may make use of individuals that were naturally reared in-river or are the progeny of parents spawned in a hatchery. In some cases, reintroduction or colonization efforts may draw on captive-rearing programs, whereby juveniles captured in the wild are reared to maturity in freshwater or sea-water land-based facilities or in sea cages (Fraser 2008, O'Reilly and Kozfkay 2014).

The primary tools used to accomplish reintroductions or colonization are volitional passage and transportation of individuals via truck, barge, or in some cases, helicopter. In volitional passage, a barrier to migration (e.g. a man-made dam in the case of reintroduction or a natural waterfall in the case of colonization) is removed or altered in a way (e.g. through installation of a fishway) that allows upstream migrating salmon to pass the obstruction at their own pace to reach spawning habitat. In "trap and haul" programs, returning adults are trapped at a migratory barrier and "hauled" upstream in a tank (Anderson et al. 2014), and is hereafter referred to as "translocation".

Without a detailed understanding of how salmon exploit space when introduced to "novel" habitat, it is difficult to determine if the reintroduction and colonization programs will be able to achieve the desired outcome of enhancing population productivity via the establishment (or re-establishment) of a population. Migration patterns, habitat use, and movement by adult salmonids are influenced by a variety of extrinsic and intrinsic factors. River hydrology and geomorphological features shape river habitat and influence spawning migrations by affecting the difficulty of upstream passage, thus determining the time and energy it takes to reach spawning grounds (Milner et al. 2012). Such features also may limit the availability of suitable holding pools, where salmon recover before continuing migration (Bardonnet and Bagliniere 2000, Milner et al. 2012). Salmon metabolic rate increases with temperature, therefore, individuals incur increased travel costs at elevated river temperature (Martin et al. 2015). Increased energy costs incurred during migration can reduce reproductive fitness, either through a within-season reduction in energy stores that can be allocated to spawning activity and/or gonad development, or by increasing post-spawning mortality in iteroparous species that prevents spawning in subsequent years (Thorstad et al. 2008). Fish sex, size, and proximity to the spawning season also may affect an individual's migration pattern (Baglinière et al. 1990, Baglinière et al. 1991, Dahl et al. 2004, Thorstad et el. 2008, Richard et al. 2014). Handling stress may result in individuals moving out of the habitat chosen for colonization or reintroduction, thereby reducing the number of parents available for spawning and the potential gains in population productivity. Characterizing migration patterns and habitat use of individuals introduced to novel habitat and how they are influenced by biotic and abiotic factors would therefore help managers prioritize habitats, select individual candidates for release, and conduct transport under conditions that lead to successful establishment of a spawning population. Such information, therefore, is essential to the success of reintroduction and assisted migration programs designed to enhance and protect salmon populations (Thorstad et al. 2008).

Although reintroduction programs for salmonids are becoming more commonly adopted as a strategy to preserve and enhance salmonid populations (Anderson et al. 2014, O'Reilly and Kozfkay 2014, Askling 2015, Izzo et al. 2016), colonization programs are fairly uncommon due to risks posed to resident aquatic species (MFFP 2016). Due to the previously described negative consequences associated with hatchery propagation of salmonids, use of hatcheries to augment Atlantic salmon populations in the Province of Quebec has been greatly reduced, and is limited to only those rivers that have failed to attain a river-specific conservation threshold and face severe abundance problems (MFFP 2016). Consequently, under certain conditions, colonization of waterbodies or parts of waterbodies previously unoccupied by salmon has become an accepted strategy for population enhancement and is evaluated on a case-by-case basis. The rationale for supporting colonization as an enhancement strategy for Quebec salmon rests on the assumption that Atlantic salmon smolt production is limited by parr density, therefore, increasing habitat available for spawning will reduce density-dependent effects on parr survival, resulting in increased smolt production that will translate to greater returns of adults (Bley and Moring 1988, MFFP 2016).

1.1 Study Site

Between 2014 and 2016, a translocation program was operated on the Rivière Sainte-Marguerite Nord-Est in Québec, which provided a rare opportunity to examine movement patterns and habitat use by adult Atlantic salmon during the colonization of novel habitat. The Rivière Sainte-Marguerite Nord-Est is a salmon river that drains a catchment of approximately 1000 km^2. It joins the Rivière Sainte-Marguerite 5 km upstream of the confluence with the Saguenay Fjord (Figure 3.1). Volitional passage was initiated in the Rivière Sainte-Marguerite Nord-Est in 1981, with the installation of a fish ladder at a natural waterfall (Chute Blanche) at river kilometer (rkm) 7. Before the fish ladder was installed, returning adult salmon were only able to access 7 km of the river. The installation of the fish ladder opened an additional 18 km of river habitat for spawning and juvenile rearing. Further upstream passage is blocked by a pair of impassable waterfalls at rkm 33.7 (Chute du 16 Miles) and rkm 36.2 (Chute du 18 Miles).

In 2014, a translocation program was initiated to trap a subset of the adults returning to the fish ladder at Chute Blanche and transport them for release upstream of Chute du 18 Miles. Transported adults were able to access between13 km and 25 km of river habitat, depending on whether the natural waterfall Chute André was passable (Figure 3.1).

1.2 Objectives

The overarching objective of this dissertation was to examine migration patterns and habitat use by adult Atlantic salmon (*Salmo salar*) following transport and release into habitat upstream of Chute du 18 Miles. In attaining this objective, three research chapters were conceived.

The objective of the first chapter was to identify factors that influence whether adults remained in the novel habitat following transport. One of the key determinants of the success of a transport program involving adult salmon, regardless of the program's objective, is whether transported salmon stay and spawn in habitat where they are released. Some individuals die following release, whereas others exhibit downstream movements, termed "fallback" (Frank et al., 2009; Keefer et al., 2010). If fallback occurs over migration barriers, individuals will be removed from the spawning population in the release habitat (Keefer et al., 2010; Hagelin et al., 2015, 2016). Because fallback reduces the number of adults in the spawning population relative to the number of individuals transported, it can have serious consequences for the success of a program. The ability to predict fallback rate given intrinsic fish characteristics and environmental conditions at the time of transport, therefore, could greatly improve the success of transport programs.

The objective of the second chapter was to examine thermal refuge use by transported adults during summer 2016. Atlantic salmon are a cold-water species with a narrow temperature tolerance, however, throughout much of their range, Atlantic salmon are exposed to summer temperatures that often exceed the upper limit for temperature tolerance. Salmon survive high heat events by engaging in behavioral thermoregulation in cool water patches, termed thermal refuges. Despite considerable research on thermal refuge use by juvenile Atlantic salmon, relatively little information exists on use of refuge use by adult salmon. This is surprising, since adults return to natal rivers during summer, many months before the onset of spawning, and require access to cool thermal refuges to avoid mortality and retain sufficient energy stores for spawning. Understanding how adult Atlantic salmon use thermal refuges during the pre-spawning period may become essential for developing strategies for mitigating the effects of climate change on salmon during the in-river, pre-spawning migration and may help managers determine whether habitat targeted for colonization or reintroduction efforts contains adequate refuge habitat to allow adults to survive to the spawning season with adequate resources for successful reproduction.

The objective of the third chapter was to link Atlantic salmon movement patterns and habitat use with intrinsic fish characteristics and extrinsic environmental conditions experienced during colonization in a free-flowing river. Despite many studies of upstream migration of returning adults, a general mechanism for predicting the migratory response of salmon to environmental variables has not yet been developed (Thorstad et al. 2008, Bendall et al. 2012). Links between migration patterns and environmental variables are likely river- and context-specific, and relationships between environmental variables themselves are complex and often correlated (Jonsson 1991, Bendall et al. 2012, Martin et al. 2015). Differences in methods (e.g. counts at fish ladders vs. telemetry) used to examine the effects of environmental variables on migration make comparison among studies difficult, and studies carried out in regulated rivers will not necessarily be representative of conditions experienced by salmon in freely-flowing, natural river systems (Thorstad et al. 2008, Bendall et al. 2012). Further, adult salmon use olfactory cues generated by the chemical composition of natal river water and from the presence of conspecifics (juveniles or other adults) to navigate during in-river migration (Hasler et al. 1978, Quinn et al. 1983, Bett and Hinch 2015). Thus, the absence of such cues in novel habitat may also influence how salmon use habitat during reintroduction and colonization. Consequently, a concerted effort is needed to understand how individuals use novel habitat during colonization so as to best optimize new programs. In this chapter, I examined how salmon movement patterns vary in response to environmental conditions (river temperature, river discharge, season, diel period) and fish characteristics (sex and size) during colonization. Secondly, I attempted to determine the physical characteristics of pools (e.g. surface area, depth) that yield suitable habitat for holding by adults during in-river residence, and whether pool use changes as a function of environmental factors (e.g. river temperature and discharge).

1.3 General Methodology

Acoustic telemetry was applied to address the objectives of the three dissertation chapters, and methods are generally described in the current section. Returning adult salmon were captured at the Chute Blanche fish ladder and transported to a site 3 km upstream of Chute du 18 Miles. Each salmon was tagged with a uniquely coded 69 kHz acoustic transmitter that was implanted into the intraperitoneal cavity. The incision was closed with 3 or 4 sutures and aseptic technique was followed throughout the surgical procedure. Fish length, maxillary length, mass, and sex were recorded, as were the presence of any injuries. Maxillary length was used to confirm visual sex identification made in the field. A scale sample was collected for subsequent age analysis, and a small sample of adipose fin (2014) or caudal fin (2015 & 2016) was collected for future genetic analyses that are beyond the scope of this dissertation. Following surgery, salmon were transferred to an in-river recovery cage. Once fish regained equilibrium, an underwater door in the cage was opened. Most salmon swam out of the cage within one hour of surgery. If salmon remained in the cage after one hour, they were released by hand.

Tagged salmon were tracked after release using an array of acoustic receivers (Figure 3.1). Although the number of receivers increased with each year of the study, a core network of 8 receivers were deployed annually in the same locations and facilitated consistent detection of salmon among years. Range testing conducted during 2014 indicated that 95% of tag emissions were detected at a distance of 40 m, and 80% of tag emissions were detected at a distance of 200 m under calm conditions (Frechette et al. 2018). A reduction in detection range occurred when river discharge exceeded 60 m^3s^{-1} and during discrete rainfall events, due to an increase in ambient noise. However, redundancy produced by the combination of high frequency of signal transmission (every 30 to 90 sec) and long-term monitoring at fixed locations allowed us to successfully track salmon movements, even at the greatest river discharge recorded during the study (167 m^3s^{-1}). Receivers were deployed in June before the first transport occurred and were recovered during the spawning season in the autumn before the river froze.

Continuous river temperature and discharge data were recorded (at 15-minute intervals) during the course of this study (2014-2016). River temperature recorded by temperature loggers deployed in a shallow, well-mixed areas of the river mainstem were obtained from the RivTemp Network (Boyer et al., 2016) or from temperature loggers deployed specifically for this study. River discharge was obtained from the Government of Quebec (Station 062803; 48.267962N, –69.908823W).

2 BIBLIOGRAPHIE

Anderson JH, Pess GR, Carmichael RW, Ford MJ, Cooney TD, Baldwin CM, McClure MM (2014) Planning Pacific salmon and steelhead reintroductions aimed at long-term viability and recovery. *North American Journal of Fisheries Management.* 34:72-93.

Araki H, Schmid C. (2010) Is hatchery stocking a help or harm? *Aquaculture.* 308:S2-S11.

ASF (2011) Economic value of wild Atlantic Salmon. *Atlantic Salmon Federation.* http://www.asf.ca/.

Askling O (2015) A telemetry study for reintroducing wild Atlantic salmon (*Salmo salar* L.) in the Daugava and Ogre Rivers, Latvia. Master's Thesis. Karlstads University.

Baglinière J-L, Maisse G, Nihouarn A (1990) Migratory and reproductive behaviour of female adult Atlantic salmon, Salmo salar L., in a spawning stream. *Journal of Fish Biology.* 36:511-520.

Baglinière J-L, Maisse G, and Nihouarn A (1991). Radio-tracking of male adult Atlantic salmon, *Salmo salar* L., during the last phase of spawning migration in a spawning stream (Brittany, France). *Aquatic Living Resources.* 4:161–167.

Bardonnet A, Baglinière JL, (2000) Freshwater habitat of Atlantic Salmon (*Salmo salar*). *Canadian Journal of Fisheries and Aquatic Sciences.* 57:497-506.

Bendall B, Moore A, Maxwell D, Davison P, Edmonds N, Archer D, Solomon D, Greest V, Wyatt R, Broad K (2012) Modelling the migratory behaviour of salmonids in relation to environmental and physiological parameters using telemetry data. *Fisheries Management and Ecology.* 19:475-483.

Bett NN, Hinch, SG (2015) Attraction of migrating adult sockeye salmon to conspecifics in the absence of natal chemical cues. *Behavioral Ecology.* 26:1180-1187.

Bryant MD, Frenette BJ, McCurdy SJ (1999) Colonization of a watershed by anadromous salmonids following the installation of a fish ladder in Margaret Creek, Southeast Alaska. *North American Journal of Fisheries Management.* 19:1129-1136.

Carlson SM, Satterthwaite, WH (2011) Weakened portfolio effect in a collapsed salmon population complex. *Canadian Journal of Fisheries and Aquatic Sciences.* 68:1579–1589.

Christie MR, Marine ML, French RA, Waples RS, Blouin MS (2012) Effective size of a wild salmonid population is greatly reduced by hatchery supplementation. *Heredity.* 109:254-260.

COSEWIC (2010) COSEWIC assessment and status report on the Atlantic Salmon *Salmo salar* (Nunavik population, Labrador population, Northeast Newfoundland population, South Newfoundland population, Southwest Newfoundland population, Northwest Newfoundland population, Quebec Eastern North Shore population, Quebec Western North Shore population, Anticosti Island population, Inner St. Lawrence population, Lake Ontario population, Gaspé-Southern Gulf of St. Lawrence population, Eastern Cape Breton population, Nova Scotia Southern Upland population, Inner Bay of Fundy population, Outer Bay of Fundy population) in Canada. Committee on the Status of Endangered Wildlife in Canada. Ottawa. xlvii + 136 pp.

Dahl J, Dannewitz J, Karlsson L, Petersson E, Löf A, Ragnarsson B (2004) The timing of spawning migration: implications of environmental variation, life history, and sex. *Canadian Journal of Zoology.* 82:1864-1870.

DFO (2015) Special Report on Atlantic Salmon. Prepared by the Minister's Advisory Committee on Atlantic Salmon. *Department of Fisheries and Oceans Canada*. July 2015. 65 p.

Fisch KM, Kozfkay CC, Ivy JA, Ryder OA, Waples RS (2015) Fish hatchery genetic management techniques: integrating theory with implementation. *North American Journal of Aquaculture*. 77:343-357.

Fleming, IA (1998) Pattern and variability in the breeding system of Atlantic salmon (Salmo salar), with comparisons to other salmonids. *Canadian Journal of Fisheries and Aquatic Sciences.* 55:59–76.

Fraser DJ (2008) How well can captive breeding programs conserve biodiversity? A review of salmonids. *Evolutionary Applications*. 1: 535-86.

Hasler AD, Scholz AT, Horrall RM (1978). Olfactory Imprinting and Homing in Salmon: Recent experiments in which salmon have been artificially imprinted to a synthetic chemical verify the olfactory hypothesis for salmon homing. *American Scientist*. 66, 347-355.

Hagelin A, Calles O, Greenberg L, Nyqvist D, Bergman E (2016) The migratory behaviour and fallback rate of landlocked Atlantic salmon (*Salmo salar*) in a regulated river: does timing tatter? *River Research and Applications*. 32(6), 1402-1409.

Hagelin, A, Calles O, Greenberg L, Piccolo J, Bergman E. (2016) Spawning migration of wild and supplementary stocked landlocked Atlantic salmon (*Salmo salar*). *River Research and Applications.* 32(3), 383-389.

Hilborn R, Quinn TP, Schindler DE, Rogers DE (2003). Biocomplexity and fisheries sustainability. *Proceedings of the National Academy of Sciences.* 100:6564-6568.

Izzo LK, Maynard GA, Zydlewski J. (2016). Upstream Movements of Atlantic Salmon in the Lower Penobscot River, Maine Following Two Dam Removals and Fish Passage Modifications. Marine and Coastal Fisheries 8:448-461.

Jonsson N. (1991) Influence of water flow, water temperature and light on fish migration in rivers. *Nordic Journal of Freshwater Research*. 66:20-35.

Keefer ML, Taylor GA, Garletts DF, Gauthier GA, Pierce TM, Caudill CC (2010) Prespawn mortality in adult spring Chinook salmon outplanted above barrier dams. *Ecology of Freshwater Fish*. 19:361-372.

Kostow K. (2009). Factors that contribute to the ecological risks of salmon and steelhead hatchery programs and some mitigating strategies. *Reviews in Fish Biology and Fisheries.* 19:9-31.

Martin BT, Nisbet RM, Pike A, Michel CJ, Danner EM (2015) Sport science for salmon and other species: ecological consequences of metabolic power constraints. *Ecology Letters*. 18:535-544.

Milner NJ, Solomon DJ, Smith GW (2012) The role of river flow in the migration of adult Atlantic salmon, *Salmo salar*, through estuaries and rivers. *Fisheries Management and Ecology*. 19:537-547.

Naish KA, Taylor III JA, Levin PS, Quinn TP, Winton JR, Huppert D, Hilborn R (2008) An evaluation of the effects of conservation and fishery enhancement hatcheries on wild populations of salmon. *Advances in Marine Biology*. 53:61–194.

MFFP (2016) Plan de gestion du saumon atlantique 2016–2026, ministère des Forêts, de la Faune et des Parcs, Direction générale de l'expertise sur la faune et ses habitats, Direction de la faune aquatique, Québec, 40 p.

O'Reilly PT, Kozfkay C (2014) Use of microsatellite data and pedigree information in the genetic management of two long-term salmon conservation programs. *Reviews in Fish Biology and Fisheries*. 24(3):819-848.

O'Toole CL, Reed TE, Bailie D, Bradley C, Cotter D, Coughlan J, Cross T, Dillane E, McEvoy S, NO Maoiléidigh, Prodohl P, Rogan G, McGinnity P (2015) The signature of fine scale local adaptation in Atlantic salmon revealed from common garden experiments in nature. *Evolutionary Applications*. 8:881-900.

Quinn TP, Brannon EL, Whitman RP (1983) Pheromones and the water source preferences of adult coho salmon Oncorhynchus kisutch Walbaum. *Journal of Fish Biology.* 22:677–684

Ryman N, Laikre L (1991) Effects of Supportive Breeding on the Genetically Effective Population Size. *Conservation Biology*. 5:325-329.

Thorstad EB, Økland F, Aarestrup K, Heggberget TG (2008) Factors affecting the within-river spawning migration of Atlantic salmon, with emphasis on human impacts. *Reviews in Fish Biology and Fisheries* 18:345-371.

Richard A, Bernatchez L, Valiquette E, Dionne M, Jonsson B (2014) Telemetry reveals how catch and release affects prespawning migration in Atlantic salmon (Salmo salar). Canadian Journal of Fisheries and Aquatic Sciences 71:1730-1739.

Thorstad EB, Whoriskey F, Rikardsen AH, Aarestrup, K (2011) Aquatic Nomads: The Life and Migrations of the Atlantic Salmon. Page 467 *in* Ø. Aas, S. Einum, A. Klemetsen, and J. Skurdal, editors. Atlantic Salmon Ecology. John Wiley & Sons Ltd, Chichester, West Sussex, PO19 8SQ, United Kingdom.

3 FACTORS INFLUENCING FALLBACK BY SALMON FOLLOWING TRANSPORT INTO NOVEL HABITAT

Title of Article: **Factors influencing fallback by adult Atlantic salmon (*Salmo salar*) following transport into novel habitat**

Titre de l'article : **Facteurs influençant le retour vers l'aval des saumons atlantiques adultes suite à leur transport dans un nouvel habitat**

Auteurs :

Authors and affiliations:
[1]Danielle M. Frechette
[2]Elsa Goerig (goerig.elsa@gmail.com)
[1]Normand E. Bergeron (Normand.Bergeron@ete.inrs.ca)

1. Institut National de Recherche Scientifique, Centre Eau Terre Environnement, Québec, Canada
2. Museum of Comparative Zoology, Harvard University, Cambridge Massachusetts, USA

This chapter was submitted to Fisheries Management and Ecology

Submitted 3 November 2018

Contributions of authors:

D. Frechette and N. Bergeron planned the study to use acoustic telemetry to determine the fate of Atlantic salmon transported and released into novel habitat. D. Frechette conducted the fieldwork, processed the data, conducted analyses of summary statistics, and wrote the original draft of the manuscript. D. Frechette and E. Goerig conceived the idea of using survival analysis to analyse the data. E. Goerig wrote the R code to analyse the data, and D. Frechette and E. Goerig conducted and interpreted the survival analysis. N. Bergeron and E. Goerig provided valuable comments on initial drafts of the manuscript, which greatly improved the final submission.

3.1 Résumé

Le transport vers l'amont des salmonidés durant leur migration permet de contourner les obstacles tels les barrages hydroélectriques ou les chutes naturelles, et d'accéder à des habitats de reproduction et de croissance. Le retour vers l'aval suivant le transport en amont d'un obstacle est fréquent et il a pour conséquence de réduire le nombre de reproducteurs dans la population, entraînant des conséquences négatives pour la productivité de celle-ci. Une régression de Cox considérant la période précédant l'occurrence d'un événement (e.g. retour vers l'aval) a été utilisée pour déterminer les effets des caractéristiques du poisson, des conditions de transport et des variables environnementales sur les taux de mouvement vers l'aval de saumons de l'Atlantique adultes transportés en amont d'une chute infranchissable dans le cadre d'une stratégie d'amélioration de la population de la rivière Sainte-Marguerite Nord-Est. Sur les 68 saumons transportés, 19 ont effectué un mouvement vers l'aval dans les sept jours suivant leur transport. La longueur à la fourche des poissons était le seul facteur augmentant le risque de retour vers l'aval après le transport. Nous avons observé une augmentation de 5% dans la proportion des grands saumons (≥ 780 mm LF) s'étant déplacés vers l'aval au cours des sept jours suivant le transport, par rapport aux saumons de taille médiane (750 mm LF). Malgré un échantillon de petite taille, les conclusions de notre étude ont des implications pour l'optimisation du programme du transport sur la rivière Sainte-Marguerite, ainsi que pour la conception de programmes similaires dans d'autres rivières.

3.2 Abstract

Transport of salmonids allows upstream migrating adults to bypass barriers to migration, e.g. hydroelectric dams or adverse habitats. Downstream movement ("fallback") after transport is common and removes individuals from spawning populations, with possible detrimental consequences for population productivity. Time-to-event analysis was used to determine effects of fish characteristics, transport conditions, and environmental variables on fallback by adult Atlantic salmon transported into novel habitat as a population enhancement strategy on the Rivière Sainte-Marguerite Nord-Est (Québec, Canada). Of 68 salmon transported, 19 exhibited post-transport fallback within seven days of transport. Fork length (FL) was the only factor that increased risk of post-transport fallback; there was a 5% increase in the proportion of large salmon (≥ 780 mm FL) exhibiting post-transport fallback relative to individuals of median size (750 mm FL). Although the present study was limited by small sample size, the findings will help inform design of transport programmes in freshwater systems.

3.3 Introduction

The Atlantic salmon (*Salmo salar*) is an anadromous fish that occurs in temperate and subarctic catchments that drain into the Atlantic Ocean (Thorstad, Whoriskey, Rikardsen & Aarestrup, 2011). Historically, the species was distributed in North American catchments ranging from southern New England to Ungava Bay in the north and Eurasian catchments ranging from Portugal to Russia. Human impacts in freshwater and marine environments have caused decreases in Atlantic salmon populations throughout much of their global range, and many stocks are currently endangered or extirpated (Thorstad, Whoriskey, Rikardsen & Aarestrup, 2011). In eastern Canada, populations are listed as endangered, threatened, or of concern by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC), with population declines attributed to loss of freshwater habitat and decreased marine survival (COSEWIC, www.cosewic.gc.ca). Consequently, there is a concerted effort to conserve and augment salmon populations (DFO, 2015).

Translocation of salmon, i.e. capture of salmon in one location and release in a different location, is used to meet a variety of conservation objectives. Most commonly, transport via truck or barge enables salmon to bypass man-made barriers to migration (e.g. dams) or habitat where mortality may be high, thus reconnecting fragmented habitat (Ebel, 1980; Hagelin et al., 2015, 2016; Keefer et al., 2010). Transport of adults is also used in reintroduction programmes whereby adults are transplanted into areas from which salmon were extirpated, either to augment natural recolonisation by migrating adults, or in cases where reintroduction sites are isolated from breeding populations (Anderson et al., 2014; Keefer et al., 2010).

Transport of adults also may be used to enable salmon to colonise novel habitat as part of an assisted migration programme. Assisted migration has been defined as "the intentional translocation or movement of species outside of their historic ranges" (Hewitt, 2011), which has been proposed as a means of mitigating effects of climate change on species distributions (Thomas, 2011). With regards to salmon, assisted migration can be more broadly defined as allowing individuals to access portions of rivers that have appropriate spawning and rearing habitat, but are currently inaccessible to upstream migrating adults because of natural barriers to migration (e.g. large, natural waterfalls). Allowing adults to colonise inaccessible habitat may increase population productivity by enabling expansion of the breeding population into unoccupied, high quality habitat, subsequently reducing density-dependent effects on growth and survival of offspring (Anderson et al., 2014; Pess et al., 2011).

One of the key determinants of the success of a transport programme involving adult salmon, regardless of the programme's objective, is whether transported salmon stay and spawn in habitat where they are released. Some individuals die following release, whereas others may exhibit downstream movements, termed "fallback" (Frank et al., 2009; Keefer et al., 2010). If fallback occurs over migration barriers, then individuals will be removed from the spawning population in the release habitat (Hagelin et al., 2015, 2016; Keefer et al., 2010). Because fallback reduces the number of adults in the spawning population relative to the number of individuals transported, it can have serious consequences for the success of a programme. The ability to predict fallback rate given intrinsic fish characteristics and environmental conditions at the time of transport, therefore, could greatly improve the success of transport programmes.

Most previous studies examining fallback related to migration barriers were conducted in impounded rivers, where fallback occurred over hydroelectric dams (e.g., Hagelin et al., 2015, 2016; Keefer et al., 2004; Naughton et al., 2006). The present study represents a rare case where it was possible to evaluate post-transport fallback over natural barriers to migration. Adult salmon returning to the Rivière Sainte-Marguerite Nord-Est (Quebec, Canada) were captured for transport into previously inaccessible habitat upstream of a pair of impassable, natural waterfalls as part of an assisted migration programme that operated from 2014 to 2016. The goal of the transport programme was to increase population productivity through a reduction in density dependent effects on juvenile growth and survival to compensate for a recent decrease in the number of adults returning to the river (Ministère des Forêts, de la Faune et des Parcs, 2018). The objective of the present study was to identify factors that influence fallback after transport, more specifically to determine whether: 1) characteristics of individual salmon predisposed them to exhibiting fallback and 2) environmental or transport conditions influenced the propensity of salmon to exhibit fallback. The findings are of primary importance for local managers, but they also have more far-reaching implications, as they can help inform transport programmes for Atlantic salmon in both impounded and free-flowing river systems.

3.4 Materials and methods

3.4.1 Study area

The Rivière Sainte-Marguerite Nord-Est (hereafter, Rivière Nord-Est) is a salmon river in Quebec, Canada, that drains an area of ≈ 1000 km^2, and joins the Rivière Sainte-Marguerite ≈ 5 km upstream from its confluence with the Saguenay River (Figure 3.1). A recreational fishery for Atlantic salmon has existed on the Rivière Nord-Est since 1860. Catch and release angling was first recorded in 2000, and mandatory release of large, multi-sea-winter salmon has been in place since 2003. A large, natural waterfall (Chute Blanche) located at river kilometre (rkm) 7 prevented salmon from moving further upstream until 1981, when a fish ladder was installed that allowed salmon to bypass the waterfall. Construction of the fish ladder was an attempt to increase spawning and rearing habitat and reduce density-dependent effects on juvenile growth and survival, with the ultimate goal of producing more returning adults to augment the local recreational fishing economy. Salmon that ascended the fish ladder had access to approximately 18 km of habitat before upstream passage was blocked by a pair of large, natural waterfalls at rkm 33.7 (Chute du 16 Miles) and rkm 36.2 (Chute du 18 Miles).

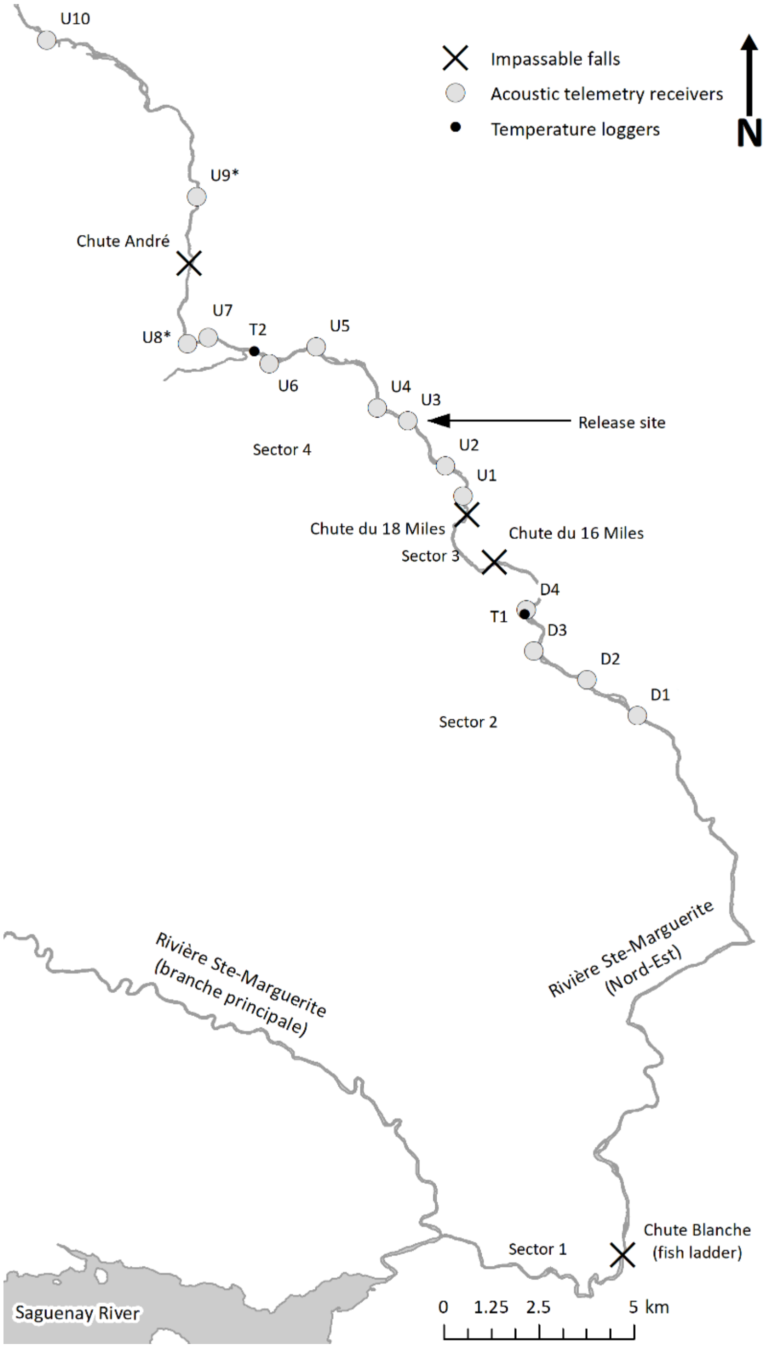


Figure 3.1 : Map of study area

Impassable waterfalls bounding the river sectors are indicated with an X. Receiver positions are indicated with solid grey circles. Receivers in the upstream sector of the river are labelled U1-U10 and receivers in the downstream sector are labelled D1-D5. Receivers marked with an asterisk were not deployed all three years (U8 was deployed in 2015 and 2016, U9 was deployed in 2015). Temperature loggers are indicated with small dark black circles and were deployed in the river main stem (T1 at rkm 30 and T2 at rkm 45). The release site is indicated with an arrow. The map was created using ArcGIS software by ESRI.

Data regarding run size and composition of returning adults is available from 1984 to the present (Ministère des Forêts, de la Faune et des Parcs, 2018). From 1984 to 1998, the mean number of adults returning to the Nord-Est (Sectors 1 and 2) was 784 (minimum–maximum: 299–1736), while mean escapement was 619 salmon (min–max: 250–1376). From 1999–2013, the mean annual run size was 478 (min–max: 261–921) and mean escapement was 392 (min–max: 185–809). During the ten years prior to the start of this study, the mean number of adults captured in the fish ladder was 273, and ranged from a low of 192 in 2006 to a high of 630 in 2011 (Ministère des Forêts, de la Faune et des Parcs, 2018). The relative proportion of one-sea-winter (1SW) and multi-sea-winter (MSW) adults fluctuated among years; MSW salmon outnumbered 1SW salmon in some years, while 1SW salmon predominated in other years. For the period 2012–2016, 1SW salmon represented 26–89% of returning adults ($\bar{x} = 57, \mathrm{SD} = 28$).

Between 2014 and 2016, a subset of adult Atlantic salmon returning to the Chute Blanche fish ladder were trapped, transported by truck, and released into novel habitat upstream of Chute du 18 Miles. Translocated adults were able to access ≈ 13 km of river habitat before further upstream passage is blocked by Chute André, another natural waterfall (Frechette, unpublished data). For the purposes of this study, the Rivière Nord-Est was divided into four sectors (Figure 3.1). Sector 1 begins at the confluence with the Rivière Sainte-Marguerite and ends at Chute Blanche. Habitat between Chute Blanche and Chute du 16 Miles is hereafter referred to as Sector 2. The 3.5 km between Chute du 16 Miles and Chute du 18 Miles (Sector 3) is inaccessible due to steep canyon walls and rapids and was not monitored during this study. Sector 4 begins at Chute du 18 Miles and ends at Chute André.

Between 1984 and 2011, hatchery-produced salmon were planted in various locations throughout the Rivière Nord-Est with the goal of further enhancing recreational fishing opportunities. Salmon were planted as eggs (1986 and 1987), fry (1988, 1991, 1997, 1998, and 2000–2011), and 1+ parr (1984, 1985, and 1988). The number of hatchery salmon planted ranged from 5821 (1+ parr) in 1988 to 43,780 unfed fry in 2004. A previous study on the Rivière Nord-Est indicated that the majority of smolts out-migrated at age-3+ (Brisson Bonenfant, 2006). Given these data, the adults returning to the Rivière Nord-Est during the study period could include 1) offspring of true wild parents; 2) offspring of hatchery-produced parents that spawned in the wild; or 3) individuals planted in the river as 0+ fry between 31 May and 3 June, thus spent the majority of their lives rearing in the wild. Fry planted in the river were not marked before release and were indistinguishable from wild-spawned salmon, therefore, all transported adults were considered to have been wild-reared for the purposes of this study.

Continuous river temperature data at 15-min intervals, obtained from the RivTemp Network (Boyer et al., 2016), were measured using a HOBO UA-002-64 temperature logger (Onset, Bourne, MA) deployed in a shallow, well-mixed area of the river in Sector 2 that provided the most complete temperature time series for the Rivière Nord-Est during the three study years (48.42164N, –69.89621W; Figure 3.1). Results of linear regression between the Sector 2 temperature logger and a temperature logger deployed in Sector 4 (48.482775N; –69.992417W) indicate that the Sector 2 logger provided an adequate representation of the thermal regime experienced by adults in sectors 4 and 2 (adjusted $R^2 = 0.92$, $P < 0.01$). River discharge at corresponding 15-min intervals was obtained from the Government of Quebec (Station 062803; 48.267962N, –69.908823W).

3.4.2 Fish trapping and transport

The fish ladder at Chute Blanche is a 23-basin pool-type ladder with lateral notches and submerged orifices. The first main basin contains a capture cage. All salmon enter the capture cage and are prevented from ascending the fish ladder until an operator raises the cage and opens a hatch at the upstream end. This design permits a complete count of all salmon that ascend the ladder each year. Although river entry of returning adults may occur from early June to early September, the fish ladder opens around 20 June and closes in mid- to late-August. The entry cage is routinely checked during daylight hours (6:00 to 21:00 at this latitude) for the entirety of the period when the ladder is in operation. In 2015, a retention cage was installed in the second basin, allowing salmon to be held in the fish ladder while awaiting transport.

Translocated salmon were transported in a 1600-L tank equipped with water recirculation and oxygen delivery systems. Fresh water was pumped into the tank before each transport. No transport occurred when river temperature exceeded 20°C. All salmon transported in 2014 and most salmon transported in 2015 and 2016 were transferred directly from the capture cage to the transport tank using a soft mesh net. The remainder of the salmon were transferred to the tank using the retention cage. The retention cage was lifted and moved over the transport tank via a winch and boom and a trap-door mechanism on the underside of the retention cage was used to open the floor of the cage so that salmon fell directly into the tank. Individuals that entered the fish ladder after 18:00 were held overnight in the retention cage. Salmon became agitated and were attempting to jump out of the retention cage beginning at sunrise, so efforts were made to transport individuals that were held overnight within one hour of sunrise. No salmon were held in the retention cage for more than 12 hours.

3.4.3 Fish tagging and telemetry

Transported salmon were tagged with acoustic tags (Vemco V13–H, 13 mm diameter) within one hour of arrival at the release site. Tag mass (6 g in water) was considerably less than the maximum recommended tag body burden of 2% for all individuals (Winter, 1983). Fish were anaesthetised in a bath containing acetyleugenol (30 mg/L). Dosage time varied depending on water temperature and ranged from 105 sec to 488 sec (mean = 267 sec; SD = 73 sec). Once adequately anesthetised, determined by gill respiration rate and strength of the reflex response, the salmon was transferred to a V-shaped surgery table for tagging. A maintenance dose of acetyleugenol (15 mg/L) and water was administered over the gills during tagging using a custom-designed reservoir. The acoustic tag was inserted into the abdominal cavity through an incision using aseptic technique. The incision (20 mm in length) was placed anterior to the pelvic girdle (lateral to the ventral midline), and closed with three or four simple interrupted sutures (c. 5 mm spacing). No antiseptic treatment was applied, however, surgical materials were sterilised before all surgeries using a 1% Virkon solution (LANXESS Corporation, Pittsburg Pennsylvania) for 10 min.

During handling, maxillary length and fork length (FL) were measured. Large salmon (> 63 cm FL) were classified as multi-sea-winter (MSW) salmon and small salmon (FL < 63 cm FL) were classified as one-sea-winter (1SW) salmon (DFO, 1998). External secondary sexual characteristics were used to assign sex in the field. Established regression relationships were applied between maxillary length and FL to determine sex of individuals that did not have evident external sexual characteristics (Maisse et al., 1988; Prévost et al., 1991). The established regression relationships did not apply to 1SW salmon, therefore, all transported 1SW salmon were assumed to be males because most had evidence of a prominent kype and males comprise 85% of 1SW salmon returning to rivers in the province of Quebec (Ministère des Forêts, de la Faune et des Parcs, 2016). Individuals were assigned an injury score based on a 6-point scale, where zero represented no injury (Annex 1). Scale samples were collected to determine fish age and a small piece of caudal fin (c. 5 mm × 5 mm) was collected for an associated project, but these samples have not yet been analysed. After surgery, salmon were transferred to an in-river recovery cage and were checked every 15 min until they regained equilibrium and were swimming freely; a door in the cage was then opened that allowed individuals to volitionally exit the cage (self-release). Individuals that remained in the cage one hour after regaining equilibrium were released by hand (hand-release). All animal handling protocols were approved by the INRS Institutional Committee for the Protection of Animals (CIPA Protocol 1406-03).

After release, movements of tagged salmon were tracked using an array of acoustic receivers (VR2W, Vemco, Halifax, NS). Although the number of receivers increased with each year of the study, a core network of seven receivers in Sector 4 (U1–U7) and one receiver in Sector 2 (D4) were deployed annually at the same locations and used to identify fallback (Figure 3.1). Receivers were installed in pools of > 0.5 m depth. Under calm conditions, 95% of tag emissions were detected at a distance of 40 m, and 80% of tag emissions were detected at a distance of 200 m (Frechette, Dugdale, Dodson & Bergeron, 2018). Although detection range was reduced during discrete rainfall events and when river discharge exceeded 60 m^3/sec, the high frequency of signal transmission (every 30 to 90 sec) and long-term monitoring at fixed locations introduced redundancy and allowed fallback to be identified with certainty.

In previous studies, fallback has been defined as directed downstream movement by fish following release after transport or handling, or after ascent of a dam or other artificial barrier to migration (Hagelin et al., 2015; Havn et al., 2015; Holbrook et al., 2009; Jokikokko, 2002). Under the assumption that salmon normally travel in a directed, upstream direction during migration (Finstad, Økland, Thorstad & Heggberget, 2005; Økland et al., 2001), these downstream movements have been used as a proxy for handling stress (Frank et al. 2009; Havn et al., 2015; Mäkinen, Niemelä, Moenb & Lindström, 2000). For the purpose of the present study, fallback was defined as movement over the impassable falls downstream of the release site, because 1) downstream movements may occur naturally as part of migration and homing behaviour (Frank et al., 2009; Heggberget, Hansen & Naesje, 1988; Keefer, Peery & Caudill, 2006; Lennox et al., 2015; Naughton et al., 2006); and 2) only downstream movements that removed individuals from the population spawning in the novel habitat were of interest in the present study. Any salmon that remained upstream of the impassable falls had the potential to remain in the colonising population, regardless of initial direction of movement. Two types of fallback were defined: complete, and partial. Complete fallback occurred when a salmon was detected by receiver D4, indicating that the individual had passed over both impassable waterfalls. Partial fallback occurred when a salmon ceased to be detected upstream of Chute du 18 Miles and was not recorded at receiver D4, indicating that the fish remained in the habitat between Chute du 16 and Chute du 18 (Sector 3).

3.4.4 Statistical Analyses

Fallback was described as a binary event occurring at a discrete time during the study, thereby allowing the probability of fallback to be predicted using a logistic model. The use of a logistic model, however, omits useful information, namely the amount of time elapsed before the event occurs (Kleinbaum & Klein, 2005). Because the amount of time an individual remains upstream (i.e. the pre-fallback interval) may be as informative as whether or not the individual exhibits fallback, time-to-event analysis (also called survival analysis), was used to identify the variables that influence the propensity of an individual to exhibit fallback. This technique has previously been applied to assess motivation and attempt rate for salmonids to pass culverts or hydro-electric dams (Castro-Santos, 2004; Goerig & Castro-Santos, 2017; Nyqvist et al., 2017). Specifically, Cox proportional hazards regression was used to estimate the instantaneous event rate, referred to as the “hazard”. The hazard rate is the conditional probability that an individual experiences the event at a particular time, given that it is in the population at risk at that time (Allison, 2014). In addition to use of survival time in the estimation of the hazard function, Cox regression also: 1) allows for inclusion of time-varying covariates (e.g. discharge or water temperature); and 2) deals well with cases in which the exact survival time for an individual is unknown. Such individuals are referred to as “censored” (Allison, 2014; Kleinbaum & Klein, 2005). In the present study, censored individuals were those that either did not exhibit fallback during the study or that left the study through death or tag loss. The Cox model allows data from censored individuals to contribute to the estimation of the hazard function (Allison, 2014). Thus, for the present study, the hazard represents the instantaneous probability that an individual will exhibit fallback given that it is in Sector 4, is not dead, and has a functioning acoustic transmitter.

Cox regression models were fitted to the data using the coxph function from the package survival (version 3.4.3) in R Studio (R Studio Team, 2016; R Core Team, 2017; Therneau & Grambsch, 2000; Therneau, 2015). The Cox regression model is given in Equation 1, where $\lambda(t)$ is the baseline hazard function (fallback rate) modelled as a function of time (t) and the term $X\,\beta$ represents the explanatory variables:

$$(t) = \lambda_0(t)e^{X\beta} \tag{1}$$

The explanatory variables hypothesised to affect fallback were classified into one of three groups: fish characteristics, river characteristics, and transport characteristics. Year was also included as an explanatory variable to identify any potential inter-year variation in fallback rates.

Fish characteristics included fish FL, sex, and injury class (Inj). River characteristics were mean hourly main stem river temperature (RT) and mean hourly river discharge (Q). Only transport characteristics that were recorded for all transports (n = 43) were included in the time-to-event analysis (Table 3.1, Figure 3.2): duration of transport (DUR), temperature in the fish ladder at departure (LT), and the temperature difference between the fish ladder at departure and the river at the upstream release site upon arrival (TDR). Other transport conditions were recorded but not included in the analysis because they were not available for all transports: tank temperature at departure (n = 42 transports; n = 66 salmon), tank temperature at arrival (n = 40 transports; n = 61 salmon) and oxygen saturation at arrival and departure (n = 37 transports; n = 55 salmon). The number of fish held overnight was low (n = 10) relative to the total number of transported fish (n = 68). The number of salmon that were hand released (n = 16) was also low relative to those that volitionally swam out of the recovery cage (n = 52). Samples were considered too unbalanced to test the effect of holding fish overnight and release type on fallback rate using time-to-event analysis.

Table 3.1 : Continuous variables included in time-to-event analysis

Covariate Class	Variable	Mean	SD	Min	Max
Fish	FL: Fork Length (mm)	725.7	118.8	520.0	975.0
Transport	LT: Ladder Temperature (°C)	17.6	1.3	13.9	20.5
	TDR: Difference between ladder and release site (°C)	-0.02	0.6	-1.5	1.4
	DUR: Duration (min)	52.6	8.3	40.0	75.0
River	T: River temperature (°C)	14.6	4.8	1.4	23.0
	Q: River discharge (m^3s^{-1})	23.9	20.1	6.6	190.3

Summary statistics for continuous variables that were measured but not included as explanatory variables in the time-to-event analysis. For all variables, sample size was 43 transports (68 salmon).

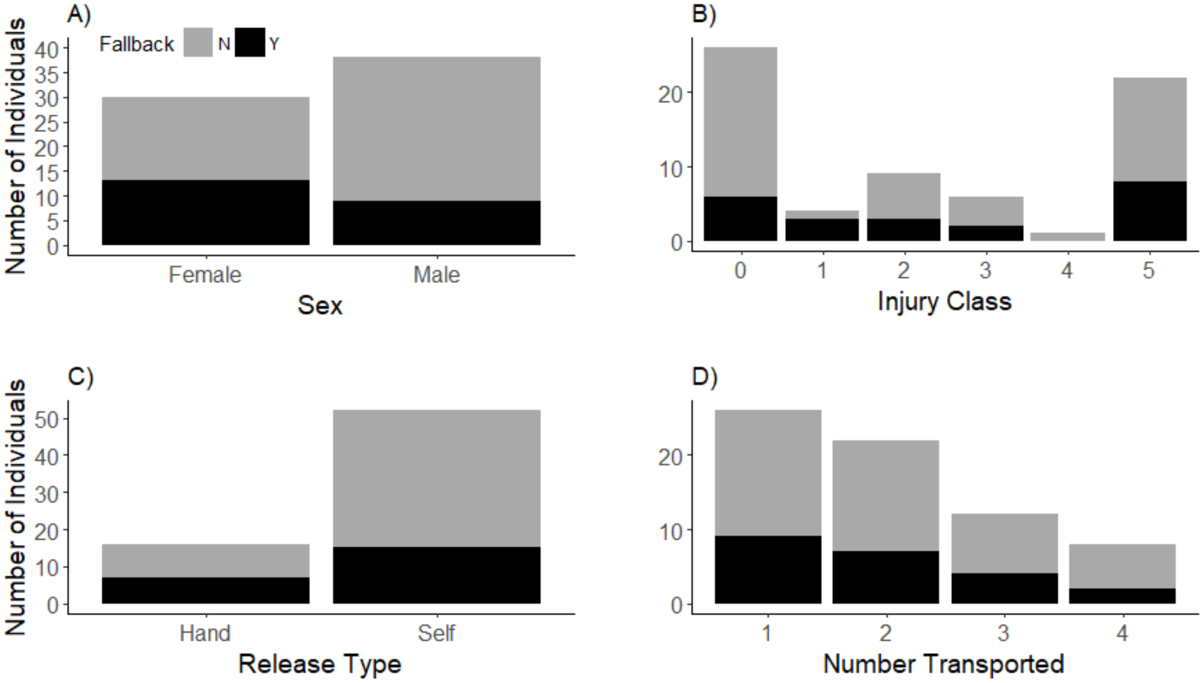


Figure 3.2 : Categorical variables used in time-to-event analysis

Distribution of categorical variables included as covariates in the time-to-event analysis. Black bars represent the number of individuals that exhibited post-transport fallback (partial and complete fallback); grey bars represent the number of individuals that did not exhibit post-transport fallback (including individuals that exhibited post-spawn fallback). Note the different y-axes.

Fish and transport characteristics were constant; that is, each individual was associated with a fixed value for FL, sex, transport duration, etc. The time-varying covariates of river temperature and discharge were incorporated into the data set such that each value of river temperature and discharge had a discrete start and end time. The start of the pre-fallback interval began at the time a salmon exited the recovery cage. The exact time that receivers were removed from the water was not recorded, so the end of the study was defined as 23:00 on the day before receivers were removed from the river. The event (fallback) time was assigned as the time of the last detection on Receiver U1 for those individuals that experienced fallback (coded as “1”). Right censoring (coded as “0”) occurred when an individual: 1) died/lost a tag before the end of the study or b) had not yet exhibited fallback at the end of the study. Tag loss/mortality were assigned when a tag failed to move from a location for the duration of the study year, however, it was not possible to distinguish between a lost tag and the death of an individual.

It can be assumed that stress of handling and transport only influences the probability of fallback for a certain period of time after transport. Rather than setting an arbitrary time period, moving-point regression was used to empirically identify the number of days over which to evaluate post-transport fallback. Specifically, the number of days since release was computed for each day that an individual was present in Sector 4, which was used as a threshold value in the moving-point regression. A global Cox regression model was fitted (Eqn. 2) using the coxph function where the covariate “Break” was a binary variable that was assigned a value of zero if the number of days since release was less than the given threshold or a value of one if it was greater:

$$\mathrm{Break+FL+Sex+Inj+RT+Q+DUR+NO+LT+TDR} \qquad (2)$$

The global model was sequentially fitted such that each value for the number of days since release was used as the threshold. The number of days since release that minimised the Akaike Information Criterion (AIC; Akaike, 1974) was selected as the breakpoint (Burnham & Anderson, 2002). This breakpoint was then used to subset the data to assess the effect of explanatory variables on post-transport fallback via Cox regression. Complete observations existed for individuals that exhibited fallback before the breakpoint. Individuals that did not exhibit fallback before the breakpoint were right censored.

Fixed effects were assigned to the Cox regression models using one of two approaches. First, a suite of candidate models was generated that grouped explanatory variables into three classes: fish characteristics (FL, Sex, and Inj), transport characteristics (DUR, LT, and TDR), and river characteristics (RT and Q), hereafter referred to as the “group-wise approach”. All models were fitted with and without the explanatory variable Year. Variables that were highly correlated ($R \geq 0.5$ or ≤ -0.5) were not allowed to co-occur in a model and no more than four covariates were allowed in a given model because the number of fallback events was low, resulting in few degrees of freedom. Cox regression was fit to the suite of candidate models using the coxph function and the model that minimised AIC was selected as the most likely model given the data (Burham & Anderson, 2002).

In the second approach, forward step-wise model selection was used to assign fixed effects. Cox regression was fitted to a suite of candidate models that included a single explanatory variable (FL, Sex, Inj, DUR, LT, TDR, RT, Q, or Year). The model that minimised AIC was selected to generate the candidate model set for the second step. In the second step, the suite of candidate models included the variable identified from step one in combination with each of the other variables. The process was repeated until the number of covariates in the model either reached four (again, because the number of fallback events was low, resulting in few degrees of freedom) or no further substantial reduction in AIC was observed. As in the group-wise approach, variables that were highly correlated ($R \geq 0.5$ or ≤ -0.5) were not allowed to co-occur in a model. No interactions were included in the candidate model set due to the low number of fallback events and associated degrees of freedom.

For both the group-wise and the forward stepwise approach, coefficients and their standard errors were extracted from the selected model and hazard ratios were computed by taking the exponent of the model coefficients. A critical assumption of the Cox proportional hazards model is that effects of the covariates on the hazard are proportional, i.e. the effect of explanatory covariates is constant over time. This assumption was assessed by visually examining plots of the Schoenfeld residuals (Allison, 2014) extracted from the selected model(s). The baseline hazard was also extracted and was used to plot survival curves adjusted for covariate values.

3.5 Results

3.5.1 Fish trapping, transport, and tagging

This study included the year with the lowest number of adults to return to the Rivière Nord-Est on record: only 185 salmon returned in 2014 (escapement = 172). Run size was 418 (escapement = 357) during 2015 and 352 during 2016 (escapement = 293; Ministère des forêts, de la Faune et des Parcs, 2018). The number of salmon that entered the fish ladder was 148 in 2014, 92 in 2015, and 217 in 2016. Fork length data were available for all salmon that entered the fish ladder during 2015 and 2016: mean FL was 71 cm (min–max: 50–107 cm). The first salmon entered the fish ladder on 24 June 2014, 30 June 2015, and 23 June 2016.

The transport target each year was 30 adults: 15 males and 15 females. During 2014, permitting restrictions prevented transport before 75 salmon had ascended the fish ladder. Thus, the first salmon was not transported until 22 July. After this date, few fish entered the fish ladder when river temperature was cool enough (< 20°C) for transport. Although the fish ladder remained open until mid-September, the last individuals entered the ladder on 5 September 2014, and a total of 12 salmon (3F, 9M) were transported and tagged. Twenty-five salmon (12F, 13M) were transported and tagged during 2015 and 33 salmon (15F, 16M) were transported and tagged during 2016. In total, 68 salmon were released with acoustic transmitters in the novel habitat from 2014 to 2016 and were included in the analysis of fallback (Annex 2).

Forty-three transports were required to transport the 68 salmon included in the analysis. The majority of transports (26 of 43) consisted of one fish (Figure 3.2D). Mean transport time was 53.6 min (SD = 8.3 min), mean water temperature in the fish ladder at departure was 17.6°C (SD = 1.3°C), and the temperature at the ladder was on average 0.2°C cooler than at the release site (TDD, Table 3.1). Air temperature ranged from 9°C to 24°C (mean = 17 °C) during the 35 transports for which it was recorded (Appendix 3). Tank water temperature at departure from the fish ladder was on average 0.6°C warmer than both the temperature at the fish ladder at departure (SD = 0.4) and the river temperature at the release site (SD = 0.6). Mean % O_2 exceeded 100% at both departure from the fish ladder (SD = 21.0) and arrival at the release site (SD = 16.0).

More males (*n* = 38) were transported than females (*n* = 30). Females were larger (mean FL = 79.8 cm, SD = 7.7 cm) than MSW males (mean FL = 70.2 cm, SD = 11.2), however the difference was not statistically significant (ordinary least squares Regression, *t* = -0.8; *p* = 0.4). One-sea-winter males had a mean FL of 56 cm (SD = 1.6 cm). Fork lengths of transported salmon represented nearly the full range of FLs observed in the fish ladder during 2015 and 2016. Mass was not recorded in 2014, however, during 2015 and 2016, females had a mean mass of 4.7 kg (SD = 1.9), MSW males had a mean mass of 3.2 kg (SD = 1.3), and 1SW males had a mean mass of 1.5 kg (SD = 0.3).

3.5.2 Incidence and Rate of Fallback

Twenty-nine of the 68 transported salmon exhibited fallback (32%). Complete fallback (*n* = 17) was more common than partial fallback (*n* = 12, Table 3.2). Owing to lack of river access in Sector 3, it was impossible to confirm whether salmon that exhibited partial fallback died as a result of the decent of Chute du 18 Miles, or whether they spawned in Sector 3. During 2016, however, one male (M37364) that moved into Sector 3 after 4.11 days in Sector 4 was ultimately detected in Sector 2 near the end of the spawning period. Three females and one other male were also present in Sector 3 and it is hypothesised that at least some of the salmon that exhibited partial fallback spawned in Sector 3.

The breakpoints that most minimised AIC in the moving-point Cox regression occurred at 3 (AIC = 216.2) and 7 (AIC = 220.4) days post-transport, which corresponded well with decreases in the proportion of salmon exhibiting fallback as observed in the Kaplan-Meier curve (Figure 3.3). Transport and handling effects appeared most likely to influence fallback in the first week after release and seven days was set as the threshold for assessing the effects of explanatory variables on post-transport fallback rate using time-to-event analysis. In total, 19 salmon exhibited fallback within this seven-day post-transport fallback window. Among the individuals that exhibited post-transport fallback, partial fallback (n = 11) was more common than complete fallback (n = 8). Three additional salmon exhibited fallback (2 complete, 1 partial) during the summer pre-spawning period, which removed them from the Sector 4 spawning population. These three salmon (pre-spawn fallback, Table 3.2) were not included in the time-to-event analysis because fallback occurred more than seven days after transport.

A second wave of fallback, which began approximately 90 days post-transport, was evident from the Kaplan-Meier curve (Figure 3.3). When translated to day of year, this second wave of fallback occurred after the observed onset of redd building in mid-October and likely represented natural downstream migration after spawning, thus was termed post-spawn fallback (Table 3.2). The seven salmon that exhibited post-spawn fallback (10%; 7 of 68) remained in Sector 4 between 72 and 106 days post-transport (mean = 91 days; Table 3.2). The risk that snow and ice would prevent access to the river forced the recovery of receivers on 22 October 2014, 20 October 2015, and 31 October 2016, before the end of the spawning season. More incidences of post-spawn fallback may have been observed had receivers been recovered later in the season.

Forty percent of females (12 of 30) and 18% of males (7 of 38) exhibited fallback within 7 days post-transport (Figure 3.2A). The majority of transported salmon (52 of 68) swam out of the release cage, either on their own or when hand release was attempted (Figure 3.2C). Twenty-three percent of the individuals that self-released exhibited post-transport fallback (12 of 52). Forty-four percent of the salmon that were hand-released exhibited fallback (7 of 16). Of the salmon that were held overnight, 40% (4 of 10) exhibited post-spawn fallback, and 20% exhibited tag loss/mortality (2 of 10).

The majority of salmon that exhibited post-transport fallback initially moved downstream after release in 17 of 19 cases (89%), whereas 2 individuals made an initial upstream movement. Of the 46 salmon remained upstream until spawning, 32 made an initial upstream movement (70%) and 14 (30%) made an initial downstream movement. The frequency of fallback was dependent on the direction of the initial movement post-release (Yates-corrected $X^2_{(1,\, n = 68)}$, $p < 0.01$).

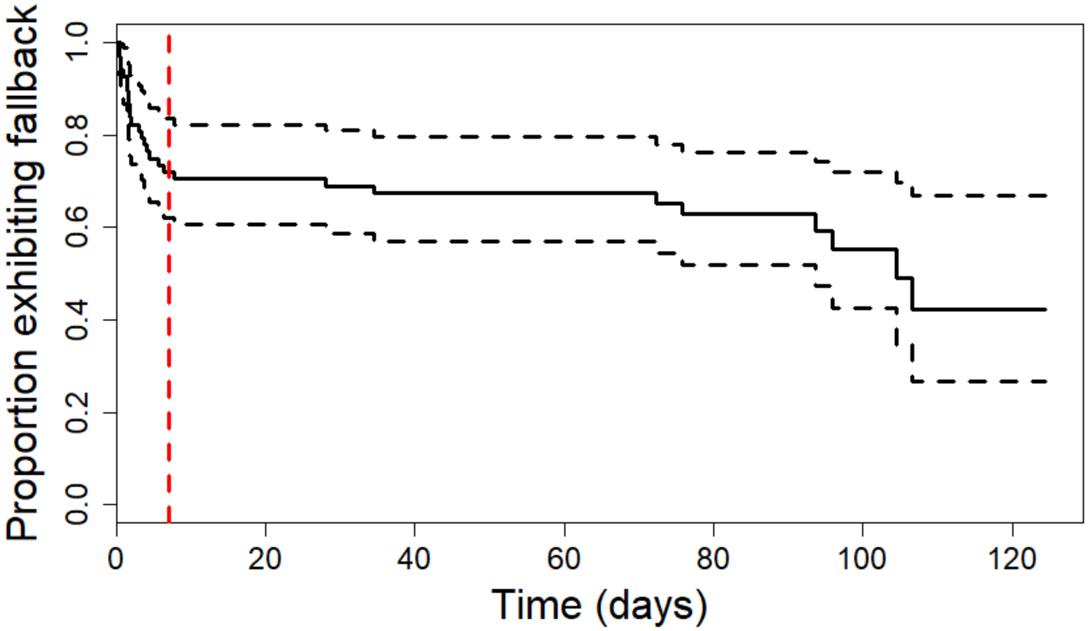


Figure 3.3 : Survival curve generated using Kaplan-Meier estimation

Survival curve indicating the proportion of salmon exhibiting fallback over the course of the study (solid black line) with 95% confidence intervals (dashed black lines). The red vertical dashed line indicates the break-point of 7 days, used for assessing the effects of explanatory variables on fallback rate.

Table 3.2 Duration of the pre-fallback interval by fallback type and year

	Year				Pre-fallback Interval (d)	
Fallback type	2014	2015	2016	Total	Mean	SD
Complete						
Post-Transport	1	2	5	8	1.8	1.4
Pre-Spawn	0	2	0	2	31.2	4.50
Post-spawn	0	1	6	7	91.4	14.40
Partial						
Post-Transport	3	3	5*	11	2.8	1.90
Pre-Spawn	1	0	0	1	7.68	0

Mean duration (and SD) of the pre-fallback interval by fallback type and year. The pre-fallback interval (in days) was measured from time of release to the last recorded detection in Sector 4. *Includes one male that arrived in Sector 4 on 28 October after 92.6 days in Sector 3.

The two approaches used to assign fixed effects to candidate model sets produced the same result: the model that minimised AIC in each case included only FL as a predictor of fallback (ΔAIC > 2 relative to closest competing model; Table 3.3 and 3.4). According to the Burnham and Anderson (2002) "rule of thumb", it would not generally be concluded that the FL only model is better than the FL+Sex or FL+Injury models because the ΔAIC between these models was less than two. The evidence ratios (w_i/w_j), however, indicate that the FL model received nearly two times more support than the FL+Sex model and nearly three times more support than the FL+Injury model. Using the forward stepwise selection method, the FL-only model received three times more support in the first round of model selection than the second best model (sex only). When combined, the results of the group-wise and forward-stepwise approaches indicate that the FL-only model was the most parsimonious model in describing the fallback rate of transported salmon.

As assessed by examining a plot of the Schoenfeld residuals, the FL-only model did not violate the proportional hazards assumption, indicating that the effect of FL did not vary with time. Fork length had a significant, positive effect on post-transport fallback: larger fish exhibited a greater rate of fallback ($\beta \pm$SE = 0.0052±0.002; $p = 0.018$). An increase of 1 mm FL produced a 0.5% increase in the hazard of exhibiting fallback (HR = 1.005). This means that the largest salmon included in the study (975 mm FL) had a predicted fallback rate that was 10.6 times faster than the smallest salmon (520 mm FL). Further, a MSW salmon of mean size (792 mm FL) had a predicted fallback rate that was 3.2 × faster than a 1SW salmon (mean size = 568 mm FL). Estimates from the selected Cox model also predicted that by seven days post-transport, nearly 30% of salmon of median size (50th percentile = 750 mm FL) and just over 10% of salmon in the 25th percentile for size (580 mm FL) would exhibit fallback (Figure 3.4). There was an ≈ 5% estimated increase in the proportion of large individuals (75th percentile for size = 780 mm FL) exhibiting fallback by seven days post-transport relative to median-sized (750 mm FL) salmon, with the divergence in the fallback rates occurring approximately two days post-transport (Figure 3.4).

Table 3.3 : Groupwise model selection

Model	Log Liklihood	AIC	ΔAIC	w_i	w_i/w_j
FL	-74.28	150.57	NA	**0.20**	**NA**
FL+Sex	-73.95	151.90	1.33	0.10	1.95
FL+Inj	-74.27	152.53	1.97	0.07	2.67
FL+Year	-73.38	152.77	2.20	0.07	3.01
Sex	-75.40	152.79	2.23	0.07	3.04
DUR	-75.43	152.87	2.30	0.06	3.16
TDR+DUR	-74.82	153.64	3.07	0.04	4.64
FL+Inj+Sex	-73.91	153.82	3.25	0.04	5.08
FL+Sex+Year	-72.94	153.88	3.32	0.04	5.25
Inj+Sex	-75.15	154.29	3.73	0.03	6.45

The top 10 (of 51) models with the lowest AIC scores are presented with estimated log likelihood, ΔAIC (the difference between the model and the "best" model) AIC weights (w_i), and the evidence ratio (w_i/w_j) for the model relative to the best model. Explanatory variables were FL= fork length (mm); Sex = male or female; Inj = ranked injury score from 0 to 5; DUR = transport duration (min); LT = temperature at the fish ladder at departure (°C); TDR = difference between LT and the river temperature at release site, RT = river temperature measured in Sector 3 (°C); and Q = river discharge (m^3s^{-1}); LT, RT, and Q did not make it into the set of ten "best" models.

Table 3.4 : Forward stepwise model selection

Step	Model	Log Liklihood	AIC	ΔAIC	w_i	w_i/w_j
1	**FL**	**-74.28**	**150.57**	**NA**	**0.48**	**NA**
	Sex	-75.40	152.79	2.23	0.16	3.04
	DUR	-75.43	152.87	2.30	0.15	3.16
	RT	-76.63	155.26	4.69	0.05	10.43
	Inj	-76.73	155.45	4.89	0.04	11.51
	TDR	-77.04	156.08	5.52	0.03	15.78
	NO	-77.29	156.59	6.02	0.02	20.29
	LT	-77.36	156.73	6.16	0.02	21.77
	Q	-77.37	156.74	6.17	0.02	21.90
	Year	-76.71	157.41	6.85	0.02	30.68
2	FL+RT	-73.20	150.40	NA	0.18	NA
	FL	-74.28	150.57	0.16	0.16	1.08
	FL+DUR	-73.41	150.81	0.41	0.14	1.22
	FL+TDR	-73.48	150.97	0.57	0.13	1.32
	FL+Sex	-73.95	151.90	1.50	0.08	2.11
	FL+LT	-74.11	152.22	1.81	0.07	2.47
	FL+Q	-74.24	152.49	2.08	0.06	2.83
	FL+Inj	-74.27	152.53	2.13	0.06	2.89
	FL+NO	-74.28	152.55	2.15	0.06	2.92
	FL+Year	-73.38	152.77	2.36	0.05	3.25
	FL+RT+DUR	-71.89	149.77	NA	0.21	NA
3	FL+RT	-73.20	150.40	0.63	0.16	1.34
	FL	-74.28	150.57	0.79	0.14	1.46
	FL+RT+TDR	-72.38	150.75	0.98	0.13	1.60
	FL+RT+Sex	-72.97	151.94	2.17	0.07	2.90
	FL+RT+LT	-73.08	152.17	2.39	0.06	3.24
	FL+RT+NO	-73.20	152.40	2.62	0.06	3.64
	FL+RT+Q	-73.20	152.40	2.63	0.06	3.65
	FL+RT+Inj	-73.20	152.40	2.63	0.06	3.65
	FL+RT+Year	-72.48	152.95	3.18	0.04	4.81
	FL+RT+DUR+TDR	-70.63	149.28	NA	0.23	NA
	FL+RT+DUR	-71.89	149.79	0.51	0.18	1.27
4	FL+RT	-73.20	150.41	1.13	0.13	1.74
	FL	-74.28	150.57	1.29	0.12	1.88
	FL+RT+DUR+LT	-71.65	151.31	2.03	0.08	2.72
	FL+RT+DUR+Sex	-71.71	151.42	2.14	0.08	2.88
	FL+RT+DUR+Q	-71.83	151.67	2.39	0.07	3.26

FL+RT+DUR+NO	-71.88	151.77	2.50	0.07	3.44
FL+RT+DUR+Year	-71.67	153.35	4.07	0.03	7.55

Explanatory variables were FL= fork length (mm); Sex = male or female; Inj = ranked injury score from 0 to 5; DUR = transport duration (min); LT = temperature at the fish ladder at departure (°C); TDD = difference between LT and the river temperature at release site; RT = river temperature measured in Sector 3 (°C); Q = river discharge (m^3s^{-1}).

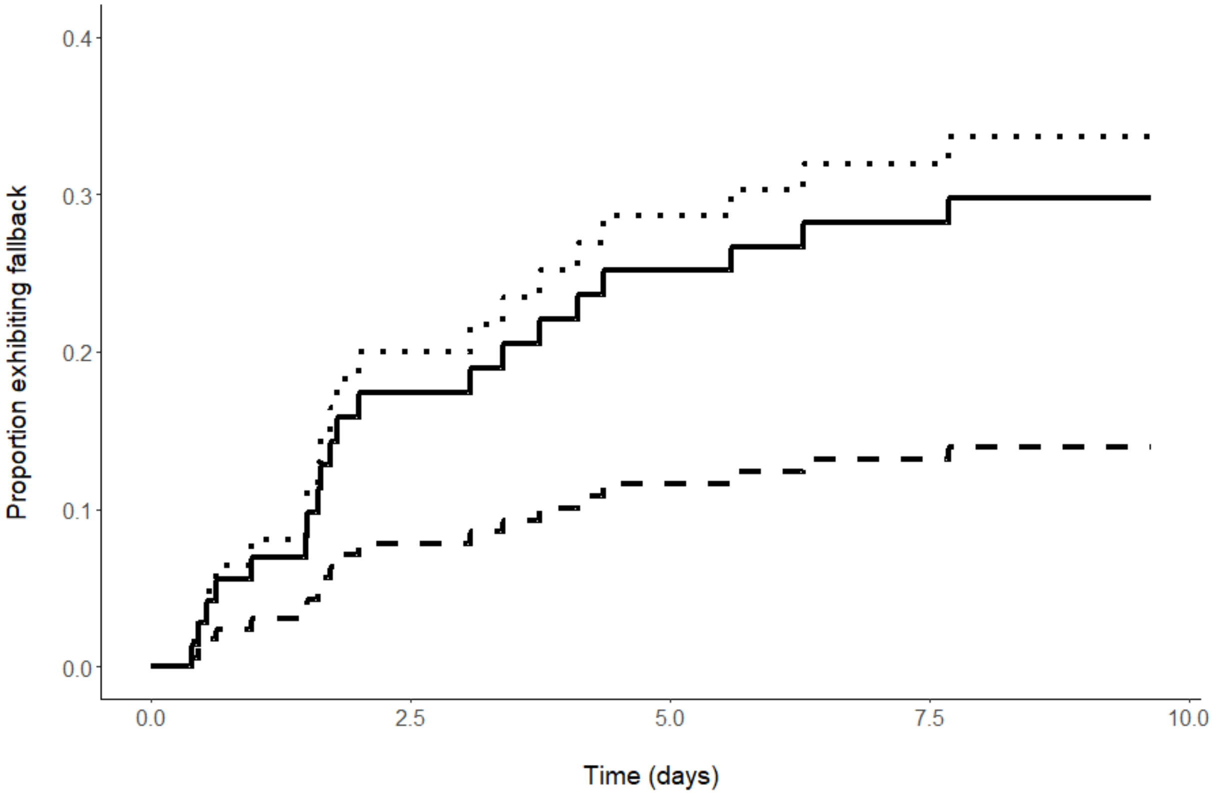


Figure 3.4 : Estimation of fallback by day and FL

Proportion of salmon exhibiting fallback (y-axis) as a function of time (x-axis) and fork length, generated from the estimated Cox regression mixed model. Fallback rate increases with size. Dashed line: 580 mm FL (25th percentile); solid line: 710 mm FL (50th percentile); dotted line: 780 mm FL (75th percentile).

3.6 Discussion

The present study represents one of the first attempts to assess factors affecting fallback by adult Atlantic salmon over natural barriers. Two primary forms of fallback were identified. Post-transport fallback occurred within one week of transport and is thought to be associated with transport and handling stress. Post-spawn fallback occurred during the spawning season and is thought to represent natural downstream movement of salmon to over-wintering areas. Fish length was the sole factor that emerged as positively influencing post-transport fallback. Specifically, larger (MSW) salmon were at greater risk for exhibiting fallback and had a much faster rate of fallback than smaller (1SW) individuals. Neither conditions experienced during transport nor environmental conditions experienced in-river after transport appeared to significantly affect fallback rate, and there was no apparent variability in fallback rate among years. The direction a fish initially moved following release into novel habitat, though not included in the time-to-event analysis, may be a good indicator of whether an individual exhibits fallback, as the majority of salmon that fell back initially moved in the downstream direction after release, whereas 70% salmon that remained in the novel habitat initially moved upstream after release.

There are few studies with which to compare post-transport fallback rates for Atlantic salmon; those that exist are confined to regulated rivers. In the Penobscot River (Maine), 11 of 25 (44%) of Atlantic salmon captured and transported upstream of the Veazie (hydro-electric) Dam fell back after release (Holbrook et al., 2009). Fallback rates for salmon transported upstream of impassable hydro-electric dams in the River Klarälven (Sweden), were 50% (out of 28) for hatchery-reared Atlantic salmon and 11.8% (out of 34) for wild salmon (Hagelin et al., 2015). In the same river, Atlantic salmon transported in June and July had a greater fallback rate (42.8% in 2012 and 51.7% in 2013) than those transported in August and September (15.1% in 2012 and 3.4% in 2013) and fallback occurred an average of 9 (2012) and 16 (2013) days following transport (Hagelin et al., 2016). Run-timing was not included as a covariate in the present study because it was not possible to classify individuals as early or late migrants with any certainty: in the Rivière Nord-Est, the wild-reared salmon transported at any given time included individuals that were both new arrivals to the river and those that had remained below the fish ladder for an unknown period of time before entering the ladder. Although fallback rate was greater than that observed for wild Atlantic salmon in the River Klarälven, it was less than the rates observed for hatchery-reared salmon and salmon transported earlier in the season (Hagelin et al., 2015, 2016) and less than the rate observed by Holbrook et al. (2009) in the Penobscot River.

The consequences of size-biased fallback on the assisted migration programme in the Rivière Nord-Est are difficult to predict, and will likely be linked to the sex of the individuals that fell back because fecundity is related to fish size in females but not in males (Jonsson & Jonsson, 2011). Larger females produce proportionally fewer but larger eggs than smaller females, which may confer a survival advantage to offspring, because larger eggs result in larger offspring (Fleming, 1996). In the absence of larger, dominant males, smaller (normally subordinate) males may have more mating opportunities and greater individual reproductive success (Fleming, 1996). Although sex was not retained in the selected model, proportionally more females exhibited post-transport fallback than males. Consequently, loss of larger females from the novel habitat could result in the production of more juveniles by the smaller females that remained upstream, but that are smaller and have lower survival rates.

Transport and handling produce a stress response in fish (Portz, Woodley & Cech, 2006). If transport and handing produce a greater stress response in larger individuals and fallback is indicative of handling stress, then larger individuals should be expected to exhibit greater fallback rates. In an impounded river in Sweden, however, Hagelin et al. (2016) found no apparent effect of fish length on the probability that adult Atlantic salmon exhibited fallback following transport upstream of impassable hydro-electric dams. In a study assessing the effects of catch and release on migratory behaviour in Atlantic salmon, Havn et al. (2015) reported that total length was the only variable that influenced whether or not salmon moved in a downstream direction after release. Contrary to the results of the present study, Havn et al. (2015) found that the smallest salmon (50 cm TL, or ≈ 49 cm FL) had a probability of downstream movement that was two times greater than the largest salmon (90 cm TL, or ≈ 88 cm FL). Further, the magnitude of physiologic stress exhibited by angled Atlantic salmon in the River Alta (Norway) was not greatly affected by fish size (Thorstad, Næsje, Fiske & Finstad, 2003). Consequently, the size-biased fallback observed in the Rivière Nord-Est likely does not result solely from handling stress.

The greater fallback rates exhibited by larger individuals could be explained by an increased propensity for these individuals to return to natal spawning sites. There is evidence that adult Atlantic salmon return not only to natal rivers, but to natal river reaches (Heggberget, Lund, Ryman & Sdhl, 1986), a trait that has been observed in the Sainte-Marguerite catchment (Dionne, Caron, Dodson & Bernatchez, 2009; Garant, Dodson & Bernatchez, 2000; Landry & Bernatchez, 2001). Homing to natal reaches enables individuals to spawn where they themselves were successful during early development, which may increase the chance that their offspring will survive (Hasler, Scholz & Horrall, 1978). Further, hatchery-reared, repeat spawners returned to rivers they were acclimated to as smolts, rather than the river of genetic origin (Hansen & Jonsson, 1994). In the Rivière Nord-Est, larger salmon are individuals that have either spent more years at sea or are repeat spawners (i.e., individuals that have already made at least one previous spawning migration). Salmon that have spent more time at sea before making a maiden spawning migration will have invested more into reproduction, in terms of attaining increased body size at the risk of at-sea mortality, than individuals that spent less time at sea and returned to spawn at smaller sizes. Large virgin spawners and repeat spawners, therefore, might have a greater drive than smaller, virgin spawners to leave the novel habitat and return to natal reaches located in river sectors 1 and 2.

Salmon transport on the Rivière Nord-Est occurred from late June to early September, thus individuals were exposed to a wide range of river discharge and temperature conditions; however, no predictive links between environmental variables and fallback were observed. Hagelin et al. (2016) found that mean daily discharge influenced the probability of fallback by adult Atlantic salmon over impassable hydro-electric dams in a Swedish river. The fish ladder on the Rivière Nord-Est has low attraction efficiency at high river discharge and low temperature (Frechette, St-Hilaire & Bergeron, 2019). To reduce thermal stress on fish, salmon were not transported when river temperature exceeded 20°C because it is thought to induce stress in adult Atlantic salmon (Breau, 2013; Brett, 1956; Portz, Woodley & Cech 2006). Because salmon rarely entered the fish ladder at high river discharge (> 20 m^3/s) when water was cool enough to permit transport, salmon were only transported when river discharge was relatively low, which may explain the lack of association between river discharge and fallback rate.

In the Penobscot River (Maine, USA), nearly 100% of Atlantic salmon that fell back after transport and release into a reservoir upstream of a dam equipped with fish passage occurred when river temperature exceeded 22°C, which may have been driven by salmon attempting to reach cool thermal refuges located downstream of the dam (Holbrook et al., 2009). Cool refuge use is a behavioural adaptation that allows salmon to mitigate the deleterious effects of high temperature (Shepard, 1995; Torgersen, Price, Li & McIntosh, 1999). Although in some cases, river temperature approached 22°C within hours to days of release, salmon had ready access to thermal refuges in the novel habitat (Sector 4). In fact, a thermal refuge was identified in the pool < 100 m downstream of the release site (Frechette, Dugdale, Dodson & Bergeron, 2018), which may explain the lack of a relationship between river temperature and fallback rate.

Conditions during fish transport and holding are well known to affect the magnitude of the physiologic stress response (reviewed by Portz, Woodley & Cech, 2006). Conditions experienced by salmon during transport were purposely held to very narrow ranges, therefore, it is not surprising that they were not retained in the selected Cox model. Salmon were exposed to only minor changes in temperature (< 0.6°C) and no salmon were transported when water temperature in the fish ladder > 20.5°C. Stress due to overcrowding (Portz, Woodley & Cech, 2006) in the tank was not considered to be an issue, as reflected by failure to retain the variable “number of fish” in the selected Cox model, likely because the number of fish transported was much less than the ten large salmon that tank was designed to transport.

In telemetry studies, fish are held for a period of time (sometimes up to 24-h) for recovery after tagging. Confinement of fish for even short periods, however, can induce a stress response (Portz, Woodley & Cech, 2006). For example, sockeye salmon *Oncorhynchus nerka* that were held in a net pen for 24 hours after capture exhibited greater physiological stress disturbance and had dramatically reduced survival relative to individuals that were released immediately after capture (Donaldson et al., 2011). Physiological disturbance due to holding was thought to be compounded by the second capture (via dip-netting) of sockeye held in the net pen for sampling and release (Donaldson et al., 2011). Holding salmon overnight in the retention cage or hand releasing salmon after surgery, therefore, could result in physiological stress that might influence the propensity for fallback. Although it was not possible to test for the effect of holding salmon overnight due to low sample size, 4 of 10 salmon held overnight fellback and two others were among the four individuals that either lost their tags or died. Further, two additional salmon escaped from the retention cage by jumping over the barrier into the main fish ladder. It appears, therefore, that overnight holding induced a stress response but more data is necessary before recommendations can be made to managers.

The conclusions presented in the present study are limited by sample size. The number of fish that exhibited post-transport fallback was relatively low (20 individuals), which limited available degrees of freedom and prevented us from including more than four covariates in a given candidate model. Further, small sample size for some of the variables of interest (e.g. holding overnight, release type, oxygen saturation), prevented their inclusion in the candidate model set. Fish length, however, appears to be a strong driver of fallback after transport, suggesting that transport of large (> 780 mm) MSW individuals will result in the greatest rates of fallback. Simply preventing transport of larger individuals (that may be more prone to fallback) will likely have unintended consequences for the total productivity in habitat selected for colonisation because: 1) not all large salmon exhibited fallback; and 2) reproductive success is related to size in salmon (Fleming 1996). When selecting individuals for transport, therefore, both the differential reproductive capacity of large versus small salmon and the risk of size-biased fallback should be taken into account. Given that the selected Cox model predicted that 30% of median-sized salmon (50th percentile for size: FL = 750 mm) would exhibit fallback within seven days of transport, it may be necessary to increase the number of individuals transported by 30% in order to meet the programme target for colonisation of the novel habitat on the Rivière Nord-Est. These findings may be useful for setting initial transport targets when implementing similar programmes in other free-flowing systems.

3.7 Acknowledgements

This work was supported by the Programme de mise en valeur des habitats du saumon de la Côte-Nord of the Fédération Québécoise du Saumon Atlantique, and the Atlantic Salmon Conservation Foundation. Financial support for D. Frechette was provided by the Fonds de recherche du Québec - Nature et technologies (FRQNT) Merit Scholarship Program for Foreign Students. We would like to thank the Ministere de la Faune, des Fôrets, et des Parcs du Québec, the Association de la Rivière Sainte-Marguerite, and the Corporation de Pêche Ste-Marguerite for their collaboration and support of this research. We also thank T. Castro-Santos for his invaluable statistics advice. The Ocean Tracking Network provided data hosting and archiving. Finally, it took an army to get this program up and running, deploy and recover acoustic receivers, and to transport the salmon over the course of our study. In particular, we wish to thank I. Bergeron, A. Boivin, F. Caron, J. Carrier, V. Cauchon, M. Dionne, R. Gagnon, S. Gravel, J. Isabelle, M. Murdock, V. Maltais, M. St-Amour, J.B. Toteroto, T. Suskiewicz, and M. Valentine.

4 BIBLIOGRAPHIE – CHAPITRE 3

Akaike, H. (1974). A new look at the statistical model identification. *IEEE Transactions on Automatic Control,* 19, 716–723. doi:10.1109/TAC.1974.1100705

Allison, P. D. (2014). *Event history and survival analysis* (2nd ed.). Thousand Oaks, CA: SAGE.

Anderson, J. H., Pess, G. R., Carmichael, R. W., Ford, M. J., Cooney, T. D., Baldwin, C. M., & McClure, M. M. (2014). Planning Pacific salmon and steelhead reintroductions aimed at long-term viability and recovery. *North American Journal of Fisheries Management, 34,* 72–93.

Boyer, C., St-Hilaire, A., Bergeron, N. E., Daigle, A., Curry, R. A., & Caissie, D. (2016). RivTemp: A water temperature network for Atlantic salmon rivers in eastern Canada. *Water News, 35,* 10–15.

Breau, C. (2013). Knowledge of fish physiology used to set water temperature thresholds for in-season closures of Atlantic salmon (*Salmo salar*) recreational fisheries. Canadian Science Advisory Secretariat, Research Document 2012/163, Department of Fisheries and Oceans, Moncton, N.B.

Brett, J. R. (1956). Some principles in the thermal requirements of fishes. *The Quarterly Review of Biology, 31*, 75–87.

Brisson Bonenfant, C. (2006). *Stratégie conditionelle et migration chez le saumon atlantique* (*Salmo salar*) *juvénile*. M.Sc. thesis, Université Laval, Quebec, QC.

Burnham, K. P., & Anderson, D. R. (2002). Model selection and multimodal inference: A practical information-theoretic approach (2nd ed.). New York, NY: Springer-Verlag.

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

DFO (1998). Atlantic Salmon Eastern Canada Overview 1997. Ottawa, Ontario.

DFO (2015). Special Report on Atlantic Salmon. Prepared by the Minister's Advisory Committee on Atlantic Salmon. Department of Fisheries and Oceans Canada. July 2015. 65 p.

Dionne, M., Caron, F., Dodson, J. J., & Bernatchez, L. (2009). Comparative survey of within-river genetic structure in Atlantic salmon; relevance for management and conservation. *Conservation Genetics, 10,* 869–879. doi:10.1007/s10592-008-9647-5

Donaldson, M. R., Hinch, S. G., Patterson, D. A., Hills, J., Thomas, J. O., Cooke, S. J., Raby, G. D., Thompson, L. A., Robichaud, D., English, K. K., & Farrell, A. P. (2011). The consequences of angling, beach seining, and confinement on the physiology, post-release behaviour and survival of adult sockeye salmon during upriver migration. *Fisheries Research, 108,* 133–141. doi:10.1016/j.fishres.2010.12.011

Ebel, W. J. (1980). Transportation of Chinook salmon, *Oncorhynchus tshawytscha*, and steelhead, *Salmo gairdneri*, smolts in the Columbia River and effects on adult returns. *Fishery Bulletin*, *78*, 491–505.

Finstad, A. G., Økland, F., Thorstad, E. B., & Heggberget, T. C. (2005). Comparing upriver spawning migration of Atlantic salmon *Salmo salar* and sea trout *Salmo trutta*. *Journal of Fish Biology, 67,* 919–930. doi:10.1111/j.1095-8649.2005.00792.x

Fleming, I. A. (1996). Reproductive strategies of Atlantic salmon: ecology and evolution. *Reviews in Fish Biology and Fisheries, 6,* 379–416.

Frank, H. J., Mather, M. E., Smith, J. M., Muth, R. M., Finn, J. T., & McCormick, S. D. (2009). What is "fallback"?: Metrics needed to assess telemetry tag effects on anadromous fish behaviour. *Hydrobiologia, 635,* 237–249. doi:10.1007/s10750-009-9917-3

Frechette, D. M., Dugdale, S. J., Dodson, J. J., & Bergeron, N. E. (2018). Understanding summertime thermal refuge use by adult Atlantic salmon using remote sensing, river temperature monitoring, and acoustic telemetry. *Canadian Journal of Fisheries and Aquatic Sciences, 75,* 1999–2010. doi:10.1139/cjfas-2017-0422

Frechette, D, St-Hilaire, A et Bergeron, NE (2019). Statistical analysis of fish ladder attractivity on the Nord-Est Sainte-Marguerite River. Research Report R1834. Institut national de la recherche scientifique, Quebec, QC.

Garant, D., Dodson, J. J., & Bernatchez, L. (2000). Ecological determinants and temporal stability of the within-river population structure in Atlantic salmon (*Salmo salar* L.). *Molecular Ecology, 9,* 615–628.

Goerig, E., & Castro-Santos, T. (2017). Is motivation important to brook trout passage through culverts? *Canadian Journal of Fisheries and Aquatic Sciences, 74,* 885–893. doi:10.1139/cjfas-2016-0237

Hagelin, A., Calles, O., Greenberg, L., Piccolo, J., & Bergman, E. (2015). Spawning migration of wild and supplementary stocked landlocked Atlantic salmon (*Salmo salar). River Research and Applications, 32,* 383–389. doi:10.1002/rra.2870

Hagelin, A., Calles, O., Greenberg, L., Nyqvist, D., & Bergman, E. (2016). The migratory behaviour and fallback rate of landlocked Atlantic salmon (*Salmo salar*) in a regulated river: Does timing matter? *River Research and Applications, 32,* 1402–1409. doi:10.1002/rra.3007

Hansen, L. P., & Jonsson, B. (1994). Homing of Atlantic salmon: Effects of juvenile learning on transplanted post-spawners. *Animal Behaviour, 47,* 220–222. doi:10.1006/anbe.1994.1027

Hasler, A. D., Scholz, A. T., & Horrall, R. M. (1978). Olfactory imprinting and homing in salmon: Recent experiments in which salmon have been artificially imprinted to a synthetic chemical verify the olfactory hypothesis for salmon homing. *American Scientist, 66*, 347–355.

Havn, T. B., Uglem, I., Solem, O., Cooke, S. J., Whoriskey, F. G., & Thorstad, E. B. (2015). The effect of catch-and-release angling at high water temperatures on behaviour and survival of Atlantic salmon *Salmo salar* during spawning migration. *Journal of Fish Biology, 87,* 342–359. doi:10.1111/jfb.12722

Heggberget, T. C., Hansen, L. P., & Naesje, T. F. (1988). Within-river spawning migration of Atlantic salmon (*Salmo salar*). *Canadian Journal of Fisheries and Aquatic Sciences, 45,* 1691–1698.

Heggberget, T. C., Lund, R. A., Ryman, N., & Ståhl, G. (1986). Growth and genetic variation of Atlantic salmon (*Salmo salar*) from different sections of the River Alta, North Norway. *Canadian Journal of Fisheries and Aquatic Sciences, 43,* 1828–1835.

Hewitt, N., Klenk, N., Smith, A. L., Bazely, D. R., Yan, N., Wood, S., MacLellan, J. I., Lipsig-Mumme, C., & Henriques, I. (2011). Taking stock of the assisted migration debate. *Biological Conservation, 144,* 2560–2572. doi:10.1016/j.biocon.2011.04.031

Holbrook, C. M., Zydlewski, J., Gorsky, D., Shepard, S. L., & Kinnison, M. T. (2009). Movements of prespawn adult Atlantic salmon near hydroelectric dams in the lower Penobscot River, Maine. *North American Journal of Fisheries Management, 29,* 495–505. doi:10.1577/m08-042.1

Jokikokko, E. (2002). Migration of wild and reared Atlantic salmon (*Salmo salar* L.) in the river Simojoki, northern Finland. *Fisheries Research, 58,* 15–23.

Jonsson, B., & Jonsson, N. (2011). *Ecology of Atlantic salmon and brown trout: Habitat as a template for life histories* (D. L. G. Noakes ed., Vol. 33). New York, NY: Springer Netherlands.

Keefer, M. L., Peery, C. A., Bjornn, T. C., Jepson, M. A., & Stuehrenberg, L. C. (2004). Hydrosystem, dam, and reservoir passage rates of adult Chinook salmon and steelhead in the Columbia and Snake Rivers. *Transactions of the American Fisheries Society, 133,* 1413–1439. doi:10.1577/t03-223.1

Keefer, M. L., Peery, C. A., & Caudill, C. C. (2006). Long-distance downstream movements by homing adult chinook salmon. *Journal of Fish Biology, 68,* 944–950. doi:10.1111/j.1095-8649.2006.00958.x

Keefer, M. L., Taylor, G. A., Garletts, D. F., Gauthier, G. A., Pierce, T. M., & Caudill, C. C. (2010). Prespawn mortality in adult spring Chinook salmon outplanted above barrier dams. *Ecology of Freshwater Fish, 19*, 361–372. doi:10.1111/j.1600-0633.2010.00418.x

Kleinbaum, D. G., & Klein, M. (2005). *Survival analysis: A self-learning text* (2nd ed.). New York, NY: Springer.

Landry, C., & Bernatchez, L. (2001). Comparative analysis of population structure across environments and geographical scales at major histocompatibility complex and microsatellite loci in Atlantic salmon (*Salmo salar*). *Molecular Ecology, 10,* 2525–2539.

Lennox, R. J., Uglem, I., Cooke, S. J., Næsje, T. F., Whoriskey, F. G., Havn, T. B., Ulvan, E. M., Solem, Ø., & Thorstad, E. B. (2015). Does catch-and-release angling alter the behaviour and fate of adult Atlantic salmon during upriver migration? *Transactions of the American Fisheries Society, 144*, 400–409. doi:10.1080/00028487.2014.1001041

Mäkinen, T. S., Niemelä, E., Moenb, K., & Lindström, R. (2000). Behaviour of gill-net and rod-captured Atlantic salmon (*Salmo salar* L.) during upstream migration and following radio tagging. *Fisheries Research, 45*, 117–127.

Maisse, G., Baglinière, J. L., Landry, G., Caron, F., & Rouleau, A. (1988). Identification externe du sexe chez le Saumon atlantique (*Salmo salar* L.). *Canadian Journal of Zoology, 66,* 2312–2315.

Ministère des Forêts, de la Faune et des Parcs. (2016). Plan de gestion du saumon atlantique 2016–2026, ministère des Forêts, de la Faune et des Parcs, Direction générale de l'expertise sur la faune et ses habitats, Direction de la faune aquatique, Québec, 40 p.

Ministère des Forêts, de la Faune et des Parcs. (2018). Bilan de l'exploitation du saumon au Québec en 2017, ministère des Forêts, de la Faune et des Parcs, Secteur de la faune, 302 p.

Naughton, G. P., Caudill, C. C., Keefer, M. L., Bjornn, T. C., Peery, C. A., & Stuehrenberg, L. C. (2006). Fallback by adult sockeye salmon at Columbia River Dams. *North American Journal of Fisheries Management, 26,* 380–390. doi:10.1577/m05-015.1

Nyqvist, D., Nilsson, P.A., Alenäs, I. Elghagen, J. Hebrand, M., Karlsson, S., Kläppe, S., & Calles, O. (2017). Upstream and downstream passage of migrating adult Atlantic salmon: Remedial measures improve passage performance at a hydropower dam. *Ecological Engineering, 102,* 331–343. doi:10.1016/j.ecoleng.2017.02.055

Økland, F., Erkinaro, J., Moen, K., Niemelä, E., Fiske, P., McKinley, R. S., & Thorstad, E. B. (2001). Return migration of Atlantic salmon in the River Tana: Phases of migratory behaviour. *Journal of Fish Biology, 59,* 862–874. doi:10.1111/j.1095-8649.2001.tb00157.x

Pess, G. R., Kiffney, P. M., Liermann, M. C., Bennett, T. R., Anderson, J. H., & Quinn, T. P. (2011). The influences of body size, habitat quality, and competition on the movement and survival of juvenile coho salmon during the early stages of stream recolonization. *Transactions of the American Fisheries Society, 140,* 883–897. doi:10.1080/00028487.2011.587752

Portz, D. E., Woodley, C. M., & Cech, J. J. (2006). Stress-associated impacts of short-term holding on fishes. *Reviews in Fish Biology and Fisheries, 16,* 125–170. doi:10.1007/s11160-006-9012-z

Prévost, E., Vauclin, V., Baglinière, J. L., Brana-Vigil, F., & Nicieza, A. G. (1991). Application d'une méthode de détermination externe du sexe chez le Saumon atlantique (*Salmo salar* L.) dans les rivières des Asturies (Espagne). *Bulletin Français de la Pêche et de la Pisciculture, 323,* 149–159. doi:10.1051/kmae:1991002

R Core Team. (2017). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. Available from: www.R-project.org [accessed 15 June 2017]

R Studio Team. (2016). RStudio: Integrated development for R. RStudio, Inc., Boston, MA. Available from: www.rstudio.com [accessed 15 June 2017]

Shepard, S.L. (1995). *Atlantic salmon spawning migrations in the Penobscot River, Maine: Fishways, flows, and high temperatures*. M.Sc. thesis, University of Maine, Orono, ME.

Therneau T. M. (2015). A Package for Survival Analysis in S. version 2.38. URL: https://CRAN.R-project.org/package=survival

Therneau T. M., & Grambsch P. M. (2000). *Modeling survival data: Extending the Cox model.* New York, NY: Springer. ISBN 0-387-98784-3

Thomas, C. D. (2011). Translocation of species, climate change, and the end of trying to recreate past ecological communities. *Trends in Ecology & Evolution, 26,* 216–221. doi:10.1016/j.tree.2011.02.006

Thorstad, E. B., Næsje, T. F., Fiske, P., & Finstad, B. (2003). Effects of hook and release on Atlantic salmon in the River Alta, northern Norway. *Fisheries Research, 60,* 293–307.

Thorstad, E. B., Whoriskey, F., Rikardsen, A. H., & Aarestrup, K. (2011). Aquatic nomads: The life and migrations of the Atlantic salmon. In O. Aas, S. Einum, A. Klemesten, & J. Skurdal (Eds.), *Atlantic salmon ecology* (pp. 1–23). Chichester, UK: John Wiley & Sons Ltd.

Torgersen, C. E., Price, D. M., Li, H. W., & McIntosh, B. A. (1999). Multiscale thermal refugia and stream habitat associations of Chinook salmon in northeastern Oregon. *Ecological Applications, 9,* 301–319.

Winter, J. D. 1983. Underwater biotelemetry. In L. A. Nielsen and D. L. Johnson (Eds.), *Fisheries Techniques* (pp. 371–395). Bethesda, MD: American Fisheries Society

5 UNDERSTANDING SUMMERTIME THERMAL REFUGE USE BY ATLANTIC SALMON USING COMBINED METHODS

Title of Article: **Understanding summertime thermal refuge use by adult Atlantic salmon using remote sensing, river temperature monitoring, and acoustic telemetry**

Titre de l'article : **Évaluation de l'utilisation estivale des refuges thermiques par les saumons atlantiques adultes à l'aide de la télédétection, du suivi de la température en rivière et de la télémétrie acoustique**

Authors and affiliations:
[1]Danielle M. Frechette
[2]Stephen J. Dugdale (s.j.dugdale@bham.ac.uk)
[3]Julian J. Dodson (Julian.Dodson@bio.ulaval.ca)
[1]Normand E. Bergeron (Normand.Bergeron@ete.inrs.ca

1. Institut National de Recherche Scientifique, Centre Eau Terre Environnement, Québec, Canada
2. University of Birmingham, Birmingham, United Kingdom
3. Université Laval, Québec, Canada

This chapter was published by the Canadian Journal of Fisheries and Aquatic Sciences.
Received September 29, 2017. Accepted January 15, 2018.
Published on the web 26 March 2018.

Published in print October 2018. Volume 75. Pages 1999-2010. dx.doi.org/10.1139/cjfas-2017-0422

Contributions of authors:

D. Frechette conceived the idea for the thermal refuge study using acoustic telemetry and conducted the fieldwork, data analysis, and original writing. N. Bergeron and D. Frechette wrote a grant application to obtain funding for the fieldwork and thermal image analysis. S. Dugdale and N. Bergeron conceived the idea for the aerial thermal infrared imaging survey. S. Dugdale and D. Frechette analysed the thermal images, and S. Dugdale created Figure 3.1. N. Bergeron and J. Dodson provided guidance regarding the data analyses and outline of the manuscript. N. Bergeron, J. Dodson, and S. Dugdale, provided valuable comments on initial drafts of the manuscript, which greatly improved the final submission.

5.1 Résumé

Les saumons atlantiques (*Salmo salar*) adultes reviennent dans leurs rivières natales plusieurs mois avant le frai et, durant l'été, peuvent être exposés à des températures dépassant leur limite de tolérance thermique supérieure. Bien que les saumons utilisent fréquemment les refuges thermiques pour minimiser leur exposition aux températures élevées, peu d'information existe sur la thermorégulation comportementale des saumons atlantiques adultes. Nous avons examiné la thermorégulation comportementale de saumons atlantiques durant leur période de résidence estivale dans une rivière du Québec en utilisant une combinaison novatrice de télédétection infrarouge thermique, de mesure de la température de la rivière et de télémétrie acoustique. Les adultes font preuve de thermorégulation comportementale à des températures ambiantes plus faibles (17–19 °C) que celles observées antérieurement pour cette espèce et maintiennent leur température corporelle dans une fourchette restreinte (16–20 °C) en utilisant des refuges frais et chauds. Les adultes utilisent les fosses profondes thermiquement stratifiées comme refuges stables, ce qui permet à de multiples individus de réguler en même temps leur température sans quitter la fosse. Les faibles débits et les températures élevées peuvent constituer des barrières physiques à la migration des saumons, les empêchant d'accéder à des refuges convenables (p. ex. fosses). La reconnaissance des refuges thermiques et le maintien de leur connectivité pourraient être essentiels à la persistance des populations de saumons atlantiques dans un contexte de changements climatiques et de réchauffement des rivières.

5.2 Abstract

Adult Atlantic salmon (*Salmo salar*) return to natal rivers several months before spawning and during summer can be subjected to temperatures that exceed their upper temperature tolerance limits. Salmon use thermal refuges to minimize exposure to high temperatures, but little information exists regarding behavioral thermoregulation by adult Atlantic salmon. We examined behavioral thermoregulation by Atlantic salmon during summer in-river residence in a Quebec river with a novel combination of thermal infrared remote sensing, river temperature monitoring, and acoustic telemetry. Adults engaged in behavioural thermoregulation at cooler ambient river temperatures (17–19 °C) than previously recorded for this species and maintained body temperature within a narrow range (16–20 °C) via use of cool and warm refuges. Adults used large, stable, stratified pools as refuges, allowing multiple individuals to thermoregulate simultaneously without leaving the pool. Low river discharge and high temperatures can be physical barriers to salmon migration, preventing them from accessing suitable refuges (e.g., pools). Identifying and maintaining connectivity to thermal refuges may be critical for persistence of Atlantic salmon populations as climate changes and rivers warm.

5.3 Introduction

Salmonid species have narrow temperature tolerance ranges, making them highly susceptible to environmental warming resulting from climate change (Brett 1956; Pörtner and Farrell 2008; Jonsson and Jonsson 2009). Outside their range of optimal temperatures (where aerobic scope is greatest and growth and metabolism are maximized), capacity for aerobic activity decreases to the point where aerobic scope is zero and metabolism depends on anaerobic processes (Pörtner and Farrell 2008; Jonsson and Jonsson 2009). Above the incipient lethal temperature, fish become thermally stressed and long-term survival is not possible unless access to cooler water is available (Elliott and Elliott 2010). Although the upper incipient lethal temperature varies among species and populations of salmonids, it generally falls between 20° and 28°C (Goinea et al. 2006; Jonsson and Jonsson 2009; Elliott and Elliott 2010).

Salmonids cope with high temperatures using behavioural thermoregulation, whereby individuals actively seek out and use cold-water refuges, i.e. discrete patches of water that are cooler than the surrounding ambient river temperature (Kaya et al. 1977; Berman and Quinn 1991; Torgersen et al. 1999). Such cold water patches may be formed by cool tributaries and their associated confluence plumes, groundwater seeps, thermal stratification of deep pools or alcoves, or hyporheic exchange (Bilby 1984; Ebersole et al. 2003; Torgersen et al. 2012). Behavioural thermoregulation has been observed in multiple species of salmonids during all phases of the life cycle (Gibson 1966; Berman and Quinn 1991; Tanaka et al. 2000) and records of Atlantic salmon (*Salmo salar*) using cool water refuges during high temperature events were described as early as 1939 (Huntsman 1942).

Atlantic salmon return to natal rivers during summer, many months before the onset of spawning. While over-summering in rivers, Atlantic salmon can be subject to temperatures that approach or surpass the upper incipient lethal level. Although the optimal and critical temperatures are not explicitly known for adult Atlantic salmon, temperatures of 26° to 27°C have been associated with mortality of migrating adult Atlantic salmon and there is consensus in the literature that temperatures between 20° and 23°C are stressful (Shepard 1995; Wilke et al. 1997; Breau 2013). High summer temperatures, therefore, may reduce the number of adult salmon that survive to spawn during the autumn, with associated negative impacts on population productivity. Because salmon metabolism increases with water temperature, high temperatures also reduce the energy available for individuals to engage in costly reproductive efforts, e.g. gamete production, mate selection, male-male competition, and nest construction by females (Gilhausen 1980; Berman and Quinn 1991; Hasler et al. 2012). Such non-lethal effects of high temperature on reproductive capacity can negatively impact productivity, even in the absence of heat-induced mortality. In order to retain sufficient energy stores for spawning, therefore, some adult salmon require access to cool thermal refuges during their long, in-river pre-spawning residence (Berman and Quinn 1991; Newell and Quinn 2005; Hasler et al. 2012).

Given the importance of thermal refuges to persistence and management of salmon populations, it is surprising that to date, there has been little research directed at understanding the temperatures that trigger refuge use by adult Atlantic salmon or the specific refuge types used. Studies of thermal refuge use by juvenile Atlantic salmon (e.g. Cunjak et al. 2005; Breau et al. 2007; Dugdale et al. 2016) have been widely conducted, whereas records of refuge use by adult salmonids largely have been restricted to species of Pacific salmon (e.g. Goniea et al. 2006; Donaldson et al. 2009; Keefer et al. 2009).

Several tools are now available for monitoring river temperature and tracking fish movements in rivers across a range of temporal and spatial scales. Remote sensing of river temperature via aerial thermal infrared (TIR) imagery permits estimation of river temperature at a single time point over large spatial scales, whereas monitoring via temperature loggers can provide a long-term record of temperature at specific locations (Torgersen et al. 2001; Torgersen et al. 2012; Dugdale 2016). Temperature sensors built into very high frequency (VHF) and ultrasonic (acoustic) transmitters allow direct measurement of internal body temperature of tagged fish (Brewitt and Danner 2014; Gutowsky et al. 2017). We used a unique combination of TIR imagery, river temperature monitoring, and acoustic telemetry to 1) characterize the types of thermal refuges used by adult Atlantic salmon during the pre-spawning in-river residence and 2) identify the temperatures at which adults initiated thermal refuge use in a gravel bed river in Quebec, Canada. We expected that adult Atlantic salmon would engage in behavioural thermoregulation to remain within a narrow temperature range (Berman and Quinn 1991; Newell and Quinn 2005; Gotkowsky et al. 2017). Specifically, we expected that adults would use cool water patches when river temperatures reached the range thought to be stressful to adult Atlantic salmon (i.e. 20° to 23°C, Shepard 1995; Wilke et al. 1997; Breau 2013). We further expected that patterns in behavioural thermoregulation would follow the diurnal cycle of heating and cooling patterns, with adults using cool refuges during the warmest hours of the day (Ebersole et al. 2001).

5.4 Materials and methods

5.4.1 Study area

The Rivière Sainte-Marguerite Nord-Est (hereafter, Nord-Est) is a salmon river in Quebec, Canada, approximately 190 km northeast of the city of Quebec. The Nord-Est drains a catchment of ~1000 km^2, and joins the Rivière Sainte-Marguerite 5 km upstream from its confluence with the Saguenay River (Fig. 5.1). During summer, river temperature routinely exceeds 22°C and during some years (2005, 2007, 2012, 2014), river temperatures greater than 26°C were recorded in the lower seven kilometres of the river (Boyer et al. 2016).

A natural waterfall (Chute Blanche) at river kilometre (rkm) 7 blocked upstream migration of returning adult salmon until 1981, when a fish ladder was installed to allow adult salmon to bypass the waterfall. The installation of the fish ladder opened approximately 18 km of additional river habitat to salmon for spawning and juvenile rearing. All adult Atlantic salmon that return to the fish ladder are captured in an entry cage for counting and measurement before being allowed to pass into the main fish ladder. A pair of impassable waterfalls at rkm 33.7 (Chute du 16 Miles) and rkm 36.2 (Chute du 18 Miles) currently prevent further upstream movement by returning adults.

In 2014, a translocation program was initiated to trap a subset of the adults returning to the fish ladder at Chute Blanche for transport upstream of the pair of impassable falls. Transported adults are able to access approximately 13 km of river habitat, before further upstream passage is blocked by another natural barrier. As part of the evaluation of the success of the translocation program, all salmon transported between 2014 and 2016 were tagged with acoustic transmitters to assess post-transport movement patterns. Our study leveraged the existing infrastructure and tagging program on the Nord-Est to assess thermal refuge use by adult Atlantic salmon during summer 2016, by tagging a subset of transported salmon with temperature sensing acoustic tags (V13T–H, Vemco, Halifax, NS). We conducted our study in two river reaches; the river reach between Chute Blanche and Chute du 16 Miles (hereafter, the downstream sector) and upstream of Chute du 18 Miles (hereafter, the upstream sector). Due to challenging river access, we were unable to deploy acoustic receivers throughout the entirety of the downstream sector, so we focused our efforts on the seven kilometres immediately downstream of Chute du 16 Miles, which are accessible by canoe (Fig. 5.1).

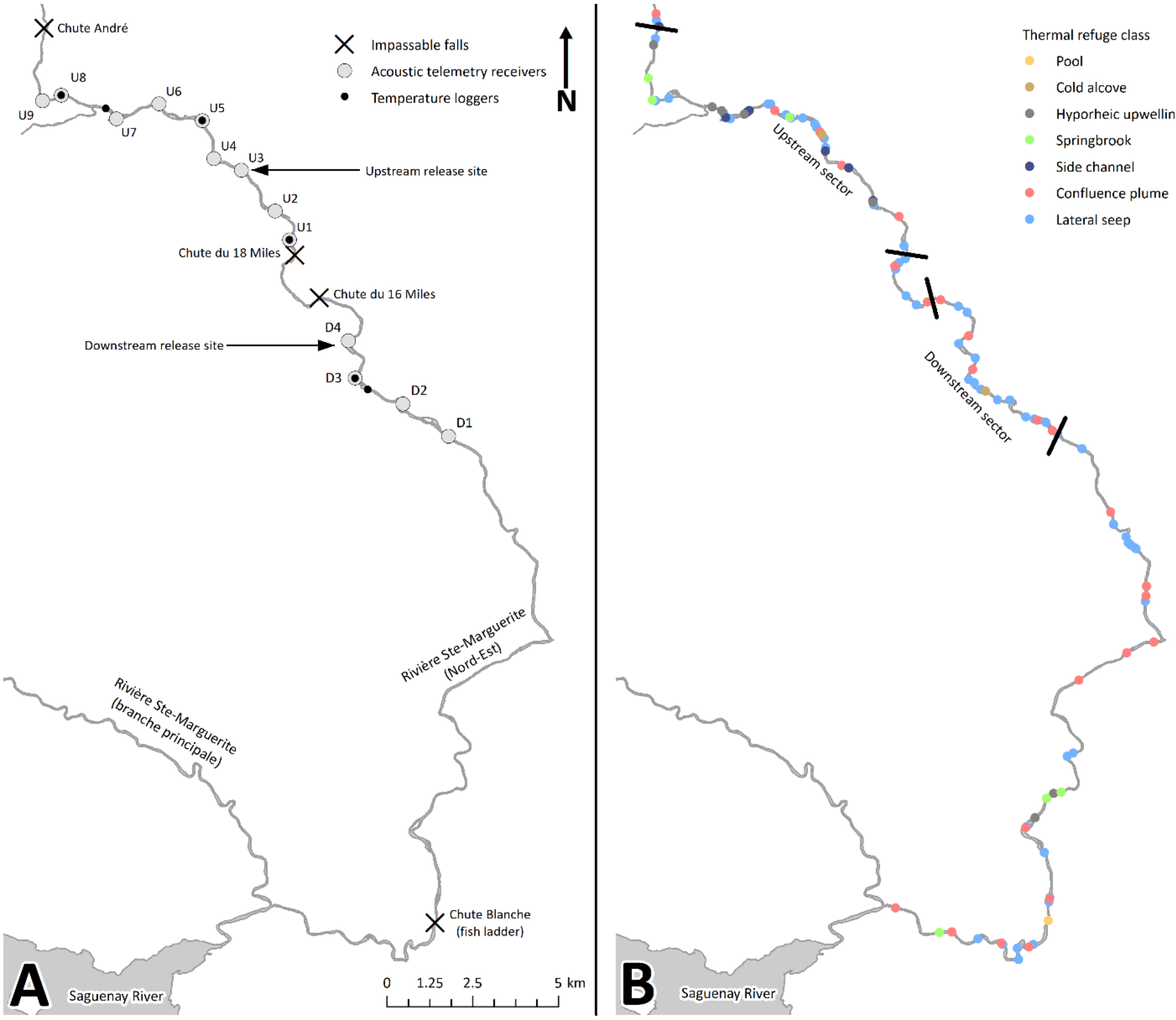


Figure 5.1 : Study area map with receiver position and thermal refuges

Panel A indicates the fish ladder where adult salmon were captured, sites where salmon were released after transport, and placement of acoustic receivers and temperature loggers. Impassable waterfalls bounding the upstream and downstream river sectors are indicated with an X. Receiver positions are indicated with solid grey circles. Receivers in the upstream sector of the river are labelled U1-U9 and receivers in the downstream sector are labelled D1-D4. Temperature loggers are indicated with small dark black circles and were deployed in the river mainstem (at rkm 30 and rkm 45), or in association with acoustic receivers in confluence plumes (U1 and U5) or deep pools (1 logger in D3; 2 loggers in U8 to test for thermal stratification). Panel B depicts the location of all cool patches identified from TIR imagery. Boundaries delineating each study sector are identified with solid black lines. The map was created using ArcGIS software by ESRI.

5.4.2 TIR imagery and acoustic telemetry array

We used TIR imagery to locate cold patches at the riverscape scale, which we subsequently used to inform placement of an acoustic receiver array designed to monitor movements and body temperatures of tagged Atlantic salmon. Airborne thermal and optical imagery (resolution of approximately 2.6 cm and 18.7 cm respectively from ~300 m AGL) was obtained from an aerial survey of the Nord-Est conducted on 25 August 2014 using the same method as Dugdale et al. (2013). We processed images and identified cool patches using the custom MATLAB graphical user interface and methods described by Dugdale et al. (2013). Briefly, thermal images were used to identify surface temperature anomalies, which were verified against the corresponding optical images to distinguish true water temperature anomalies from landscape features (e.g. shading on bedrock or vegetation). True surface anomalies that were ≥ 0.5˚C cooler than ambient river temperature were classified as cool thermal refuges (Dugdale et al. 2013). Identified refuges were classified by type according to the definitions of Ebersole et al. (2003) and Torgersen et al. (2012), which are described in detail by Dugdale et al. (2013).

We deployed acoustic receivers in TIR-identified cool patches that were ≥ 0.5 m depth, the minimum depth required for receiver deployment. This depth requirement was deemed unlikely to bias the results of the present study because refuges shallower than this threshold are unlikely to provide thermal habitat suitable for long-term use by adult salmonids (Torgersen et al. 1999; Baird and Krueger 2003; Torgersen et al. 2012). Because only cool water patches that intersect the river surface can be identified by TIR (Dugdale 2016), acoustic receivers were also deployed in five deep pools known to be used by adult salmon for holding during in-river residence (Frechette, unpublished data). Deployment of acoustic receivers in deep pools enabled identification of subsurface cool refuges that otherwise would have been missed via evaluation of TIR imagery. Receivers were deployed in late June before tagging commenced and were recovered towards the end of the spawning period in late October. Raw telemetry data were downloaded from receivers using VUE software (Vemco, Halifax, NS) and processed using the VTrack package for R (Campbell et al. 2012).

5.4.3 River temperature monitoring

Water temperature within the Nord-Est was recorded at 15-min intervals using temperature loggers (HOBO UA-002-64, Onset, Bourne, MA) installed at a number of sites (Fig. 5.1a). Before deployment, we cross-calibrated temperature loggers and temperature-sensing transmitters in an ice-water bath to develop a correction factor. Temperature responses varied among individual loggers (0.010 – 0.678˚C, mean = 0.2˚C) so logger-specific correction factors were applied to each temperature logger prior to use in subsequent analyses. Temperature loggers (N = 7) were housed in white PVC tubes to shield them from direct sunlight and shifting river sediment, and were either attached to the anchoring blocks used to deploy acoustic receivers or attached to rock-filled plastic sacks. Temperature loggers were deployed in well-mixed areas of the river mainstem (one in the upstream sector at rkm 45 and one in the downstream sector, at rkm 30), in the two confluence tributary plumes identified in the upstream sector (U1 and U5), and in two deep pools known to be used by salmon during in river residence (U8 in the upstream sector and D3 in the downstream sector). We suspected that the upstream pool (U8) might be thermally stratified, so we deployed a second temperature logger c. 10 cm below the surface float that was attached to the anchor for the acoustic receiver. The difference between the temperatures measured 10 cm below the surface and 10 cm above the substrate allowed us to test for the presence of thermal stratification in pool U8.

5.4.4 Salmon capture and tagging

Salmon included in this study were part of the translocation program detailed in the ‘study area’ section. Twenty individuals were captured at the fish ladder and transported to upstream release sites (Fig. 5.1a) where they were tagged with acoustic transmitters equipped with temperature sensors (Vemco V13T–H), allowed to recover in-river, and released. The temperature-sensing transmitters allowed us to obtain measurements of instantaneous internal fish temperature whenever tagged salmon were detected by an acoustic receiver. Sixteen salmon were released in the upstream sector, c. 3 km upstream of Chute du 18 Miles (adjacent to pool U3) and four salmon were released in the downstream sector, c. 3 km downstream of Chute du 16 Miles (adjacent to pool D4).

Fish were transported in a 1 600-L tank with a water recirculation system and supplied with oxygen. No transport occurred when water temperatures exceeded 20˚C and a maximum of four fish were transported at the same time. Tagging was accomplished within one hour of arrival at the release site. Before tagging, salmon were placed in an aerated anaesthetic bath containing 30 mg L^{-1} acetyleugenol. Dosage time varied depending on water temperature. Once the salmon was adequately anesthetized (determined by gill respiration rate and strength of the reflex response), it was placed on a V-shaped surgery table. During the surgical procedure, salmon received a maintenance dose of acetyleugenol (15 mg L^{-1}) and water administered over the gills using a custom-designed reservoir. The acoustic tag was inserted into the abdominal cavity anterior to the pelvic girdle through an incision using aseptic technique. The incision was closed with three or four simple interrupted sutures. During handling, fish length (fork and total length) and maxillary length were measured. Established regression relationships between maxillary length and fork length permitted sex identification for individuals that had not yet developed evident external sexual characteristics (Maisse et al. 1988; Prévost et al. 1991). Following surgery, fish were placed in an aerated recovery tank to be weighed before transfer to a water-filled stretcher for transport to the in-river recovery cage.

Salmon were held in the recovery cage and checked every 15 minutes until they regained equilibrium and were swimming freely. The recovery cage in the upstream sector was equipped with a door that was opened once salmon were swimming freely, allowing individuals to volitionally exit the cage. If an individual remained in the cage one hour after regaining equilibrium, it was released by hand. The recovery cage in the downstream sector did not have a door so individuals were released by hand one hour after they regained equilibrium.

5.4.5 Seasonality and location of refuge use

We obtained consistent position and temperature recordings from 15 of the 20 tagged salmon during July and August 2016 (Table 5.1). Four salmon tagged in the upstream sector and one salmon tagged in the downstream sector left the study area within two days of tagging and were not included in analyses. Two of the salmon tagged in the upstream sector (Fish D-01 and Fish D-02) moved downstream over the impassable falls within six days of release (termed fallback) and were detected in the downstream sector. As these fish were present in the downstream sector for the majority of the study period, they were grouped with the individuals released in the downstream sector for all analyses. Statistical analyses were conducted using R version 3.3.0 (R Core Team 2014) within R Studio version 1.0.136 (R Studio Team 2016).

To identify when and where salmon used thermal refuges, we computed the difference (ΔT) between salmon body temperature (T_B) recorded by acoustic receivers and mainstem river temperature (T_R) measured by temperature loggers. Because fish temperature was logged intermittently (only when a fish was in proximity of the receiver), while ambient temperature was logged at 15-minute intervals, we used cubic spline interpolation to estimate mainstem river temperature at the exact moment that fish temperature was measured and logged by the acoustic receiver, which allowed us to calculate the instantaneous difference (ΔT_I) between interpolated mainstem river temperature (T_{RI}) and fish temperature (T_B). We generated plots of ΔT_I by day for each individual, and color-coded the location (receiver identity) where the detections were recorded (Fig. 5.2).

In the literature, cool refuges have been defined either using a specific temperature differential between the mainstem and cool patches, e.g. 2˚C (Torgersen et al. 2012) or 3˚C (Ebersole et al. 2001; 2003), or as simply water that is cooler than the mainstem (Baird and Krueger 2003). Donaldson et al. (2009), however, found evidence of behavioural thermoregulation in sockeye salmon (*Oncorhynchus nerka*) when the differential between body and river temperatures was 1˚C. Given the inconsistency in the literature regarding definitions of thermal refuges and/or behavioural thermoregulation, we chose to use a threshold of 1˚C to identify the location and timing of refuge use. We classified fish as using cool refuges when $\Delta T_I \leq -1$˚C. Conversely, values of $\Delta T_I \geq 1$˚C indicated that fish were located in water that was warmer than the ambient mainstem river temperature.

5.4.6 Identification of behavioural thermoregulation

We assessed trends in behavioural thermoregulation over the course of the summer using the difference (ΔT_H) between mean hourly internal fish temperature (T_{BH}) and mean hourly ambient mainstem river temperature (T_{RH}). We used mean hourly measurements because river temperature did not change substantially within the hour. To determine whether salmon exhibited behavioural thermoregulation, we regressed T_{BH} against T_{RH} for each individual (Berman and Quinn 1991). If salmon did not behaviourally thermoregulate (i.e., fish temperature depended on mainstem river temperature), we would expect a 1:1 relationship between T_{BH} and T_{RH}. If a fish did behaviourally thermoregulate (i.e., salmon actively selected water that was warmer or cooler than ambient mainstem river temperature), we would expect a significant departure from the 1:1 relationship (Hillyard and Keeley 2012). We accounted for temporal autocorrelation in the data by applying weighted stratified sampling to the time series of T_{BH} and T_{RH}. Specifically, the observations of each individual salmon were divided into four strata, with each stratum representing one week during the month of August (each stratum consisted of 8 days, except for the fourth stratum, which was 7 days). One half of the total observations for each fish were randomly sampled, with the number of samples taken from each stratum weighted by the proportion of observations in the stratum relative to total number of observations during the month of August. The subsampled data were used in the linear regression model and a bootstrapping routine (1000 replicates) was used to confirm that estimates of model coefficients remained constant. Regression assumptions of normality and homogeneity were assessed by visually examining residual plots and the assumption of independence was assessed using the autocorrelation function (Zuur et al. 2009). We used a Student's t-test to test the null hypothesis that the slope of the regression coefficient did not differ from unity.

To determine mainstem river temperatures at which salmon exhibited behavioural thermoregulation, we subset the mainstem river temperature into 1˚C bins for the range of ambient mainstem temperatures observed within each river sector. We then plotted the frequency histogram for values of ΔT_H within each 1˚C river temperature bin. We computed the median value of ΔT_H within each 1˚C river temperature bin and generated 95% confidence intervals (CI) around the estimate of median ΔT_H via bias corrected and accelerated (BCa) bootstrap resampling, which adjusts for bias and skewness using the 'boot' package in R (Efron and Tibshirani 1993; Davison and Hinkley 1997; Canty and Ripley 2017). If the 95% CI did not overlap zero, then median ΔT_H (hereafter ΔT_{Hmed}) was considered to differ significantly from zero. A negative value of ΔT_{Hmed} indicated that at a given river temperature, salmon were predominantly detected in cool patches (i.e. they used patches of water that were cooler than ambient mainstem river temperature), whereas a positive ΔT_{Hmed} indicated that salmon were predominantly detected in warm patches. No significant difference between ΔT_{Hmed} and zero indicated that there was no preferential use of cool or warm patches at the given temperature.

To examine diurnal patterns in refuge use, we merged records of ΔT_H for all fish, and for each hour of the day, summed the amount of time that fish occupied a) cool patches [$\Delta T_H \leq -1^{\circ}C$], b) the main stem [$-1^{\circ}C > \Delta T_H > 1^{\circ}C$] and c) warm patches [$\Delta T_H \geq 1^{\circ}C$]. We used Chi-square contingency table analysis to test the null hypothesis that the water type occupied (cool patch, main stem, or warm patch) was independent of the hour of the day, and graphically examined diurnal patterns in refuge use.

5.4.7 Within-pool behavioural thermoregulation

We hypothesized that salmon using large pools containing cool water patches would behaviourally thermoregulate within the pool to occupy cool patches, ambient pool temperature, or warm patches as needed to maintain a narrow range of body temperatures (e.g. Nielsen et al. 1994; Newell and Quinn 2005; Gutowsky et al. 2017). We tested this hypothesis using temperature data from the loggers attached to the VR2 anchors in pools. The temperature difference between internal fish temperature and ambient temperature measured in the pool allowed us to assign fish to patch type (ambient pool temperature, cool patch, or warm patch) for all detections of individuals that occurred in the pool.

We estimated instantaneous ambient pool temperature (T_{AI}) for each measurement of fish temperature (T_B) that was logged by the acoustic receiver using the cubic spline interpolation, as described previously. We then calculated instantaneous pool-specific ΔT ($\Delta T_{IP} = T_B - T_{AI}$), which we used to assign patch state (cool, ambient, or warm patch) to all detections of each individual in the pool. We again used $1^{\circ}C$ as a threshold to distinguish between the use of cool patches ($\Delta T_{IP} \leq -1^{\circ}C$), ambient river temperature ($-1^{\circ}C > \Delta T_{IP} > 1^{\circ}C$), or warm patches ($\Delta T_{IP} \geq 1^{\circ}C$).

We employed empirical cumulative density functions to determine the temperatures at which salmon moved into cool or warm patches. To ensure that a new detection of an individual in a patch truly represented the initiation of patch use, and not an individual that was simply on the edge of a cool or warm patch (in which case it might appear to sporadically move into and out of the patch), we set a threshold of 15 min to define a patch residence. That is, for a fish to be considered resident in a warm or cool patch, it must have remained in the patch for a minimum of 15 min. The threshold of 15 min was chosen because this was the sampling resolution of our in-river temperature loggers.

5.5 Results

5.5.1 TIR imagery and acoustic telemetry array

Although we classified thermal refuges throughout the Nord-Est (Fig. 5.1b), here we present counts of only those cool refuges located in the accessible study reaches. We identified 18 cool patches in the downstream sector and 36 in the upstream sector. Three classes of cool patch were identified downstream: lateral seep (n = 12), confluence plume (n = 5), and cold alcove (n = 1). As in the downstream sector, lateral seeps (n = 16) were the most prevalent cool patch type identified in the upstream sector. The other classes identified upstream, in order of prevalence, were: cool side channel (n = 6), confluence plume (n = 5), hyporheic upwelling (n = 5), springbrook (n = 3), and cold alcove (n = 1). Although we did not directly measure the size of most cool patches identified using TIR imagery, we used the optical images coupled with knowledge of the system to determine that the majority had a surface extent of less than 1 m^2 and were in water less than 0.5 m depth, making them too shallow for receiver deployment.

We deployed 13 acoustic receivers during summer 2016 (Fig. 5.1a). The only cool patches identified from TIR imagery that were deep enough for receiver deployment (≥ 0.5 m) were either seeps located in deep pools or confluence plumes (Fig. 5.1a). Maximum water depth within pools was measured on 25 July 2016 at a river discharge of 26 m^3s^{-1} using a single beam echo sounder (Hydroball, CIDCO, Rimouski, QC). Confluence plume depth was measured with a meter stick during receiver deployment. In the downstream sector, we deployed receivers in two pools containing lateral seeps (D1 = 2.1 m deep and D2 = 5.8 m deep). In the upstream sector, lateral seeps were identified in three large pools (U3, U4, and U7), which had maximum depths ranging between 3 and 4 m. A small patch of cool hyporheic upwelling was identified in a fourth large pool (U8), which was the deepest pool in both study sectors (maximum depth = 6.2 m). Three of five confluence plumes were deep enough for receiver deployment (1 – 1.5 m at a river discharge of 21 m^3s^{-1}). We were only able to deploy receivers in two of these sites (U1 and U5) because a strong counter-current prevented receiver deployment at the third confluence plume. We deployed receivers in all remaining accessible large pools (maximum depth: 2.7 – 5.3 m) in the upstream (n = 3) and downstream (n = 2) sectors.

Our analyses focused on data from 15 individuals that were consistently detected during July and August (Table 5.1). Internal body temperature was logged whenever salmon were in proximity of a receiver, i.e., when they were in confluence plumes or pools containing receivers. Temperature records were not obtained when salmon were transiting between pools or in habitat not monitored by a receiver.

Table 5.1 : Characteristics of tagged Atlantic salmon.

River Sector	Fish ID	FL (mm)	Sex	Release site	Date Available Upstream	Date Available Downstream	Number of Records
Upstream	U-01	820	M	Upstream	29-Jun	NA	17 248
	U-02	720	F	Upstream	10-Jul	NA	14 270
	U-03	740	F	Upstream	12-Jul	NA	13 416
	U-04	820	M	Upstream	12-Jul	NA	22 760
	U-05	770	M	Upstream	12-Jul	NA	14 196
	U-06	770	F	Upstream	13-Jul	NA	14 596
	U-07	830	M	Upstream	11-Aug	NA	4 048
	U-08	680	M	Upstream	11-Aug	NA	8 080
	U-09	750	M	Upstream	18-Aug	NA	8 016
	U-10	630	M	Upstream	22-Aug	NA	4 005
Downstream	D-01	790	M	Upstream	13-Jul	16-Jul	31 406
	D-02	780	F	Upstream	13-Jul	23-Jul	14 926
	D-03	770	F	Downstream	NA	30-Jul	14 019
	D-04	775	F	Downstream	NA	31-Jul	12 124
	D-05	760	F	Downstream	NA	31-Jul	4 560
Removed	R-01	720	F	Upstream	29-Jun	NA	1 611
	R-02	975	F	Upstream	1-Jul	NA	269
	R-03	920	F	Upstream	3-Aug	NA	1 494
	R-04	780	F	Upstream	18-Aug	NA	174
	R-05	665	M	Downstream	NA	2-Aug	1 353

Size and sex of Atlantic salmon implanted with temperature sensing acoustic transmitters (Vemco V13T–H) during summer 2016, by river sector, site of release, and dates individuals were first available for detection in each river sector, and number of times each individual was detected (number of records). Tagging data for fish removed from analyses are included for reference.

Range testing conducted during the summer of 2014 indicated that under calm conditions, the detection efficiency of V13 acoustic tags by VR2W receivers deployed in pools in the Nord-Est was 95% at a distance of 40 m and 80% at 200 m (water depth ≥ 0.5 m). Reduced receiver detection range was only observed when river discharge exceeded 60 m^3s^{-1} or during discrete heavy rainfall events (Frechette, unpublished data). During the study period, median river discharge was 18.7 m^3s^{-1} (range = 8.8–39.4 m^3s^{-1}) and only two rain events occurred during summer 2016 (both during July) that could have interfered with tag detection over a period of less than 12 hours. In cases when multiple salmon were present within a pool, there was some evidence of tag collision, which prevented temperature records from being registered by a receiver despite the salmon being within range of the receiver. Given the high temporal frequency at which data was transmitted to the receivers (i.e. every 30 to 90 sec), data lost because of tag collisions represents only a tiny fraction of the total number of detections recorded from each individual (Table 5.1). Consequently, we do not expect that the loss of tag detections from rainfall or tag collisions biased our analysis of behavioural thermoregulation.

5.5.2 Seasonality and location of refuge use

All observed cool patch use occurred during August (Fig. 5.2), which was the only month when measured mainstem river temperature remained within the range considered to be stressful to adult Atlantic salmon (20-23°C, Breau 2013) for more than a few hours at a time (Annex 4). Three high temperature events, defined as periods during which mainstem river temperature exceeded 22°C in the upstream sector and approached or exceeded 20°C in the downstream sector, occurred during August 2016. The initial onset of behavioural thermoregulation was linked to the high temperature event that occurred 4-6 August (day 217-219), when mainstem river temperature approached 23°C and remained greater than 20°C for three days. Before this event, river temperature was rarely greater than 19°C (Annex 4) and there was no evidence of cool patch use (Fig. 5.2). During or immediately following the first high temperature event, all salmon moved into pools containing thermal refuges.

Cool refuge use ($\Delta T_I \leq -1^{\circ}C$) occurred in six locations (Fig. 5.2): D3 (downstream sector) and U2, U3, U6, U7, and U8 (upstream sector). Of the pools where cool patch use occurred, only three had cool patches that were also identified from TIR images (U3, U7 and U8). Data from temperature loggers installed at the bed and surface of U8 (cross-validated with spot measurements from a temperature probe) indicated that U8 was thermally stratified during August 2016 (Annex 5). Temperature recorded 10 cm below the surface ranged from 0.77°C to 1.7°C warmer than the temperature recorded 10 cm above the substrate. This temperature differential is greater than the thresholds used to define thermal stratification used by Matthews et al. (1994; 0.5°C) and Gendron (2013; 0.1°C), despite the fact that the bottom logger was not placed in the coolest area of the pool. No cool patch use was identified in either of the confluence plumes (U1 and U5), nor in other pools containing lateral seeps (U4 and D1) that were identified via thermal imagery. Fish used cool patches for extended periods of time (≥ 2 weeks), in pools U8 (upstream sector) and D3 (downstream sector), which were the only pools where of $\Delta T_I \leq -2^{\circ}C$ was recorded. Minimum ΔT_I ranged from -2.97 to -3.79°C in D3 and -4.83 to -5.03°C in U8. Aside from brief forays into other pools, all tagged fish remained in D3 or U8 during the warmest part of August, with up to 90% of available individuals in the upstream sector (8 of 9) detected in pool U8 and 100% of available individuals in the downstream sector (5 of 5) detected on a given day.

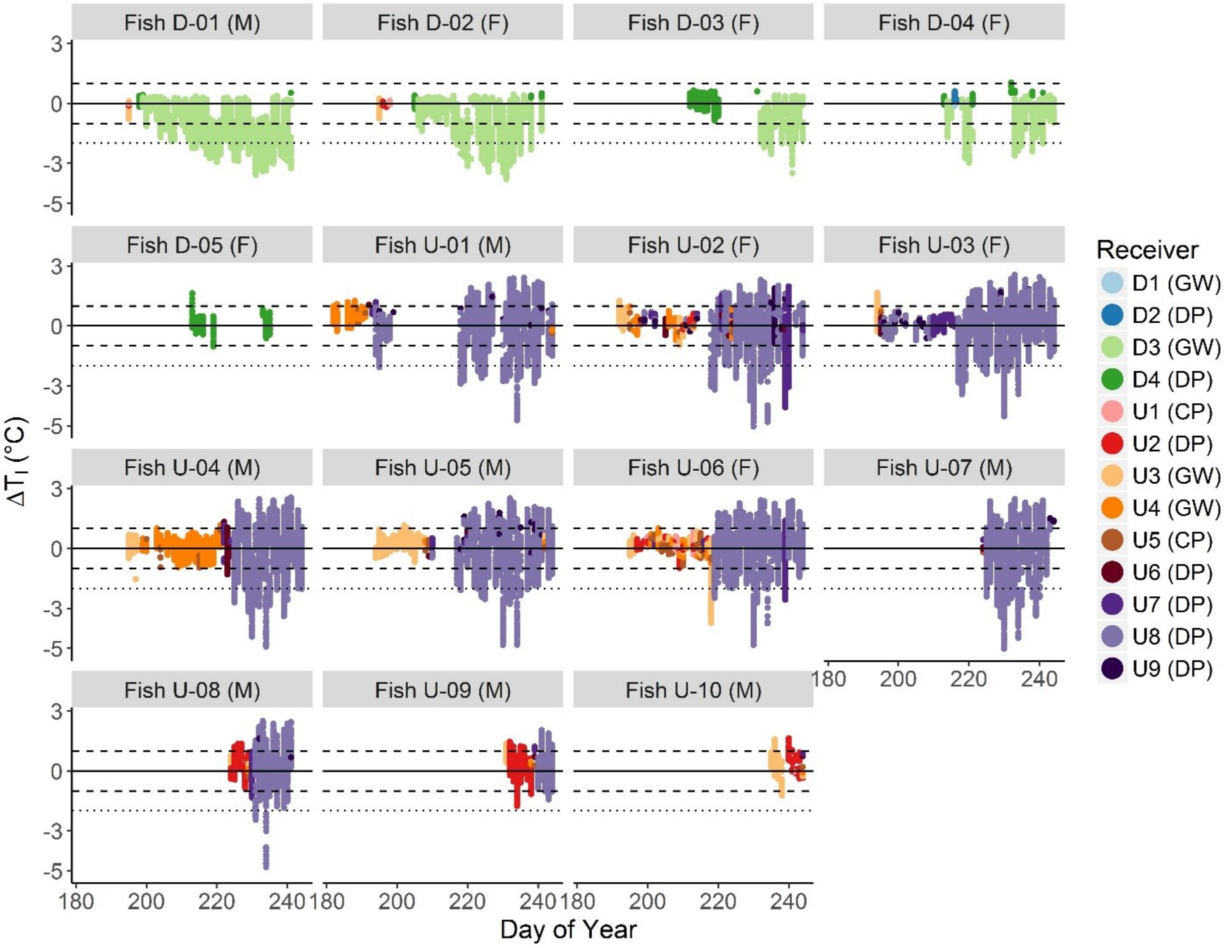


Figure 5.2 : Temporal variation in behavioural thermoregulation

Temporal variation in behavioural thermoregulation by individual adult Atlantic salmon tagged with temperature-sensing acoustic tags during summer 2016 from June 29 (day 181) to August 31 (day 244). Behavioral thermoregulation is represented as the difference between body temperature and instantaneous mainstem temperature (ΔT_I, where mainstem river temperature was measured at rkm 45 (upstream sector) and rkm 30 (downstream sector). Fish identity corresponds to Table 5.1 and is presented in the gray box above each individual plot along with sex (M = male, F = female). Each point marks a detection of an individual by a given receiver, with receiver location coded by color. Habitat type is specified for each receiver (DP = deep pool; GW = groundwater seep; CP = confluence plume).

5.5.3 Identification of behavioural thermoregulation

Although all tagged salmon engaged in behavioural thermal regulation, individuals that were in the downstream sector during August exhibited less behavioural thermoregulation than salmon in the upstream river sector and salmon tagged after the high temperature events exhibited less behavioural thermoregulation than fish tagged earlier in the summer. A linear relationship with a slope that differed from 1:1 was observed between mean hourly mainstem river temperature and mean hourly internal fish temperature for all individuals (1-tailed Student's t-test, $\alpha = 0.05$, Fig. 5.3) and no substantial departure from the assumptions of normality and homogeneity were evident in residual plots. In the downstream sector, greater than 70% of the variation in internal fish temperature was explained by the mainstem river temperature (measured at rkm 30). In the upstream sector, however, mainstem river temperature (measured at rkm 45) explained little of the variance in internal fish temperature for individuals that experienced the high temperature events (Fig. 5.3). The remaining variation in fish temperature (42 to 73%) was explained by fish using areas of the river that were cooler or warmer than the ambient mainstem temperature. Ambient mainstem river temperature explained approximately 80% of variation in fish temperature for the two individuals that were tagged during late August, after the high temperature events (Fish U-09 and Fish U-10).

In the upstream sector, ΔT_{Hmed} was significantly greater than zero when ambient mainstem river temperature was between 14.0 and 16.9°C (bootstrapped 95% CI did not overlap zero, Fig. 5.4a), indicating that salmon were using warm patches at these cooler temperatures. When ambient mainstem river temperature was between 17 and 18.9°C, median ΔT_{Hmed} was not significantly different than zero (bootstrapped 95% CI contain zero), indicating that salmon did not seek out warm or cool patches. Once ambient mainstem river temperature reached 19°C, however, ΔT_{Hmed} began to skew significantly negative, indicating that fish were actively using cool patches. At water temperatures $\geq$ 21.0°C, nearly 100% of detections of tagged salmon were in cool refuges, and ΔT_{Hmed} was approximately -2°C.

Fish in the downstream sector showed no evidence of warm patch use, and cool patch use began at lower ambient mainstem river temperatures than in the upstream sector (Fig. 5.4b). When mainstem river temperature was between 14 and 16.9°C, ΔT_{Hmed} was not significantly different than zero (bootstrapped 95% CI contain zero). Once mainstem river temperature reached 17°C, ΔT_{Hmed} began to skew significantly negative, a threshold that was two degrees cooler than in the upstream habitat. At water temperatures $\geq$ 19.0°C, nearly 100% of detections of tagged salmon were in cool refuges and ΔT_{Hmed} was greater than -2°C.

There was a clear diurnal pattern in behavioural thermoregulation in the upstream sector and the thermal habitat type occupied (cool patch, ambient mainstem temperature, or warm patch) was not independent of the hour of the day (Fig. 5.5a; $\chi^2_{(46, N = 4526)}$, $P < 0.05$). Cool patch use increased throughout the afternoon, when river temperature generally increases due to solar heating, and was greatest at 16:00 before decreasing again. Warm patch use increased during the early morning, and was greatest at 06:00. There was no clear diurnal pattern in behavioural thermoregulation in the downstream sector and no warm patch use was observed (Fig. 5.5b), however, water type occupied (cool patch or ambient mainstem temperature) was not independent of the hour of the day ($\chi^2_{(23, N = 1765)}$, $P < 0.05$).

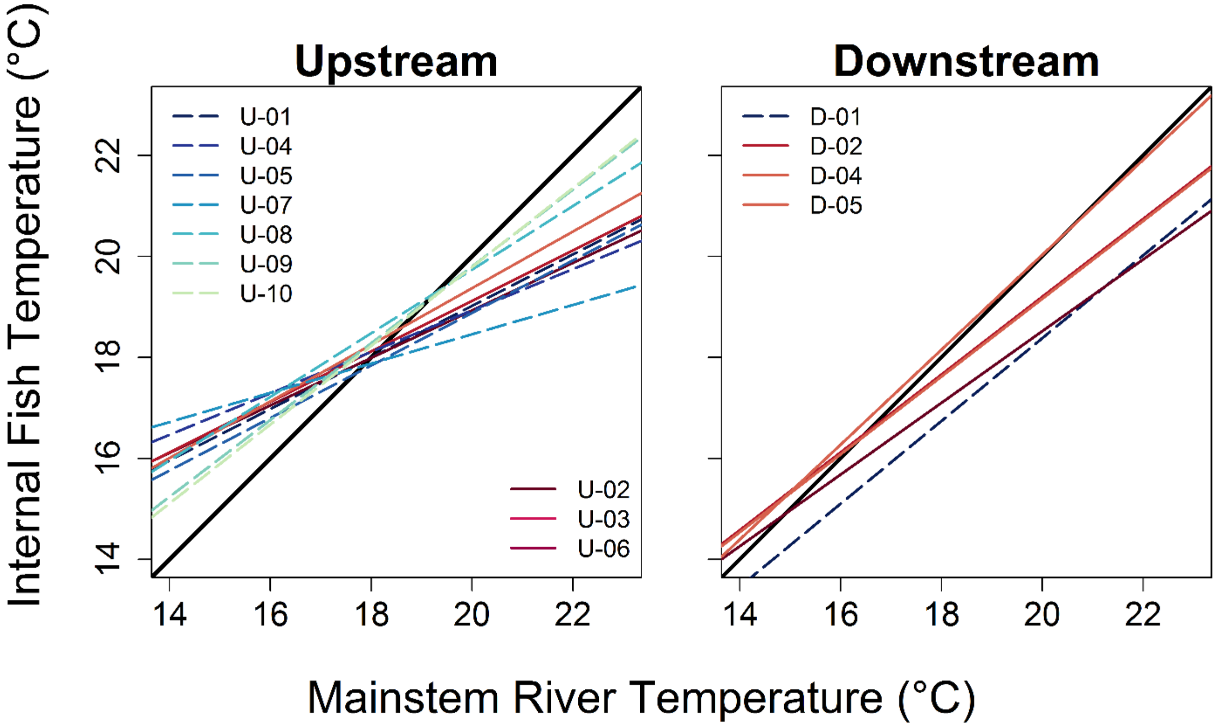
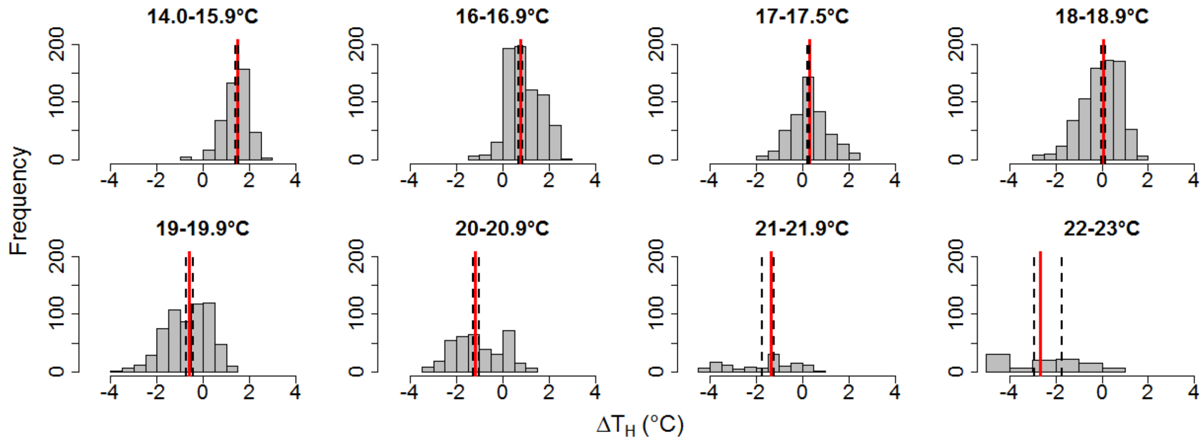


Figure 5.3 : Relationship between internal fish temperature and mainstem river temperature

Slope plots depicting the median slope and median intercept obtained via bootstrapping (1000 replicates) for the linear relationship between mean mean hourly internal fish temperature (T_{BH}) and mean hourly ambient mainstem river temperature (T_{RH}) in the upstream and downstream river sectors for all fish included in analyses. The solid black line represents a 1:1 relationship between T_{BH} and T_{RH}. Males are represented by dashed lines in shades of blue, females by solid lines in shades of red. Fish identity corresponds to Table 5.1.

A) Upstream Sector



B) Downstream Sector

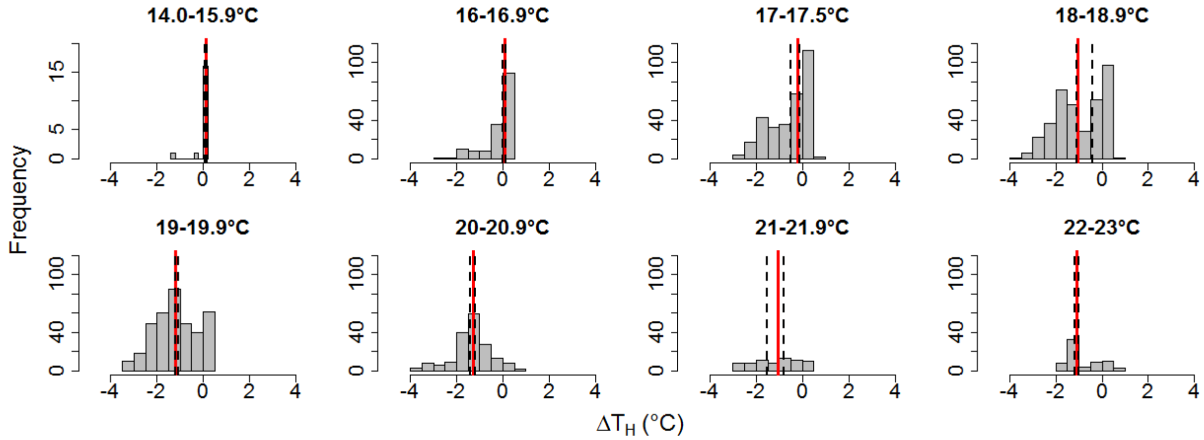


Figure 5.4 : Frequency histograms binned by mainstem river temperature.

Frequency histograms of the difference (ΔT_H) between mean hourly internal fish temperature and mean hourly mainstem river temperature for the A) upstream sector (n = 10 salmon) and B) downstream sector (n = 6 salmon), binned by mainstem river temperature (measured at rkm 45 for the upstream sector and at rkm 30 for the downstream sector), for August 2016. Solid red vertical lines denote the median (ΔT_{Hmed}) and dashed black vertical lines denote the 95% CI, generated using 5,000 Bca bootstrap replicates. Note different y-axes between panel A and panel B, and in the 14-15.9°C bin in Panel B.

There was a clear diurnal pattern in behavioural thermoregulation in the upstream sector and the thermal habitat type occupied (cool patch, ambient mainstem temperature, or warm patch) was not independent of the hour of the day (Fig. 5.5a; $\chi^2_{(46,\, N = 4526)}$, $P < 0.05$). Cool patch use increased throughout the afternoon, when river temperature generally increases due to solar heating, and was greatest at 16:00 before decreasing again. Warm patch use increased during the early morning, and was greatest at 06:00. There was no clear diurnal pattern in behavioural thermoregulation in the downstream sector and no warm patch use was observed (Fig. 5.5b), however, water type occupied (cool patch or ambient mainstem temperature) was not independent of the hour of the day ($\chi^2_{(23,\, N = 1765)}$, $P < 0.05$).

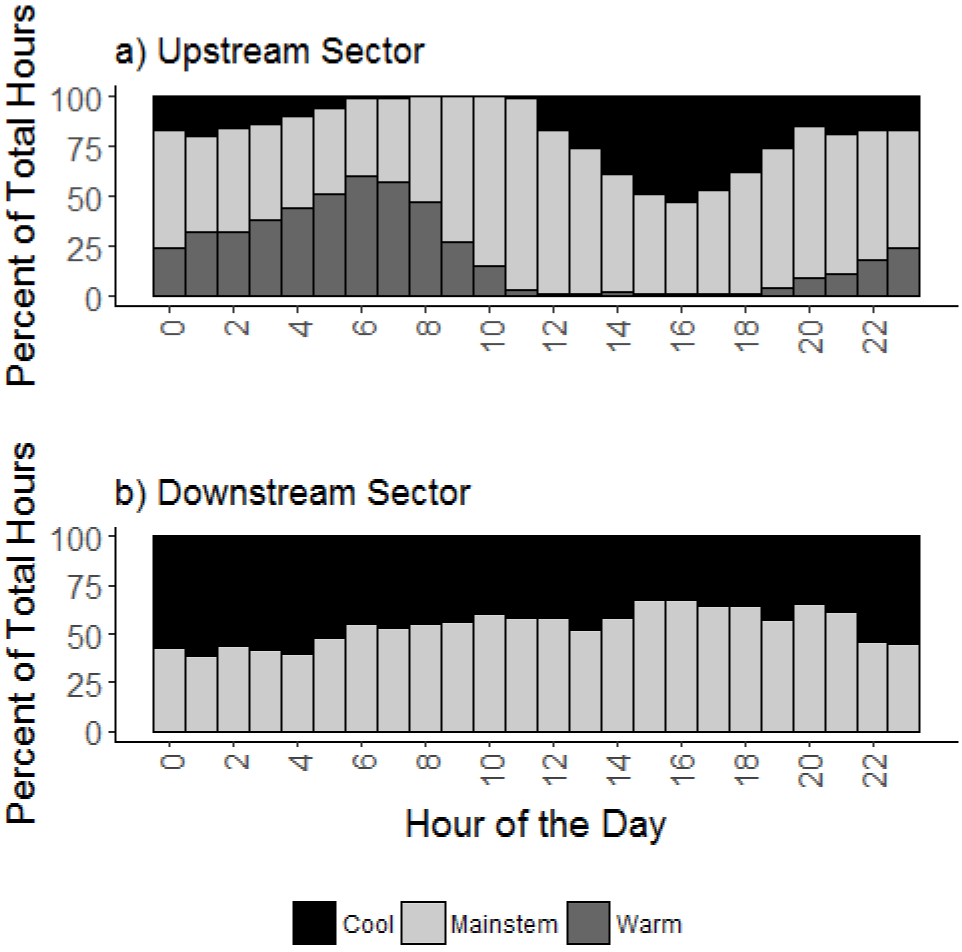


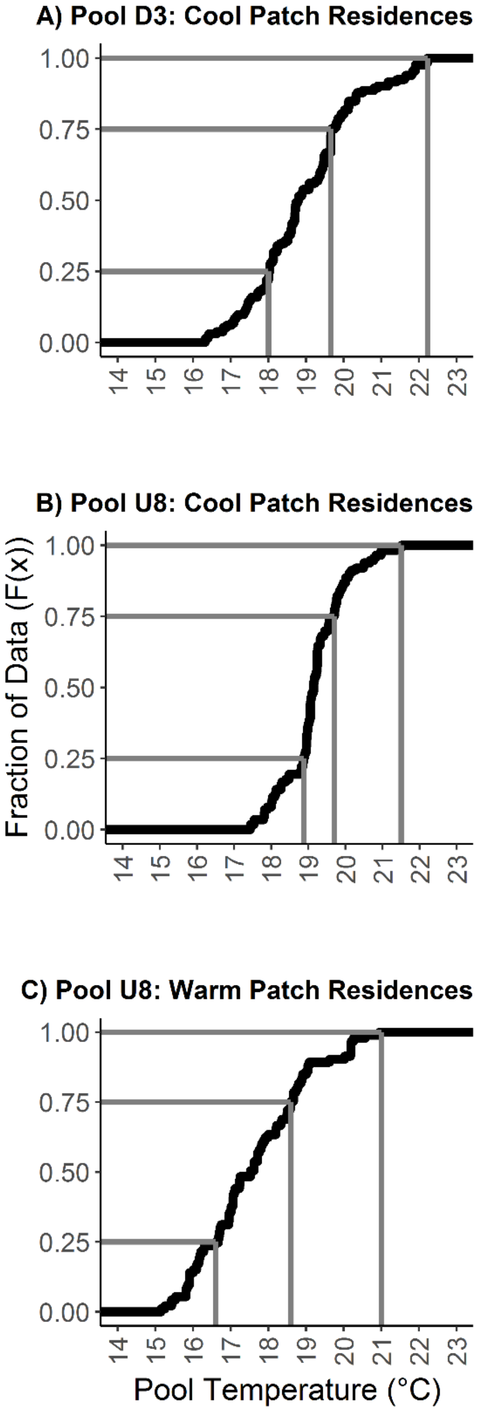
Figure 5.5 : Distribution of thermal habitat use by hour of the day.

Percent of total hours that salmon used cool patches ($\Delta T_H \leq -1^\circ C$; black bars) mainstem river temperature ($-1^\circ C > \Delta T_H > 1^\circ C$; light gray bars), and warm patches as ($\Delta T_H \geq 1^\circ C$; dark gray bars) in the upstream (a) and downstream (b) sectors during August 2016.

5.5.4 Within-pool refuge use

We examined within-pool behavioural thermoregulation in the pools where the majority of cool patch use occurred (D3 and U8). During August 2016, three salmon (2 females, 1 male) were detected in D3 on ≥ 18 days. During the same period, seven salmon (3 females, 4 males) were detected in U8 on ≥ 19 days. Measured ambient temperature in pool D3 was always cooler than downstream ambient mainstem temperature (mean = 0.42˚C; range = 0.27˚ to 0.77˚C). Measured ambient temperature in pool U8 was 3.4˚C cooler to 2.4˚C warmer than the upstream ambient mainstem temperature (on average, U8 was 0.12˚C cooler than the mainstem). The temperature range recorded at the bottom of U8 was 15.1˚C to 21.5˚C, whereas the temperature range recorded in D3 was slightly broader (15.7˚C to 22.2˚C). The locations of thermal refuges within these pools, however, were not known before deployment of temperature loggers. Consequently, temperature loggers were not placed directly in the thermal refuges and recorded pool temperature did not represent the coolest or warmest temperatures available in each pool.

The initiation of cool patch residences in pool D3 increased steadily between 16.5˚C and 20.5˚C (Fig. 5.6a) and no warm patch residences were observed. In pool U8, cool patch residences increased dramatically between 18.9˚C and 19.7˚C, and reached a plateau at approximately 21˚C (Fig. 5.6b). Initiation of warm patch residences increased steadily between 16˚C and 19˚C, however, very few warm patch residences began when pool temperature was > 19˚C (Fig. 5.6c).



A) Pool D3: Cool Patch Residences

B) Pool U8: Cool Patch Residences

C) Pool U8: Warm Patch Residences

Figure 5.6 : Empirical cumulative density curves.

Empirical cumulative density curves for river temperature (measured at the bottom of pool U8 in the upstream sector and at the bottom of pool D3 in the downstream sector) at the start of each patch residence (use of cool or warm patches ≥ 15 min). Vertical gray lines identify the temperature at which the proportion of fish located in a cool patch equaled 0.25, 0.75, or 1.0 (horizontal gray lines).

5.6 Discussion

All adult Atlantic salmon that were tagged with temperature-sensing transmitters engaged in behavioural thermoregulation. Although mainstem river temperature in the Nord-Est was relatively cool and did not exceed 23˚C, adult salmon used mainstem pools as cool refuges during the warmest period of the summer. Individuals exhibited behavioural thermoregulation at substantially cooler ambient river temperatures (17˚C in the downstream sector and 19˚C in the upstream sector), than expected from previous studies that described thermal refuge use by juvenile (Gibson 1966; Cunjak et al. 2005; Dugdale et al. 2016) and adult (Shepard 1995) Atlantic salmon. These results support the literature and metabolism-based assessment by Breau (2013) that temperatures above 20˚C are stressful to adult Atlantic salmon. Adult salmon predominantly used cool refuges during the afternoon when the warmest ambient mainstem water temperatures were recorded, and during refuge use body temperatures were as much as 5˚C cooler than ambient mainstem river temperature.

Our combination of TIR imagery, river temperature monitoring, and acoustic telemetry enabled us to obtain a more holistic understanding of how adult Atlantic salmon use thermal habitat than would have been possible with a single-pronged approach. Use of TIR imagery allowed us to map potential thermal refuges at the riverscape scale in a system where large sections of the river are inaccessible. The resulting refuge maps, when applied in concert with optical imagery and first-hand knowledge of the river system, helped target acoustic receiver deployment to potential cool refuges, which we were able to monitor continuously over the course of the summer using acoustic telemetry. Additional deployment of acoustic receivers in deep pools allowed us to identify subsurface cool refuges that were important refuges for adults (e.g. pool D3) but that were missed via evaluation of TIR imagery because the cool water did not extend to the river surface. Because internal salmon body temperature was recorded when salmon were in proximity of a receiver, we obtained near continuous records of salmon body temperature in potential refuge sites. When coupled with long-term measurement of ambient river temperature from temperature loggers, telemetry records allowed us to assess behavioural thermoregulation via thermal refuge use over finer temporal and larger spatial scales than would have been possible using snorkel counts or radio-telemetry, techniques that have been previously applied to study of thermal refuge use by salmonids (e.g. Torgersen et al. 1999; Ebersole et al. 2001; Brewitt and Danner 2014).

Physiological stress has been observed under laboratory conditions in adult Atlantic salmon at 23˚C (Wilkie et al 1997). Ambient mainstem river temperature in the Nord-Est first approached 23˚C during the high temperature event that occurred 4-6 August (day 217-219). We observed mass movement of individual Atlantic salmon into pools containing cool refuges during or immediately after this event. The first heat wave likely induced thermal stress, which served as trigger for individuals to search out pools containing cool refuges where they could recover physiologically (Breau 2013). Once fish entered pools containing refuges, they remained in residence for ≥ 2 weeks, similar to the residence time observed for steelhead (*Oncorhynchus mykiss*) using cold tributaries as thermal refuges in the Columbia River Basin (Keefer et al. 2009).

The degree of behavioural thermoregulation observed varied among individuals, and appeared tied to location and timing of release. Individuals in the upstream sector exhibited a greater degree of behavioural thermoregulation than salmon in the downstream sector, which may be explained by the difference in ambient mainstem temperature between the two river sectors. In the upstream sector, measured ambient mainstem temperature exceeded 20˚C and approached 23˚C during all three high temperature events, whereas in the downstream sector, ambient mainstem river temperature only approached 23˚C during the first event. Salmon that were present in the upstream sector before at least one of the three high temperature events that occurred during August 2016 exhibited a greater degree of behavioural thermoregulation than salmon that were tagged near the end of August, when water temperature was cooler (Fig. 5.3). Use of cool refuges has also been linked to run timing in Columbia River steelhead. Steelhead that migrated during the warmest part of the summer had the greatest rates of refuge use, whereas fish that migrated either early or late in the season experienced lower mainstem temperatures and had lower rates of refuge use (Keefer et al. 2009). Salmonids that migrate during periods when heat stress-inducing warm water events occur seem to have a greater need to use cool water refuges than salmonids migrating later in the summer when water is cooler.

In our study, tagged adult Atlantic salmon routinely used cool patches when river temperature in the Nord-Est was less than 19˚C, which is substantially cooler than previously reported for Atlantic salmon. Juvenile Atlantic salmon moved into cold water refuges in eastern Canadian rivers when water temperature was 22-24˚C (Gibson 1966; Cunjak et al. 2005; Dugdale et al. 2016), and adults stopped migrating and congregated in cold water tributaries in the Penobscot River in Maine at 23˚C (Shepard 1995). In the upstream sector, adult salmon used thermal refuges when ambient mainstem river temperature was as cool as 19˚C, and nearly 100% of detections were in thermal refuges when ambient mainstem temperature was ≥ 21˚C. These results are similar to the patterns of thermal refuge use exhibited by summer steelhead in the Columbia River Basin, where steelhead began using cold water tributaries as thermal refuges when mainstem river temperature reached 19˚C, and 70% of tagged fish were detected in refuges when river temperature exceeded 21˚C (Keefer et al. 2009). In the downstream sector, however, adults used thermal refuges at ambient mainstem river temperatures as low as 17˚C, with 100% of detections occurring in cold refuges when river temperature was ≥ 19˚C.

Interestingly, in the upstream sector, adult Atlantic salmon used warm water patches when river temperature was < 17˚C. Although use of warm water patches by salmonids during winter has been documented (Craig and Poulin 1975; Cunjak and Power 1986; Brown and McKay 1995), use of warm water patches during summer by migrating adult salmon has not been previously reported in the literature. Temperatures are more stable in thermal refuges created by thermal stratification or groundwater inputs than in surrounding river habitat that is more susceptible to diurnal heating and cooling cycles. Warm patch use could result from salmon remaining in refuges during periods when ambient river temperature decreases relative to refuge temperature. Alternatively, adults may actively seek out warm water patches when ambient river temperature is low. Regardless of the mechanism, warm patch use could enable adults to remain within an optimal temperature range, allowing them to balance energy conservation with gamete maturation, which can be slowed if temperature is too low (Berman and Quinn 1991; Newell and Quin 2005; Hasler et al. 2012). Taken together, the temperatures at which cool and warm patch use occurred in the Nord-Est suggest that adults may have a narrow optimal temperature range similar to that previously described to optimize growth in juvenile Atlantic salmon, i.e. approximately 16-20˚C (Elliott 1991; Jonsson and Jonsson 2009). Bull trout (*Salvelinus confluentus*) tagged with temperature-sensing V13 acoustic tags were found to occupy a narrow temperature range comparable to laboratory-derived optimal temperatures for growth and metabolism, despite a much broader range of temperatures available to free-swimming individuals in a British Columbia reservoir (Gutowsky et al. 2017). Sockeye salmon have also been observed using a narrow temperature range (9-11˚C) while over-summering in a stratified lake, despite the availability of warmer and cooler temperatures (Newell and Quinn 2005).

We observed a diurnal pattern in refuge use in the upstream sector of the Nord-Est. Cool refuge use was greatest in the afternoon and warm patch use was greatest in the early morning, corresponding to daily maximum and minimum water temperatures. Peak refuge use by rainbow trout (*O. mykiss*) in the Snake River (Oregon) drainage also occurred in the late afternoon when ambient temperature was greatest (Ebersole et al. 2001). Observations by Breau et al. 2007, however, indicated that aggregation of juvenile Atlantic salmon in cool refuges was influenced more by water temperature than by time of day. Observation of cool refuge use by Breau et al. (2007) was based on snorkel counts in one study reach, whereas our observations were based on near-continuous records of adult body temperature and river temperature, and spanned multiple potential refuges, which could explain the discrepancy between our findings and those of Breau et al. (2007). The absence of a clear diurnal pattern in the downstream sector is consistent with the observation that fish in the downstream sector exhibited less behavioural thermoregulation overall (Fig. 5.3).

Although cold water tributaries and confluence plumes served as important thermal refuges for adult salmonids in the much larger Columbia and Penobscot river systems, (Shepard 1995; Goinea et al. 2006; Keefer et al. 2009), the two confluence plumes in Nord-Est that were equipped with acoustic receivers did not serve as thermal refuges for adult Atlantic salmon. Mainstem discharge greatly influences confluence plume volume, which subsequently influences refuge carrying capacity (Gendron 2013). The monitored confluence plumes in the Nord-Est were shallow (≤ 1.5 m deep at river discharge of 21 m^3s^{-1} but ≤ 0.75 m deep when river discharge was 9 m^3s^{-1}). Discrete measurements made during August 2016 indicated that the cooling influence of confluence plumes did not extend more than 3 m from the mouth of each tributary, despite temperature differences between tributaries and the mainstem of 10-12˚C (Frechette, personal observation). Thus it is unlikely that shallower unmonitored confluence plumes were used as refuges. Our findings are similar to those of Baigun et al. (2000), who found that adult steelhead over-summering in Steamboat Creek (a mid-order stream in Oregon) did not use shallow (< 0.8 m) confluence plumes. Cool water confluence plumes in the Nord-Est, therefore, were likely too shallow to be used by adult Atlantic salmon for long-term behavioural thermoregulation (Torgersen et al. 1999; Baigun et al. 2000; Ebersole et al. 2001).

The most important thermal refuges used by over-summering Atlantic salmon adults in the Nord-Est were stratified alluvial pools (D3 and U8). Thermal stratification may form in pools where groundwater seeps or hyporheic flow is present, or in areas where channel morphology causes water velocity to slow sufficiently to prevent mixing throughout the water column (Nielsen et al. 1994). In the absence of mixing, surface water heats up during the day while bottom water maintains a relatively constant temperature. During the night, surface water cools and sinks to the bottom, maintaining a temperature gradient (Nielsen et al. 1994). Although mainstem alluvial pools are rarely stratified (Nielsen et al. 1994; Gendron 2013), pool U8 is unusually large relative to other pools in the Nord-Est. The pool inlet is shallower than the outlet, the maximum depth exceeds 6 m, and a gravel bar island in the centre of the pool may entrain cool bottom water, characteristics that are ideal for formation of thermal stratification via solar heating (Matthews et al. 1994; Nielsen et al. 1994; Gendron 2013).

We identified hyporheic flow associated with a small gravel bar near the head of pool U8 from the TIR imagery, which may enhance thermal stratification (Gendron 2013). At present, it is not possible to identify solar heating or hyporheic flow as the main mechanism producing thermal stratification in pool U8, however the temperature at the substrate was as much as 1.7˚C cooler than at the surface, which provides evidence of strong thermal stratification (Matthews et al. 1994; Gendron 2013). The source of thermal stratification in pool D3 is still under investigation, but is thought to result from resurgence of cool water originating in a cool tributary located upstream of the pool. Although the confluence plume was clearly evident in TIR images, surface evidence of the plume did not extend into pool D3. Regardless of the source of thermal stratification, pools D3 and U8 were extremely important to over-summering Atlantic salmon, a finding which corresponds with previous studies of thermal refuge use by steelhead and Chinook salmon (*Oncorhynchus tshawytscha*). Thermally stratified pools were the most heavily used pool type by summer-run steelhead in the Middle Fork Eel River, a river system in California that is comparable in size to the Nord-Est (Nielsen et al. 1994), and both over-summering spring run Chinook and summer-run steelhead disproportionately used pools as cool refuge habitat, relative to their availability in Oregon rivers (Torgersen et al. 1999; Baigun et al. 2000).

Deep pools with stable thermal refuges should allow individuals to thermoregulate with relatively little expenditure of energy (Berman and Quinn 1991). Adults holding in large pools may maintain a stable body temperature either by changing position in the pool or by remaining in a stable thermal refuge while ambient water temperature around the refuge changes throughout the day. Such behaviour would buffer adults from large temperature fluctuations associated with daily warming and cooling cycles in the river and allow them to retain valuable energy stores for spawning (Sutton et al. 2007; Hasler et al 2012). It must be noted, however, that temperature is not the only factor driving habitat selection during the in-river pre-spawning period. River discharge, proximity to spawning sites, season, and density of conspecifics may also influence choice of holding habitat. For example, large pools likely serve not only as thermal refuges, but also as hydraulic refuges, allowing fish to hold and maintain optimal temperature while waiting for discharge to increase and permit resumption of migration (Gendron 2013). Such pools are likely to be particularly important in shallow, gravel-bed rivers that are prone to low river discharge during the warmest periods of the summer when adult Atlantic salmon are present, and their abundance and location along a riverscape may influence migratory patterns of adult Atlantic salmon. Although we measured the maximum depths of the pools containing receivers, we did not make detailed measurements of physical habitat. A detailed characterization of available pools, confluence plumes, and intervening habitat would permit the effects of temperature to be disentangled from other factors that influence habitat choice by adults during in-river holding, and is the subject of on-going research in the Nord-Est.

Limitations inherent in our study give rise to potential improvements for future research. We based evidence of thermal refuge use on the difference between ambient river temperature and internal fish temperature. We selected river temperature monitoring sites in well-mixed areas of the river that were representative of mainstem temperature, therefore, choice of temperature monitoring sites was unlikely to overly influence our identification of the timing, location, and temperatures at which fish initiated behavioural thermoregulation. It is possible, however, that choice of temperature monitoring sites introduced a minor bias into our results (Torgersen et al. 1999). Such a bias could be mitigated by deploying multiple mainstem temperature loggers from which an average reach-specific ambient mainstem temperature could be calculated and used for identifying behavioural thermoregulation. Our study also represents a limited number of individuals tagged during one year in a medium-sized river that is relatively cool compared with more southerly rivers within the range of Atlantic salmon. Since thermal tolerance in salmon is related to the temperature at which they are acclimated (Elliott 1991), salmon populations in rivers that are warmer (or cooler) than the Nord-Est likely have different thresholds for initiation of thermal refuge use. Inter-annual differences in temperature regimes might also produce differences in thermal habitat use within a given river system. Additionally, refuge types that are important in large river systems (e.g. confluence pools) may be less important in smaller systems. Application of our methods in catchments of varying sizes across the range of Atlantic salmon and over multiple years would facilitate identification of refuge types and thresholds for behavioral thermoregulation under different hydrological and temperature conditions. This would further improve our understating of thermal habitat requirements of Atlantic salmon, which could prove invaluable in predicting responses of Atlantic salmon populations to climate change.

River temperatures are rising in northern latitude rivers within the range of Atlantic salmon, a trend that is expected to continue under current climate change projections (Ferrari et al. 2007; Webb and Nobilis 2007; van Vliet et al.2013). Although optimal temperature for adults likely differ among river systems due to different thermal regimes and acclimation temperatures, it is clear that adult salmon used a narrow temperature range and required access to cool refuges at much lower temperatures than are regularly measured in salmon rivers (Shepard 1995; Breau et al. 2007; Dugdale et al. 2016). Increased temperatures and reduced river discharge can serve as physical barriers to salmon migration, preventing adults from reaching the thermal refuges that are crucial to survival and energy maintenance when river temperatures become stressful (Torgersen et al. 1999; Hasler et al. 2012). Thus, the ability for adult salmon to access suitable holding pools and cool refuges will become even more important for maintaining populations in a warming climate because of the negative impacts of high temperature on survival and reproductive success. It is therefore imperative to identify, protect, and maintain connectivity among suitable thermal refuges in salmon rivers to ensure population persistence. Such protections may include controlling releases of water from dams on regulated rivers, restricting fishing and other human activities in refuges, and limiting groundwater extraction or other land use practices that reduce riverbed shading or groundwater inputs (Sutton et al. 2007; Breau and Caissie 2013; Kurylyk et al. 2015). In certain cases, enhancing existing thermal refuges or creating new refuges via channel modification or groundwater pumping may be warranted (Kurylyk et al. 2015). Presence of suitable adult thermal habitat is also essential for enhancement programs like the habitat expansion initiative currently in place on the Rivière Sainte-Marguerite Nord-Est, where adult salmon are introduced to previously inaccessible habitat via fish ladders or transport. Inventory of potential thermal refuges should therefore be included in feasibility studies before the implementation of such conservation translocation programs to ensure their success.

5.7 Acknowledgements

This work was supported by the «Programme de mise en valeur des habitats du saumon de la Côte-Nord» of the Fédération Québecoise du Saumon Atlantique and the Atlantic Salmon Conservation Foundation. Financial support for D. Frechette was provided by the Fonds de recherché du Québec - Nature et technologies (FRQNT) Merit Scholarship Program for Foreign Students. All animal handling protocols were approved by the INRS Institutional Committee for the Protection of Animals (CIPA Protocol 1406-03). The authors thank the Ocean Tracking Network for data hosting and archiving. We also thank the Quebec Minìstere de Faune, Fôrets, et Parcs, the Association de la Rivière Sainte-Marguerite, and the Corporation de Pêche Ste-Marguerite for their collaboration and support of this research. A. Boivin and the members of Team Filles (V. Maltais and J. Carrier) provided invaluable support in the field and made this project possible. Additional field help was provided by O. Flamand, S. Gravel, M. Murdock, R. Gagnon, M. St-Amour, T. Suskiewicz, and I. Bergeron. The authors also thank A. St-Hilaire and T. Suskiewicz for statistics advice, C. Narváez for assistance with figures, and M. Roy for aid with coding. We also thank M. Dionne for valuable feedback on an early draft, and the Associate Editor and two anonymous reviewers for their conscientious comments that greatly improved this manuscript.

6 BIBLIOGRAPHIE – CHAPITRE 5

Baigun, C.R., Sedell, J., Reeves, G. 2000. Influence of water temperature in use of deep pools by summer steelhead in Steamboat Creek, Oregon (USA). J. Freshwater Ecol. **15**(2): 269-279.

Baird, O.E., and Krueger, C.C. 2003. Behavioral thermoregulation of brook and rainbow trout: comparison of summer habitat use in an Adirondack River, New York. Trans. Am. Fish. Soc. **132**: 1194–1206.

Berman, C. H., and Quinn, T.P. 1991. Behavioural thermoregulation and homing by spring chinook salmon, *Oncorhynchus tshawytscha* (Walbaum), in the Yakima River. J. Fish. Biol. **39**: 301–312.

Bilby, R.E. 1984. Characteristics and frequency of cool-water areas in a western Washington stream. J. Freshwater Ecol. **2**: 593–602.

Boyer, C., St-Hilaire, A., Bergeron, N.E., Daigle, A., Curry, R.A., and Caissie, D. 2016. RivTemp: A water temperature network for Atlantic salmon rivers in eastern Canada. Water News. **35**: 10–15.

Breau, C. 2013. Knowledge of fish physiology used to set water temperature thresholds for in-season closures of Atlantic salmon (*Salmo salar*) recreational fisheries. Canadian Science Advisory Secretariat, Research Document 2012/163, Department of Fisheries and Oceans, Moncton, N.B.

Breau, C., and Caissie, D. 2013. Adaptive management strategies to protect Atlantic salmon (*Salmo salar*) under environmentally stressful conditions. Canadian Science Advisory Secretariat, Research Document 2012/164, Department of Fisheries and Oceans, Moncton, N.B.

Breau, C., Cunjak, R.A., and Bremset, G. 2007. Age-specific aggregation of wild juvenile Atlantic salmon *Salmo salar* at cool water sources during high temperature events. J. Fish. Biol. **71**: 1179–1191. doi:10.1111/j.1095-8649.2007.01591.x.

Brett, J.R. (1956). Some Principles in the Thermal Requirements of Fishes. The Quarterly Review of Biology. **31**(2): 75–87.

Brewitt, K.S., and Danner, E.M. 2014. Spatio-temporal temperature variation influences juvenile steelhead (*Oncorhynchus mykiss*) use of thermal refuges. Ecosphere. **5**(7): 1–26. doi:10.1890/es14-00036.1.

Brown, R.S., and W.C. Mackay. 1995. Fall and winter movements of and habitat use by cutthroat trout in the Ram River, Alberta. Trans. Am. Fish. Soc. **124**: 873–885.

Campbell, H.A., Watts, M.E., Dwyer, R.G., Franklin, C.E. 2012. V-Track: software for analysing and visualising animal movement from acoustic telemetry detections. Mar. Freshwater Res. **63**: 815–820.

Canty, A. and Ripley, B. 2017. boot: Bootstrap R (S-Plus) Functions. R package version 1.3-19.

Craig, P.C. and Poulin, V.A. 1975. Movements and growth of Arctic grayling (Thymallus arcticus) and juvenile Arctic char (Salvelinus alpinus) in a small Arctic stream, Alaska. J. Fish. Res. Board Can. **32**(5): 689–697. doi: 10.1139/f75-088.

Cunjak, R.A., and G. Power. 1986. Seasonal changes in the physiology of brook trout, **Salvelinus fontinalis** (Mitchill) in a sub-Arctic river system. J. Fish. Biol. **29**(3): 279–288.

Cunjak, R.A., Roussel, J.M., Gray, M.A., Dietrich, J.P., Cartwright, D.F., Munkittrick, K.R., and Jardine, T.D. 2005. Using stable isotope analysis with telemetry or mark-recapture data to identify fish movement and foraging. Oecologia. **144**: 636–646. doi:10.1007/s00442-005-0101-9.

Davison, A.C. and Hinkley, D.V. 1997. Bootstrap Methods and Their Applications. Cambridge University Press, Cambridge. ISBN 0-521-57391-2.

Donaldson, M.R., Cooke, S.J., Patterson, D.A., Hinch, S.G., Robichaud, D., Hanson, K.C., Olsson, I., Crosson, G.T., English, K.K. and Farrell, A.P. 2009. Limited behavioural thermoregulation by adult upriver-migrating sockeye salmon (*Oncorhynchus nerka*) in the Lower Fraser River, British Columbia. Can. J. Zool. **87**: 480–490. doi:10.1139/z09-032.

Dugdale, S.J. 2016. A practitioner's guide to thermal infrared remote sensing of rivers and streams: recent advances, precautions and considerations. Wiley Interdisciplinary Reviews: Water. **3**: 251–268. doi:10.1002/wat2.1135.

Dugdale, S.J., Bergeron, N.E., and St-Hilaire, A. 2013. Temporal variability of thermal refuges and water temperature patterns in an Atlantic salmon river. Remote Sens. Environ. **136:** 358–373. doi:10.1016/j.rse.2013.05.018.

Dugdale, S.J., Franssen, J., Corey, E., Bergeron, N.E., Lapointe, M., and Cunjak, R.A. 2016. Main stem movement of Atlantic salmon parr in response to high river temperature. Ecol. Freshw. Fish. **25**(3): 429–445. doi:10.1111/eff.12224.

Ebersole, J.L., Liss, W.J., and Frissell, C.A. 2001. Relationship between stream temperature, thermal refugia and rainbow trout *Oncorhynchus mykiss* abundance in arid-land streams in the northwestern United States. Ecol. Freshw. Fish. **10**: 1–10.

Ebersole, J.L., Liss, W.J., and Frissell, C.A. 2003. Cold water patches in warm streams: Physicochemical characteristics and the influence of shading. J. Am. Water Resour. Assoc. **39**: 355–368.

Efron, B. and Tibshirani, R. 1993. An Introduction to the Bootstrap. Chapman and Hall, New York, NY.

Elliott, J.M. 1991. Tolerance and resitance to thermal stress in juvenile Atlantic salmon, *Salmo salar*. Freshwater Biol. **25**: 61–70.

Elliott, J.M., and Elliott, J.A. 2010. Temperature requirements of Atlantic salmon *Salmo salar*, brown trout *Salmo trutta* and Arctic charr *Salvelinus alpinus*: predicting the effects of climate change. J. Fish. Biol. **77**: 1793–1817. doi:10.1111/j.1095-8649.2010.02762.x.

Ferrari, M.R., Miller, J.R. and Russell, G.L. 2007. Modeling changes in summer temperature of the Fraser River during the next century. Journal of Hydrology. **342**: 336–346.

Gendron, J.-F. 2013. Physical controls on summer thermal refuges for salmonids in two gravel-cobble salmon rivers with contrasting thermal regimes: the Ouelle and Ste-Marguerite Rivers. M.Sc. thesis, Department of Geography, McGill University, Montreal, QC.

Gibson, R.J. 1966. Some factors influencing the distributions of brook trout and Atlantic salmon. J. Fish. Res. Board Can. **23**: 1977–1980.

Gilhousen P. 1980. Energy sources and Expenditures in Fraser River sockeye salmon during their spawning migration. IPSFC Bulletin XXII. New Westminster, B.C.

Goniea, T.M., Keefer, M.L., Bjornn, T.C., Peery, C.A., Bennett, D.H., and Stuehrenberg, L.C. 2006. Behavioral thermoregulation and slowed migration by adult fall Chinook salmon in response to high Columbia River water temperatures. Trans. Am. Fish. Soc. **135**: 408–419. doi:10.1577/t04-113.1.

Gutowsky, L.F.G., Harrison, P.M., Martins, E.G., Leake, A., Patterson, D.A., Zhu, D.Z., Power, M. and Cooke, S. J. 2017. Daily temperature experience and selection by adfluvial bull trout (*Salvelinus confluentus*) [online]. Environ. Biol. Fishes. doi:10.1007/s10641-017-0634-x.

Hasler, C.T., Cooke, S.J., Hinch, S.G., Guimond, E., Donaldson, M.R., Mossop, B., and Patterson, D.A. 2012. Thermal biology and bioenergetics of different upriver migration strategies in a stock of summer-run Chinook salmon. J. Therm. Biol. **37**: 265– 272. doi:10.1016/j.jtherbio.2011.02.003.

Hillyard, R.W., and Keeley, E.R. 2012. Temperature-related changes in habitat quality and use by Bonneville cutthroat trout in regulated and unregulated river segments. Trans. Am. Fish. Soc. **141**: 1649–1663. doi:10.1080/00028487.2012.717517.

Huntsman, A.G. 1942. Death of salmon and trout with high temperature. J. Fish. Res. Board Can. **5**: 485–501.

Jonsson, B., and Jonsson, N. 2009. A review of the likely effects of climate change on anadromous Atlantic salmon *Salmo salar* and brown trout *Salmo trutta*, with particular reference to water temperature and flow. J. Fish. Biol. **75**: 2381–2447. doi:10.1111/j.1095-8649.2009.02380.x.

Kaya, C.M., Kaeding, L.R., and Burkhalter, D.E. 1977. Use of a cold-water refuge by rainbow and brown trout in a geothermally heated stream. The Progressive Fish-Culturist, **39**(1): 37-39. doi:10.1577/1548-8659(1977)39[37:uoacrb]2.0.co;2.

Keefer, M.L., Peery, C.A., and High, B. 2009. Behavioural thermoregulation and associated mortality trade-offs in migrating adult steelhead (*Oncorhynchus mykiss*): variability among sympatric populations. Can. J. Fish. Aquat. Sci. **66**: 1734–1747. doi:10.1139/f09-131.

Kurylyk, B.L., MacQuarrie, K.T.B., Linnansaari, T., Cunjak, R.A., & Curry, R.A. 2015. Preserving, augmenting, and creating cold-water thermal refugia in rivers: concepts derived from research on the Miramichi River, New Brunswick (Canada). Ecohydrology. **8**: 1095–1108.

Maisse, G.,L., B.J., Landry, G., Caron, F., and Rouleau, A. 1988. Identification externe du sexe chez le Saumon atlantique (*Salmo salar* L.). Can. J. Zool. **66**: 2312–2315.

Matthews, K.R., Berg, N H., Azuma, D.L., and Lambert, T.R. 1994. Cool water formation and trout habitat use in a deep pool in the Sierra Nevada, California. Trans. Am. Fish. Soc. **123**(4): 549–564. doi:10.1577/1548-8659(1994)123<0549:cwfath>2.3.co;2.

Newell, J.C., & Quinn, T.P. 2005. Behavioral thermoregulation by maturing adult sockeye salmon (*Oncorhynchus nerka*) in a stratified lake prior to spawning. Can. J. Zool. **83**(9): 1232–1239. doi:10.1139/z05-113.

Nielsen, J.L., Lisle, T.E., and Ozaki, V. 1994. Thermally stratified pools and their use by steelhead in northern California streams. Trans. Am. Fish. Soc. **123**: 613–626.

Pörtner, H.O., and Farrell, A.P. 2008. Physiology and Climate Change. Science. **322**: 690–692. doi:10.1126/science.1163156.

Prévost, E., Vauclin, V., Baglinière, J.L., Brana-Vigil, F., and Nicieza, A.G. 1991. Application d'une méthode de détermination externe du sexe chez le Saumon atlantique (*Salmo salar* L.) dans les rivières des Asturies (Espagne). Bulletin Français de la Pêche et de la Pisciculture. **323**: 149–159. doi:10.1051/kmae:1991002.

R Core Team. 2014. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. Available from http://www.R-project.org/ [accessed 15 June 2017].

R Studio Team. 2016. RStudio: Integrated Development for R. RStudio, Inc., Boston, MA. Available from http://www.rstudio.com/ [accessed 15 June 2017].

Shepard, S.L. 1995. Atlantic salmon spawning migrations in the Penobscot River, Maine: fishways, flows, and high temperatures. M.Sc.thesis, University of Maine, Orono, Maine.

Sutton, R.J., Deas, M.L., Tanaka, S.K., Soto, T., and Corum, R.A. 2007. Salmonid observations at a Klamath River thermal refuge under various hydrological and meteorological conditions. River Research and Applications. **23**: 775–785. doi:10.1002/rra.1026.

Tanaka, H., Takagi, Y., and Naito, Y. 2000. Behavioural thermoregulation of chum salmon during homing migration in coastal waters. J. Exp. Biol. **203**: 1825–1833.

Torgersen, C.E., Price, D.M., Li, H.W., and McIntosh, B.A. 1999. Multiscale thermal refugia and stream habitat associations of Chinook salmon in northeastern Oregon. Ecological Applications, **9**: 301–319.

Torgersen, C.E., Faux, R.N., McIntosh, B.A., Poage, N.J., and Norton, D.J. 2001. Airborne thermal remote sensing for water temperature assessment in rivers and streams. Remote Sensing of Environment, **76**: 386-398.

Torgersen, C.E., Ebersole, J.L., and Keenan, D.M. 2012. Primer for identifying cold-water refuges to protect and restore thermal diversity in riverine landscapes. EPA 910-C-12-001, United States Environmental Protection Agency, Seattle, WA.

van Vliet, M.T.H., Franssen, W.H.P., Yearsley, J.R., Ludwig, F., Haddeland, I., Lettenmaier, D.P. and Kabat, P. 2013. Global river discharge and water temperature under climate change. Global Environmental Change **23**: 450–464.

Webb, B.W. and Nobilis, F. 2007. Long-term changes in river temperature and the influence of climatic and hydrological factors. Hydrol. Sci. J. **52**: 74–85.

Wilkie, M.P., Brobbel, M.A., Davidson, K., Forsyth, L., and Tufts, B. L. 1997. Influences of temperature upon the postexercise physiology of Atlantic salmon (*Salmo salar*). Can. J. Fish. Aquat. Sci. **54**: 503–511.

Zuur, A.F., Saveliev, A.A., Ieno, E.N., and Smith, G.M. 2009. Mixed Effects Models and Extensions in Ecology with R. Springer , New York, N.Y

7 ATLANTIC SALMON MOVEMENT PATTERNS AND HABITAT USE DURING COLONIZATION

Title of Article: **Evolution and environment shape Atlantic salmon movement patterns and habitat use during colonization of novel habitat**

Titre de l'article : **Les patrons de déplacement et l'utilisation de l'habitat des saumons atlantique lors de la colonisation d'un nouvel habitat sont modulés par l'évolution et l'environnement**

Authors and affiliations:
[1]Danielle M. Frechette
[2] Mélanie Dionne (Melanie.Dionne@mffp.gouv.qc.ca)
[3]Julian J. Dodson (Julian.Dodson@bio.ulaval.ca)
[1]Normand E. Bergeron (Normand.Bergeron@ete.inrs.ca)

1. Institut National de Recherche Scientifique, Centre Eau Terre Environnement, Québec, Canada
2. Ministère des Forêts, de la Faune et des Parcs, Direction de la faune aquatique, Québec, Canada
3. Université Laval, Québec, Canada

This chapter is ready for submission in the journal Ecological Applications

Contributions of authors:
The authors together conceived the research program to use acoustic telemetry to evaluate habitat use and movements of adult Atlantic salmon transported into novel habitat, and wrote the initial grant application to receive the primary funding for the research program. N. Bergeron and D. Frechette wrote a grant application to obtain additional funding for the fieldwork. D. Frechette organized and conducted the fieldwork, data processing, data analysis, and original writing. M. Dionne, N. Bergeron, and J. Dodson provided guidance regarding the design of the field study. N. Bergeron and J. Dodson provided guidance regarding the data analyses and outline of the manuscript. N. Bergeron, J. Dodson, and M. Dionne provided valuable comments on initial drafts of the manuscript, which greatly improved the final submission.

7.1 Résumé

La réintroduction d'espèces et la migration assistée, associés à la biologie de la conservation, sont des outils utilisés pour prévenir ou inverser l’extinction d'espèces. Les salmonidés anadromes ont décliné sur une grande partie de leur aire de répartition mondiale. Ils font l'objet de programmes de restauration dans le cadre desquels une intervention humaine permet aux adultes de recoloniser des habitats précédemment occupés (réintroduction) ou d’en coloniser de nouveaux (migration assistée). Une application réussie de ces techniques pour les salmonidés nécessite une compréhension approfondie de la manière dont les adultes utilisent l'espace lors de la colonisation afin de garantir l’atteinte des résultats visés par ces programmes. Nous avons utilisé la télémétrie acoustique pour examiner les déplacements et l'utilisation de l'habitat par le saumon atlantique adulte lors de la colonisation d'un nouvel habitat dans une rivière de l'est du Canada, en fonction des conditions environnementales et des caractéristiques intrinsèques du poisson. Des adultes en phase de montaison ont été capturés et transportés par camion en amont d'une chute infranchissable, où ils ont été relâchés dans un nouvel habitat (auparavant inoccupé par le saumon atlantique). La probabilité de déplacements a été plus faible pendant l'été, ce qui coïncide avec des périodes d’occupation de fosses par certains individus lors d'événements avec une température de l’eau élevée et de faibles débits. La température de la rivière, le débit et le jour de l'année influencent la prédiction de la rétention du saumon dans des bassins. La taille du bassin est la caractéristique physique la plus importante pour identifier un habitat de rétention « convenable ». Les femelles se déplacent moins que les mâles, peu importe la température ou le débit de la rivière. Ce comportement leur permet de conserver l'énergie nécessaire au développement des gonades et à la construction du nid, maximisant ainsi le potentiel de reproduction. En ce qui concerne les mâles, ces derniers, ont une plus grande probabilité de mouvements et se déplacent sur de plus grandes distances (comportement « exploratoire ») quand les températures diminuent, sauf en périodes de forts débits. Ce comportement, moins de mouvements pendant les chaleurs estivales et plus de mouvements à des températures plus basses, permet aux mâles de conserver leur énergie et d'éviter la mortalité à haute température, tout en augmentant les possibilités d'accouplement grâce à une recherche plus active des femelles durant la période de frai. Les schémas de mouvements observés reflètent différentes stratégies d'évolution utilisées par chaque sexe pour optimiser la capacité de reproduction. Puisque le comportement de frai est hautement préservé chez les espèces de salmonidés, ces résultats peuvent 1) fournir une image générale de la manière dont le saumon atlantique utilise l'espace pendant la colonisation d'un habitat inoccupé et 2) être utilisés pour optimiser les programmes de réintroduction et de migration assistée.

7.2 Abstract

Species reintroduction and assisted migration are tools used in conservation biology to prevent or reverse species extinctions. Anadromous salmonids have declined throughout much of their global range and are the subject of restoration programs, whereby human intervention allows adults to colonize previously occupied (reintroduction) or novel (assisted migration) habitat. Successful application of these techniques to salmonid restoration require a thorough understanding of how adult salmon use space during colonization to ensure that programs achieve desired outcomes. We applied acoustic telemetry to examine movements and habitat use of adult Atlantic salmon during colonization of novel habitat in an eastern Canadian river in relation to environmental conditions and intrinsic fish characteristics. Returning adults were captured and transported by truck upstream of an impassible waterfall, where they were released into novel habitat (previously unoccupied by Atlantic salmon). The probability of salmon movement was lower during the summer, coincident with individuals holding in pools during high heat/low discharge events. River temperature, discharge, and day of year were influential in predicting whether salmon held in pools, and pool size was the most important physical characteristic identifying “suitable” holding habitat. Females moved less than males regardless of river temperature or discharge, a behavior that should allow females to conserve energy to dedicate to gonad development and nest building, thereby maximizing reproductive potential. Males had a greater probability of movement as temperature decreased, and engaged in more extensive movements (“exploratory” behavior) except at elevated temperature and discharge. Less movement during summer heat events and more movement at cooler temperature should enable males to conserve energy and avoid mortality at high temperature, while increasing mating opportunities through more active searching for females during the spawning period. It is suggested that the observed movement patterns reflect different evolutionary strategies employed by each sex to maximize reproductive fitness. Because spawning behavior is highly conserved within salmonid species, these findings may 1) provide a generalized picture of how Atlantic salmon use space during colonization of unoccupied habitat and 2) be used to optimize future reintroduction and assisted migration programs.

7.3 Introduction

Species reintroduction and assisted migration are practices in conservation biology that are used to prevent or reverse species extinctions (Seddon et al. 2007, Hewitt 2011, Thomas 2011). In reintroduction, captive-bred or wild-caught individuals are translocated into habitat from which the species was previously extirpated. Species reintroductions were first implemented at least as early as the beginning of the twentieth-century and have been applied to a wide range of taxa, (including birds, mammals, and fishes), and gave rise to the field of reintroduction biology (Wolf et al. 1996, Seddon et al. 2007, Dunham et al. 2011). Assisted migration can be considered an extension of reintroduction biology, with a key difference. In species reintroductions, individuals of a species are reintroduced into unoccupied habitat within the historic range of the species, whereas in assisted migration, species are allowed to colonize habitat outside of the historic range (Hewitt 2011). Assisted migration has been proposed as a means (albeit controversial) of mitigating the effects of climate change on species distributions and has been investigated for use in plants, insects, birds, mammals, fish, and amphibians (Hewitt 2011, Thomas 2011).

Reintroduction programs and assisted migration are tools that can be used to aid recovery of depleted salmonid populations (Anderson et al. 2014, Pess et al. 2011, Pess et al. 2012). Salmonid populations have decreased dramatically throughout much of their global range due to “death by a thousand cuts”: over-harvest, loss and degradation of freshwater habitat, construction of dams that block access to spawning and rearing habitat, competition and hybridization with hatchery-reared salmon, and decreased survival in the ocean related to changes in the marine ecosystem (National Resource Council 1996, Gustafson et al. 2007, Jonsson and Jonsson 2011, ICES 2018). In salmon reintroduction programs, access is facilitated to habitats previously used by salmon that are no longer accessible because dams or other anthropogenic features block access to upstream spawning and rearing areas (Anderson et al. 2014). In assisted migration, (hereafter referred to as “colonization”), salmon are given access to portions of rivers that have appropriate spawning and rearing habitat, but are historically inaccessible to upstream migrating adults because of natural barriers to migration, e.g. large waterfalls (Bryant et al. 1999). Introduction of adults to previously inaccessible habitat can enhance population productivity by allowing the breeding population to expand into unoccupied, high quality habitat, thereby reducing density-dependent negative effects on juvenile growth and survival (Pess et al. 2011, Anderson et al. 2014). The primary methods used to accomplish reintroduction and colonization programs for salmon are volitional passage and translocation. In volitional passage, the migration barrier is removed or altered in such a way (e.g. through installation of a fish ladder or fish lift) that allows upstream migrating salmon to pass the obstruction at their own pace to reach spawning habitat (Bryant et al. 1999, Pess et al. 2011, Pess et al. 2012, Izzo et al. 2016). Translocation of fish entails physical transport of fish via truck or barge and often is referred to as “trap and haul”, because of the practice of trapping fish at a migratory barrier and "hauling" them upstream in a tank (Anderson et al. 2014).

Without a detailed understanding of how salmon exploit the novel habitat during colonization, however, reintroduction and colonization programs may not achieve the desired outcome of enhancing population productivity. Migration and habitat use by adult salmonids are influenced by a variety of extrinsic and intrinsic factors. River hydrology and geomorphological features shape river habitat and influence spawning migrations by affecting the difficulty of upstream passage, thus determining the time and energy it takes to reach spawning grounds (Milner et al. 2012). Such features also may limit availability of suitable holding pools, where salmon rest and recover before continuing migration (Bardonnet and Bagliniere 2000, Milner et al. 2012). Because salmon metabolic rate increases with temperature, individuals incur increased travel costs at elevated river temperature (Martin et al. 2015). Such additional energy costs can reduce reproductive success, either through a within-season reduction in energy stores allocated to spawning activity and/or gonad development, or by increasing post-spawning mortality in iteroparous species, thereby preventing subsequent spawning (Thorstad et al. 2008). Fish sex, size, and proximity to the spawning season also may affect an individual's migration pattern (Baglinière et al. 1990, Baglinière et al. 1991, Dahl et al. 2004, Thorstad et el. 2008, Richard et al. 2014). Consequently, determining how biotic and abiotic factors affect movement patterns and habitat use during colonization is essential to the success of reintroduction and assisted migration programs designed to enhance and protect salmon populations (Thorstad et al. 2008).

Despite many studies of upstream migration of returning adults, a general mechanism for predicting the migratory response of salmon to environmental variables has not yet been developed (Thorstad et al. 2008, Bendall et al. 2012). Links between migration patterns and environmental variables are likely river- and context-specific, and relationships between environmental variables themselves are complex and often correlated (Jonsson 1991, Bendall et al. 2012, Martin et al. 2015). Differences in methods (e.g. counts at fish ladders vs. telemetry) used to examine the effects of environmental variables on migration make comparison among studies difficult, and studies carried out in regulated rivers will not necessarily be representative of conditions experienced by salmon in freely-flowing, natural river systems (Thorstad et al. 2008, Bendall et al. 2012). Further, adult salmon use olfactory cues generated by the chemical composition of natal river water and from the presence of conspecifics (juveniles or other adults) to navigate during in-river migration (Hasler et al. 1978, Quinn et al. 1983, Bett and Hinch 2015). Thus, the absence of such cues in novel habitat may also influence how salmon use habitat during reintroduction and colonization.

The objective of our study was to examine migration patterns and habitat use by adult Atlantic salmon (*Salmo salar*) during the colonization of novel habitat. The Atlantic salmon is an iteroparous salmonid that occurs in temperate and subarctic watersheds draining into the Atlantic Ocean (Thorstad et al. 2011). Historically, Atlantic salmon ranged from southern New England (USA) to Ungava Bay (Canada) in North America and from Portugal to Russia in Europe, however, many stocks currently are listed as endangered or extirpated (COSEWIC 2010, Thorstad et al. 2011). Atlantic salmon hatch from eggs in freshwater where they remain for one to several years before undergoing physiological changes that enable them to migrate to the ocean. After spending one to four years at sea, adult Atlantic salmon return to freshwater to spawn (Jonsson and Jonsson 2011). Although the majority of Atlantic salmon return to their natal river (between 97-99%), a small proportion of the returning adults stray into other river systems (Fleming 1996). Even such a low degree of straying enables salmon to colonize new habitats as they become available, for example, with glacial retreat (Schoen et al. 2017). This propensity to stray into new habitat makes Atlantic salmon an excellent candidate for population enhancement via reintroduction and colonization, and such programs are being adopted as a strategy to preserve and enhance Atlantic salmon populations (Anderson et al. 2014, Askling 2015, Izzo et al. 2016). Consequently, a concerted effort is needed to understand how individuals use novel habitat during colonization so as to best optimize new programs.

Atlantic salmon exhibit premature migration, meaning they enter rivers many months before spawning (Power 1981, Jonsson et al. 1990, Fleming et al. 1996, Klemetsen et al. 2003). In Eastern Canada, salmon enter rivers in an immature state between June and August. The maturation process occurs during the long in-river residence period, in preparation for spawning in October and November (Stabell 1984, Scott and Scott 1988). Because adult Atlantic salmon fast while in freshwater, it is likely that there is some adaptive advantage to premature migration that must outweigh additional foraging opportunities that would occur if salmon remained in the ocean until closer to the onset of spawning (Fleming 1996, Thorstad et al. 2005). Although the adaptive advantages of premature migration remain largely understudied and unknown, the extended in-river residence means that Atlantic salmon colonizing novel habitat will be exposed to a wide range of environmental conditions that affect movement patterns and habitat use (Erkinaro et al. 1999, Økland et al. 2001, Karppinen et al. 2004, Martin et al. 2015).

In this study, we linked Atlantic salmon movement patterns and habitat use with intrinsic fish characteristics and extrinsic environmental conditions experienced during colonization in a free-flowing river. Our specific questions were two-fold. First, we asked: how do salmon movement patterns vary in response to environmental conditions (river temperature, river discharge, season, diel period) and fish characteristics (sex and size) during colonization? Second, we asked: what physical characteristics (e.g. surface area, depth) make a pool suitable for holding by adults during in-river residence and does the use of pools change as a function of environmental factors (e.g. river temperature and discharge). We addressed these questions using acoustic telemetry to continuously track movements of adult Atlantic salmon that were translocated via trap-and-haul into novel habitat upstream of impassible waterfalls on the north east branch of the Sainte-Marguerite River (Rivière Sainte-Marguerite Nord-Est) in the province of Québec (Canada) during the course of three years. We simultaneously measured river temperature and discharge, and obtained discrete measures of the characteristics of individual fish and pools. Resulting telemetry records provided positions of salmon from release into the novel habitat until the onset of spawning at extremely high spatial and temporal resolution, which could be linked with environmental data. We applied generalized linear mixed modeling and machine learning to determine the key variables driving salmon movements in novel habitat and obtain a detailed picture of how adult Atlantic salmon use habitat during colonization.

7.4 Methods

7.4.1 Study Area

The Rivière Sainte-Marguerite Nord-Est (hereafter, Nord-Est) is a salmon river in the province of Québec, Canada that drains a catchment of approximately 1000 km^2. It joins the Rivière Sainte-Marguerite 5 km upstream of its confluence with the Saguenay Fjord. Prior to 1981, anadromous Atlantic salmon had access to 7 km of river habitat before further upstream passage was blocked by an impassible waterfall (Chute Blanche). The installation of a fish ladder at Chute Blanche in 1981-1982 now allows returning adults access to an additional 18 kilometers of river habitat (Fig. 1). Further upstream passage is blocked by a pair of impassable waterfalls at rkm 33.7 (Chute du 16 Miles) and rkm 36.2 (Chute du 18 Miles).

In 2014, a three-year program was initiated to capture a subset of the adult salmon returning to the Chute Blanche fish ladder for transport into the inaccessible habitat upstream of the impassible falls. The objective of this program was to increase the population productivity of the river by reducing density-dependent effects on juvenile growth and survival (Pess et al. 2011, Anderson et al. 2014). Transported adults would be able to access between 13 and 27.5 kilometers of river, depending on whether they could ascend the waterfalls Chute André and Chute du 30 Miles (Fig. 7.1). The ultimate upstream end of the potential novel habitat is a large, impassible waterfall (Chute du 35 Miles). The transport program afforded an ideal opportunity to use telemetry to examine movement patterns and habitat use by adult Atlantic salmon during the process of colonizing novel habitat.

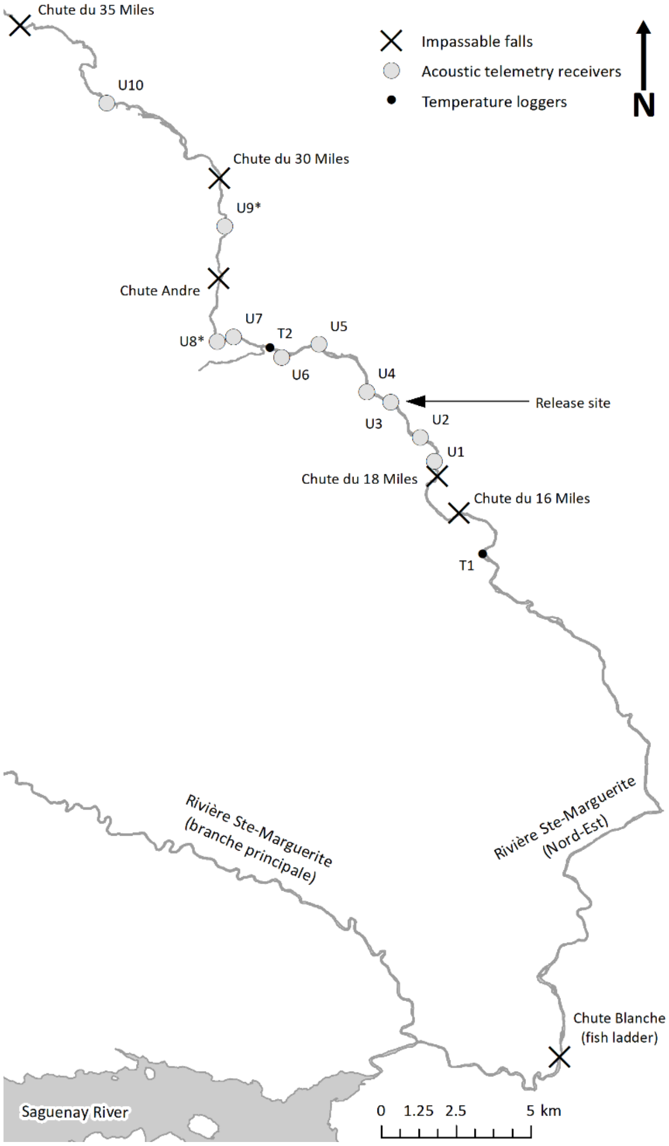


Figure 7.1 : Telemetry array used to track salmon movements

Impassable waterfalls are denoted with an X, temperature monitoring locations are denoted with a solid black circle, acoustic receivers are denoted by solid grey circles, and the release site is marked with an arrow.

7.4.2 Transport and tagging

All Atlantic salmon that enter the Chute Blanche fish ladder first arrive in a capture cage, which permits a count of the annual salmon run and length estimates of all individuals. Salmon were captured for transport either directly from the capture cage using a soft mesh net or via a retention cage that was installed in the fish ladder during 2015. The retention age allowed salmon that entered the fish ladder in the evening (between 18:00 and 21:00) to be held overnight for transport the next morning. Salmon were held in the retention cage for no more than 12 hours and were transported within one hour of sunrise.

Salmon were transported by truck in a 1600-L tank supplied with recirculating water and an oxygen delivery system. Water temperature and dissolved oxygen in the tank were measured continuously during transport using an EcoSense DO200A probe (YSI Incorporated, Yellow Springs, Ohio). Oxygen delivery was adjusted if the oxygen saturation (% O_2) exceeded 150% or dropped below 80% and blocks of ice were added if tank temperature approached 20°C or if the temperature difference between the river and the tank was greater than 2°C upon departure from the fish ladder. No transports were conducted if water temperature exceeded 20°C and no more than four salmon were transported at a given time.

We surgically implanted all transported salmon with an acoustic transmitter (Vemco V13–H, 13 mm diameter, 6 g in water) before release into the novel habitat. The average tag body burden of 0.24% (SD = 0.13%) was much less than the maximum recommended tag body burden of 2% (Winter 1983, Thorstad et al. 2000). We anesthetized individuals in a bath containing acetyleugenol (30 mg L^{-1}). Dosage time increased with decreasing water temperature (mean = 267 sec; SD = 73 sec). Once the salmon was adequately anesthetized (determined by gill respiration rate and strength of the reflex response), it was transferred to a V-shaped surgery table for tagging. We administered water and a maintenance dose of acetyleugenol (15 mg L^{-1}) over the gills during tagging via a custom-designed reservoir. The acoustic tag was inserted into the intraperitoneal cavity through an incision placed anterior to the pelvic girdle (lateral to the ventral midline). The incision was closed using three or four simple interrupted sutures and aseptic technique was followed throughout the tagging procedure.

We measured fish fork length (FL: distance from the snout to the end of the middle caudal fin rays) and mass while salmon were anesthetized. Salmon may return to the river after one winter at sea (termed one-sea-winter salmon, 1SW) or after multiple winters at sea (termed multi-sea-winter salmon, MSW salmon). The distinction between 1SW and MSW salmon is made based on size: MSW salmon are those individuals with FL > 63 cm, whereas 1SW salmon have a FL < 63 cm (DFO Science 1998). We separated 1SW and MSW individuals when comparing fish size, however, we combined 1SW and MSW individuals and used FL as continuous explanatory variable in statistical analyses.

We visually determined sex in the field using morphological features (body depth, position of the maxillary relative to the eye, presence or absence of a kype in later-returning salmon). Sex identification made in the field was verified using measurements of maxillary length and published regressions relating fork length to maxillary length (Massie et al. 1988, Prevost et al. 1991). The established regression relationships did not apply to 1SW salmon, therefore, we assumed that all transported 1SW salmon were males because most had evidence of a prominent kype and males comprise nearly 95% of 1SW salmon in the province of Quebec (Dionne et al. 2015). We attempted to transport an equal number of males and females into the novel habitat, to mimic sex ratios in Quebec salmon rivers and maximize effective population size (Foose et al. 1986, O'Reilly and Kozfkay 2014, Dionne et al. 2015).

Following tagging, salmon were transferred to a water-filled stretcher and moved to an in-river recovery cage. The recovery cage was equipped with a door that was opened once the fish was upright and swimming freely, allowing the fish to exit the cage without further handling. If salmon remained in the cage one hour after release, they were evaluated and either given more time for recovery or, more frequently, released by hand. All animal handling protocols were approved by the INRS Institutional Committee for the Protection of Animals (CIPA Protocol 1406-03).

7.4.3 Telemetry and Environmental Monitoring

We tracked movements of tagged salmon using an array of acoustic receivers (VR2W, Vemco, Halifax, NS) deployed in pools > 0.5 m depth (Fig. 7.1). Range testing conducted during 2014 indicated that 95% of tag emissions were detected at a distance of 40 m, and 80% of tag emissions were detected at a distance of 200 m under calm conditions (Frechette et al. 2018). We observed a reduction in detection range when river discharge exceeded 60 m^3s^{-1} and during discrete rainfall events, however, redundancy produced by the combination of high frequency of signal transmission (every 30 to 90 sec) and long-term monitoring at fixed locations allowed us to successfully track salmon movements, even at the greatest river discharge recorded during the study (167 m^3s^{-1}).

The number of receivers in the array increased with each year of the study, however, a core network of eight receivers were deployed each year in the novel habitat, from which movement data were analysed. A receiver placed upstream of Chute du 30 Miles was used to determine whether salmon passed both Chute André and Chute du 30 Miles. During 2015, we deployed a receiver upstream of Chute André to assess whether salmon passed this waterfall. The access to the site was extremely challenging, thus we only deployed this receiver during 2015. Receivers were deployed before the first transport occurred each year and were recovered during the spawning season in October before snow and ice formation (23 Oct 2014, 20 Oct 2015, and 31 Oct 2016). We extracted raw telemetry data from receivers using VUE software (Vemco, Halifax, NS) and processed it using the VTrack package for R (Campbell et al. 2012).

River temperature and discharge were recorded at 15-min intervals throughout the study. We obtained river temperature measurements from a temperature logger (HOBO UA-002-64, Onset, Bourne, MA) deployed by the RivTemp Network (Boyer et al. 2016) in a shallow, well-mixed area of the river downstream of Chute du 16 (T1, Fig. 7.1). Logging station T1 provided the most complete temperature time series for the Nord-Est for the three study years. It was deemed to be an adequate representation of the thermal regime experienced by adults in the novel habitat, based on the fit of a linear regression between logger T1 and T2, a temperature logger deployed in the novel habitat (Adjusted $R^2 = 0.92$, $P < 0.01$). We obtained river discharge measurements from the Centre d’expertise hydrique du Québec (CEHQ) station 062803 (48.267962N, -69.908823W).

7.4.4 Post-transport Movement Patterns

On a given day, salmon could either remain as a resident in a single telemetered pool, or they could move between pools (as evidenced by detection by more than one receiver on a given day). We assessed the probability of movement on a given day relative to fish characteristics (sex and fork length) and environmental variables (water temperature and river discharge metrics, day of year, season, and year) using a binomial generalized linear mixed model. Use of the mixed model structure allowed us to account for the fact that the response variable (move vs. no move) consisted of repeated measures on individual fish (Zuur et al. 2009 p 324). The variance associated with the random effect provided a measure of within-fish variability in the frequency of occurrence of movement types.

We standardized continuous variables by subtracting the mean and dividing by the standard deviation. We fitted models using R version 3.4.2 (R Core Team 2017) using the glmer function (package: lme4; Bates et al. 2015). We applied stepwise selection and compared models using the Akaike Information Criterion (AIC, Akaike 1974). In each round of model selection, the model that received the lowest AIC score was retained and used as the basis for the candidate model set in the next round of the selection. We considered that the selected model was better supported than a competing model when ΔAIC was ≥ 2 (Burnham & Anderson 2002). Given that data were recorded daily, we expected some degree of temporal autocorrelation, which is a problem common to studies of effects of environmental variables on migration (Trépanier et al. 1996). The glmer function does not allow for inclusion of autocorrelation structure in the model, therefore, we incorporated a first order autoregressive dependence structure to the model by using the function glmmPQL of R (package: MASS; Venables and Ripley 2002). We assessed model fit by computing the area under the receiver operating curve (Hosmer et al. 2013).

To examine patterns in fish movement, we characterized daily movements using four metrics (Roy et al. 2013): 1) number of movements per day (total number of times a fish moved between receivers each day); 2) number of sites visited per day (number of receivers where a fish was detected each day); 3) distance travelled per day (sum of the distance between successively visited receivers); and 4) daily extent (distance between the two most distant receivers). The number of movements and the number of sites provide measures of how frequently fish moved, i.e., they indicate overall activity levels. The total distance travelled represents the minimum distance moved by an individual on a given day, as fish may have moved downstream or upstream of a given receiver, but returned before entering the detection range of another receiver. Extent provides a measure of the total river length explored by a given fish on a single day.

We identified movement types by applying principal component analysis (PCA) and k-means clustering to the four daily movement metrics. Movement metrics were centered and standardized (log +1) before use in the PCA and cluster analysis. We obtained the most parsimonious number of groups (i.e. movement types) for use in the k-means clustering by comparing three methods. First, we used the NbClust package in R, which varies the number of clusters, clustering methods, and distance measures to determine the optimal number of clusters that is best supported by 30 different indices (Charrad et al. 2014). We then compared the number of clusters produced by NbClust with a plot of the within groups sum of squares (Everitt and Hothorn 2009). Finally, we examined the silhouette width for the range of the number of clusters deemed most likely from the previous two methods using the cluster package for R (Maechler et al. 2017). Silhouette values ≥ 0.51 indicate a reasonable clustering structure.

We used the results of the k-means clustering to assign a movement type to each individual on each day that it exhibited movement and computed the frequency of occurrence of each movement type. We subsequently examined the relationship between movement type and fish characteristics and environmental variables using a generalized linear mixed model. That is, we modelled the daily frequency of occurrence of each movement type as a function of fish length, sex, mean daily river temperature, the range in daily river temperature, mean daily river discharge, the range in daily river discharge, day of year, season, day length, and year. We again employed a forward stepwise selection method based on minimizing the AIC to retain or reject explanatory variables. We compared among-fish variability in the frequency of occurrence of movement types using descriptive statistics (mean and standard deviation). The variance associated with the random effect provided measure of within-fish variability in the frequency of occurrence of movement types.

We tested the hypothesis that salmon would exhibit a crepuscular movement pattern by calculating the number of movements initiated at dawn, during daylight hours, at dusk, and at night for comparison to an expected distribution. We used the time that a fish left a given receiver as the initiation of movement. To account for the loss of daylight as the year progressed from summer to autumn, we obtained sunrise and sunset times from the ‘suncalc’ package (version 0.4) for R (Agafonkin and Thieurmel 2018) using the coordinates 48.467N, -69.939W. We defined dawn as the period spanning from two hours before sunrise to one hour after sunrise, and dusk as the period spanning from one hour before sunset to two hours after sunset. This accounts for the amount of time that the sun is below the mountains bordering the river after sunrise and before sunset (approximately 1 h). Consequently, the number of dawn/dusk hours was constant throughout the study, whereas the number of hours during the day and night changed as a function of the day of the year. We summed the number of hours occurring in each time period within and across study years to obtain the total number and proportion of hours occurring within each period, which we used to calculate the expected frequency of movements initiated at dawn, during the day, at dusk, and during the night.

7.4.5 Habitat Use

We obtained measurements of physical characteristics of all pools containing acoustic receivers via remote sensing or ground surveys. We used GIS to extract measurements of pool width, river width, and surface area from aerial images (30 cm resolution) of the river obtained from the Ministère des Forêts, de la Faune et des Parcs du Québec. We obtained measurements of maximum pool depth on 25 July 2016 at a river discharge of 26 m^3s^{-1} using a single beam echo sounder (Hydroball, CIDCO, Rimouski, QC). The presence or absence of a cold thermal refuge was identified from thermal infrared (TIR) images obtained from a helicopter survey conducted 25 August 2014 (see Frechette et al. 2018 for methods) and from a bottom survey conducted 24 August 2017. The TIR images permitted us to identify cold seeps that extended to the river surface, whereas the ground survey allowed us to identify sub-surface seeps that did not extend to the river surface and would have been missed using TIR imagery alone. We conducted the ground survey by dragging the weighted probe of an EcoSense DO200A (YSI Incorporated, Yellow Springs, Ohio) along the bottom of each pool. Before surveying each pool, we measured the temperature at the surface and the bottom of the river at the inflow (when working upstream to downstream) or outflow of each pool (when working downstream to upstream). Identical temperature at the surface and bottom indicated that the river was well mixed, and was used as the reference river temperature. We traversed pools in a series of transects with the YSI probe suspended $\leq$ 10 cm above the substrate. Pool temperatures $\geq$ 0.5°C cooler than the reference temperature were classified as a cool patch (Dugdale et al. 2013, Frechette et al. 2018). We identified the locations of spawning areas during surveys conducted via canoe and snorkel during the spawning period in 2015 and 2016 (Frechette, unpublished data).

We used a random forest approach to identify the importance of physical characteristics of pools and environmental conditions in influencing pool use by adult salmon. The random forest approach is a machine learning extension to the accepted use of classification trees for analyzing ecological data. This method improves classification accuracy by generating and combining the predictions from a large number of classification trees (Breiman 2001, Cutler et al. 2007). The random forest approach avoids overfitting, and unlike many commonly applied parametric methods used in ecology, does not rely on assumptions regarding the underlying distribution of the data, so can be used in cases (like ours) where relationships between dependent and independent variables are highly non-linear (Dahl 2001, Cutler et al. 2007). Additional advantages of the random forest approach for our application are 1) the ability to include categorical and continuous predictor variables, 2) insensitivity to different units, and 3) the potential to retain correlated predictor variables that are ecologically important (Breiman 2001, Cutler et al. 2007).

We implemented the random forest approach using the package ‘randomForest’ in R (Liaw and Weiner 2002). The number of variables randomly sampled as candidates at each split was optimized using the function train within the R package ‘caret’ (version 6.0-80), where the optimal number of variables minimized the RMSE (Kuhn 2008). Environmental conditions included in the analysis were mean daily river temperature and mean daily river discharge. Physical pool characteristics included three measures of pool size (maximum depth, surface area, and expansion factor), the presence or absence of a cool thermal refuge, and the mean distance to all known spawning areas. The expansion factor was the ratio between maximum pool width and the channel width upstream of the pool, where channel width was calculated as the mean of three bank-to-bank measures of river width. We also included day of year to assess how pool use changed over time.

7.5 Results

7.5.1 Transport and tagging

We released 68 tagged salmon into the novel habitat during the three years of the study (30F, 38M). Conditions experienced by salmon during transport are described in detail in Chapter 4. Briefly, mean transit time between the fish ladder and the release site was 52.1 min (range: 40-75 min). All transport occurred when water temperature was less than 20.5˚C (mean = 17.4˚C; SD = 1.4˚C). The mean difference between the river temperature at the fish ladder and the temperature in the transport tank was 0.46˚C (SD = 0.38˚C). The mean difference between the tank temperature at departure from the fish ladder and arrival at the release site was 0.1˚C (SD = 0.2˚C).

Each year, a subset of salmon exhibited fallback, i.e., they swam back downstream over the impassible falls, generally within 7 days of release (Chapter 4). Post-transport fallback rates were 42% during 2014 (5 of 12), 28% during 2015 (7 of 25), and 32% during 2016 (10 of 31). Individuals that exhibited post-transport fallback were excluded from analysis of movement patterns and habitat use. We also excluded salmon that either died or lost their transmitter following release. Death or tag loss was assigned if a tag failed to move from a location for the duration of the study year. It was not possible to distinguish between a lost tag and the death of an individual. Four salmon either lost tags or died (Annex 6). Our analyses were thus restricted to 42 salmon (15F, 27M) that remained alive and with functioning tags in the novel habitat from release until the onset of the spawning season in October (Annex 6).

There was no significant difference in fork length between MSW females ($\bar{x}$ = 77.4 cm; N = 13, SE = 1.6) and MSW males ($\bar{x}$ = 77.2 cm; N = 12; SE = 1.8; OLS regression, t = -0.093; *P* = 0.927). There was no significant difference in mass between MSW females ($\bar{x}$ = 4.2 kg; N = 14, SE = 0.3) and males ($\bar{x}$ = 3.9 kg; N = 9; SE = 0.3; OLS regression, t = -0.530; *P* = 0.602). By definition, 1SW males were substantially smaller in fork length and mass than MSW males and females (Fig. 7.2).

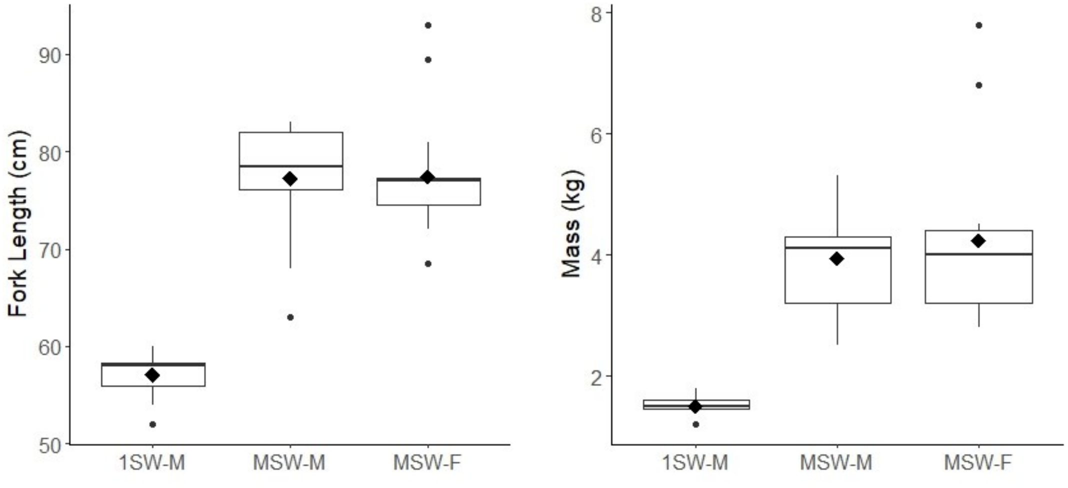


Figure 7.2 : Distribution of fish size (fork length, and mass) by age class and sex.

Multi-sea-winter salmon (MSW) are > 63 cm fork length and one-sea-winter salmon (1SW) are < 63 cm fork length.

7.5.2 Telemetry and Environmental Monitoring

Following release, 32 individuals were detected for the first time by the receiver in the pool immediately downstream (< 50 m) of the release site (pool U3), while the remaining 10 individuals were first detected by the receiver 1 km upstream of the release site (pool U4). The initial direction of movement, defined as the direction of travel between the first receiver of detection (pool U3 or U4) to the second receiver of detection, was predominantly upstream: 69% of individuals (29 of 42) initially moved upstream, whereas 31% of individuals made an initial downstream movement (Fig. 7.3). In general, post-transport migration by large, MSW-salmon could be divided into three "phases". The first phase was characterized by directed, step-wise movements in the upstream direction, which was occasionally preceded by several upstream and downstream movements following release. The second phase consisted of holding in one pool for an extended period of time, often punctuated by movements into pools immediately upstream or downstream of the holding pool. The third phase was characterized by extensive upstream and downstream movements that began in mid- to late-September (Fig. 7.3). This "search" behaviour was centered on what were subsequently identified as spawning sites (Frechette, unpublished data). Smaller, 1SW-salmon generally exhibited more extensive upstream and downstream movements. However, some 1SW salmon also exhibited the clear, three-phase migration described for MSW salmon and some MSW salmon had movement patterns that more closely resembled the extensive movements observed in 1SW-salmon (Fig. 7.3).

No salmon were detected upstream of Chute du 30 Miles during any of the three study years and no salmon were detected by the receiver deployed upstream of Chute André during 2015, the only year that a receiver was deployed between Chute André and Chute du 30 Miles. As 2015 was the wettest of the three years and had the greatest river discharge, we expect that if Chute André was passable by salmon, we would have detected salmon upstream of Chute André in that year. Under the river conditions experienced during the course of our study, therefore, Chute André appeared to be an impassable barrier to migration, limiting the colonization potential to the river reach between Chute du 18 Miles and Chute André (Fig. 7.1).

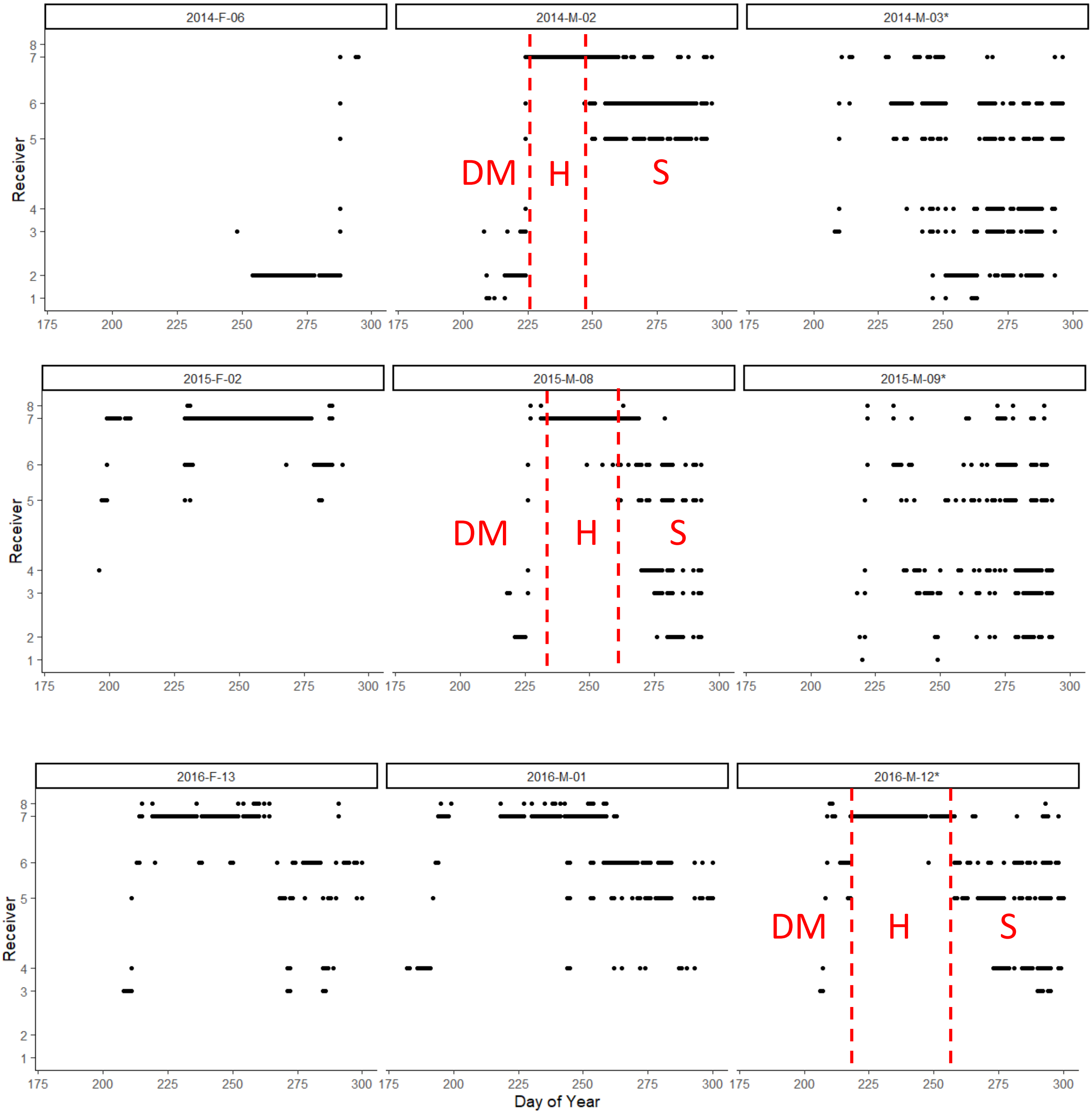


Figure 7.3 : Representative movement patterns

Movement patterns for male and female multi-sea-winter (MSW) and one-sea-winter (1SW) salmon. 1SW salmon are denoted by an asterisk. Fish identity matches the data in Supplementary Table 7.1. Day of year is on the x-axis, and receiver number (corresponding to Figure 1) are on the y-axis. Distance between receivers is to scale. Black points represent the detection of an individual fish by a receiver on a given day. Fish were often detected by multiple receivers on the same day. Vertical red dashed lines indicate the three-phase migratory pattern (directed migration, DM; holding, H; search, S) for one individual per panel that best represents the pattern.

Initial plots of movement metrics by day of the year indicated a potentially strong seasonal component, where the number of movements, number of sites visited, distance traveled, and extent all increased dramatically in mid-September (Annex 7). We fitted a piecewise linear model to the relationship between day of year and each movement metric to identify the threshold day at which the slope changed, using the segmented package for R (Muggeo 2008, Muggeo 2017). This threshold (i.e. breakpoint) was used to divide each study year into two seasons, summer and autumn. The breakpoints occurred on Day 255 (number of movements), Day 248 (number of sites), Day 255 (distance), and Day 253 (extent). Among the four metrics, the mean breakpoint occurred on Day 253. Consequently, we assigned all days up to Day 253 (10 September) as "summer" and from Day 254 to the end of the study as "autumn", which we used as an explanatory variable in our analyses of salmon movement patterns.

The years 2014 and 2016 were characterized by relatively dry summers, with low base-flow, punctuated by increases in discharge following rain events (Fig. 7.4). Discharge was consistently greater during 2015, however, the maximum mean daily discharge was greater in 2014 and 2016 than 2015 (Annex 8), due to high flow events that occurred during autumn (Fig. 7.4). The coolest maximum and minimum mean daily temperatures occurred during 2015, however, 2014 had the lowest median mean daily temperature. River temperature exceeded 21°C during August in all years, which is within the range considered stressful for adult Atlantic salmon (Breau 2013, Frechette et al. 2018).

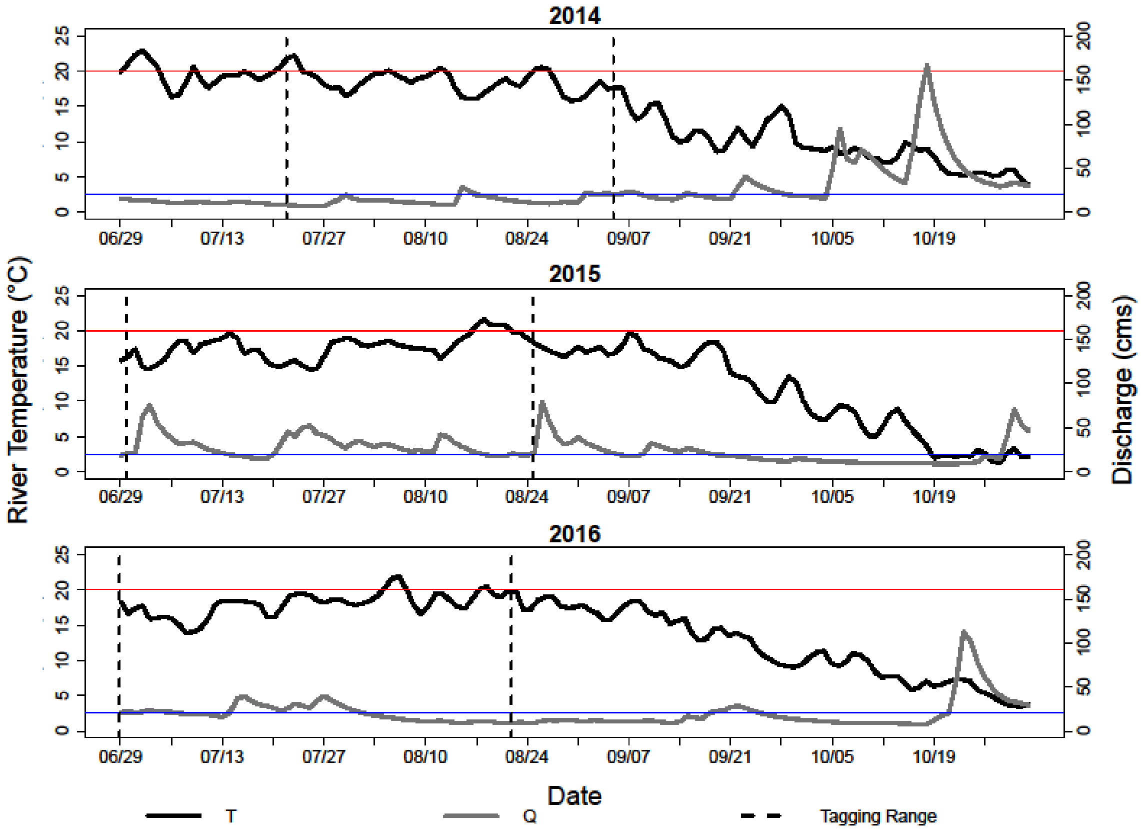


Figure 7.4 : River temperature and discharge for 2014-2016.

River temperature (left y-axis) and discharge (right y-axis) for 2014-2016. Dashed, black vertical lines indicate the date the first and last salmon was tagged in each year. Horizontal red lines denote 20°C and horizontal blue lines indicate river discharge of 20 m^3s^{-1}.

Table 7.1 : Estimated model coefficients predicting probability of movement

Fixed effects	Estimate	Std. Error	z value	Pr(>|z|)
Intercept	1.17	0.40	2.91	0.0036
Season (S)	-1.47	0.27	-5.38	< 0.0001
Qst	0.79	0.19	4.17	< 0.0001
Tst	-0.14	0.18	-0.81	0.4155
SexM	1.37	0.49	2.82	0.0049
Qst:SexM	-0.77	0.23	-3.39	0.0007
Tst:SexM	-0.66	0.18	-3.64	0.0003

Random effect	Variance	Std.Dev.
Fish ID	1.94	1.39

Model coefficients for the binomial GLM predicting probability of movement presented with associated standard error (fixed effects) or variance and standard deviation (random effect). Qst = standardized mean daily discharge and Tst = standardized mean daily temperature.

7.5.3 Post-transport Movement Patterns

In assessing the probability of moving versus residing in a pool on a given day, the selected model included the covariates season, discharge, temperature, and interactions between sex and temperature and between sex and discharge as explanatory variables (Table 7.1). Using the methods of Royston and Altman (1994), we determined the value of x^p that yielded the best model for the covariate. We determined that a linear function was appropriate to define the relationship between the response variable and both temperature and discharge. The area under the receiver operating curve (ROC) was 0.86. Using the criteria of Hosmer et al. (2013), model discrimination was considered to be "excellent". Correlation between observations made one day apart was 0.73, however, temporal autocorrelation was considered to break down quickly enough so as to not be problematic.

The significant, negative slope for the effect of season indicates that salmon were less likely to move during summer, that is, on or before 10 September (Fig. 5). The significant sex by discharge interaction indicates that females were more likely to move at high discharge (slope = 0.79) but males were not (slope = 0.02). The non-significant slope for temperature indicates that temperature did not affect the probability of moving for females, however the significant sex by temperature interaction indicates that males were less likely to move at high temperature (slope=0.8). The variance attributable to the random effect of individual was low (1.94).

All movement variables (number of movements, number of sites, total distance, and extent) were negatively correlated with the first principal axis (PCA1), representing a movement pattern characterized by a great number of movements between many sites. The number of movements was strongly negatively correlated with the second principal axis (PCA2), whereas extent was strongly positively correlated with PCA2, representing a movement pattern consisting of fewer movements but greater extent. In total, the first two principal axes accounted for 93% of the variability in the data (Table 7.2).

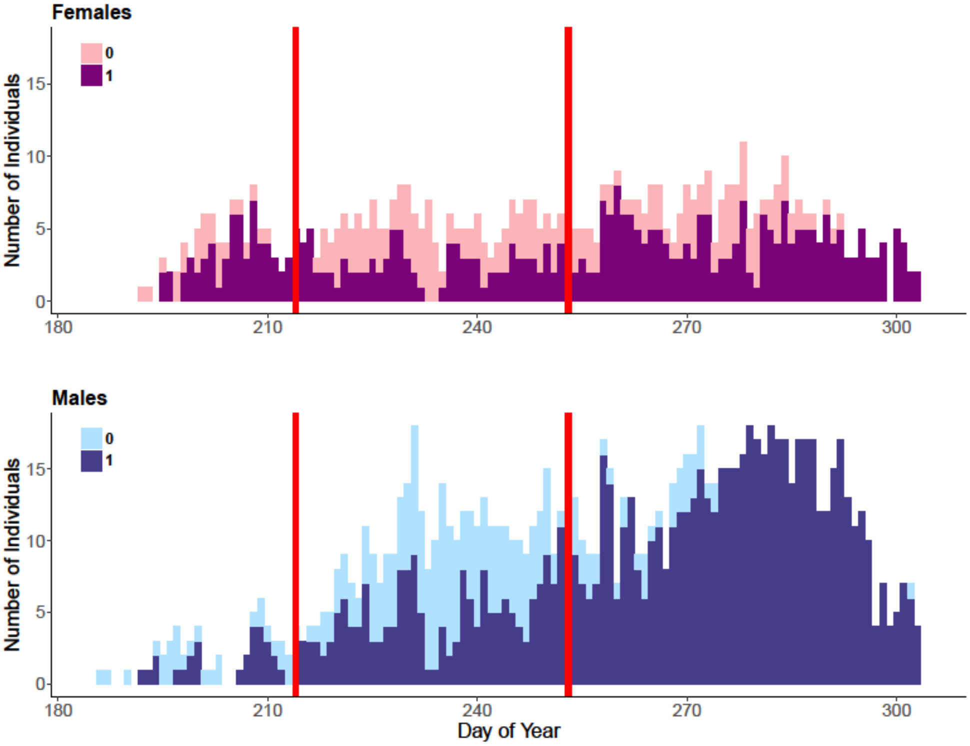


Figure 7.5 : Frequency of movement by sex

Number of females (upper panel) and males (lower panel) that were resident in a pool (0) or moved (1) each day for 2014, 2015, and 2016 combined. Red lines Red lines are included for reference and indicate 1 August and 10 September, where 10 September represents the breakpoint between "summer" and "autumn" seasons.

Table 7.2 : Pearson correlation coefficients for PCA loadings and explained variance.

	PC1	PC2	PC3	PC4
No. of movements	-0.49	-0.73	0.06	0.47
No. of sites	-0.50	0.15	0.77	-0.37
Total distance	-0.51	-0.08	-0.61	-0.60
Extent	-0.50	0.66	-0.20	0.53
Proportion of Variance	0.86	0.08	0.06	0.00
Cumulative Proportion	0.86	0.94	1.00	1.00

There was consensus among the three methods applied to determine the number of clusters to include in the k-means analysis (within-groups sum of squares, the NbClust function in R, and silhouette analysis). Examination of a plot of the within-group sum of squares by number of clusters indicated that either two or three clusters minimized the within-group sum of squares (Everitt 2007, Everitt & Hothorn 2010). Using the NbClust function in R, the greatest number of indices (10 of 30) proposed two clusters as the best solution, whereas only two indices proposed three clusters as the best solution. A comparison of silhouette values provided further support for the two-cluster solution (mean silhouette width = 0.53) relative to the three-cluster solution (mean silhouette width = 0.45).

The first cluster defined a movement type characterized by relatively low mobility, hereafter referred to as sedentary (*sensu* Roy et al. 2013). When exhibiting sedentary behavior, individuals had a low number of movements between few sites (Table 7.3). The total distance moved ($\bar{x}$ = 1.52 km) and extent were also relatively low ($\bar{x}$ = 1.18 km). As extent was the distance between the two furthest receivers visited on a given day, it may seem counter-intuitive that mean extent would be less than mean total distance. This is explained by the fact that total distance accounts for multiple movements between receivers, whereas extent describes the river distance between the most distant receivers visited by a fish in one day, irrespective of possible multiple movements between receivers within the corresponding river section. The second cluster defines a high-mobility movement type, hereafter referred to as "exploratory". The exploratory movement type was characterized by a greater number of movements, sites visited, distance travelled ($\bar{x}$ = 5.58 km) and extent ($\bar{x}$ = 3.98 km). Rate of movement was significantly greater during exploratory ($\bar{x}$ = 0.29 m/s) than during sedentary movements ($\bar{x}$ = 0.16 m/s; OLS Regression, t = 16.232; $P < 2e^{-16}$). During sedentary movements, males had a significantly greater rate of movement (0.18 m/s) than females (0.12 m/s; OSL Regression, t = 5.578; $P = 3.4e^{-8}$). Males also had a greater rate of movement during exploratory movements (0.30 m/s) than females (0.25 m/s; OLS Regression, t = 4.202; $P = 3.09e^{-5}$).

A given individual expressed only one movement type per day. That is, a salmon did not exhibit both sedentary and an exploratory movement on the same day. Overall, the frequency of occurrence (FOC) of the sedentary movement type (expressed as a percentage of the total number of days) was 60% and the variation among individuals was reasonably high (SD = 18.33%). Although males had more exploratory movements than females, both sexes exhibited the sedentary movement pattern more frequently than the exploratory movement pattern (Fig. 7.6). The frequency of occurrence of the sedentary movement type was 68% for females and 56% for males, and females had less among-individual variation in the FOC of each movement type (SD = 14.3%) than males (SD = 19%).

Table 7.3 : Daily salmon movement metrics and frequency of occurrence

	Movement Type	
	Sedentary	Exploratory
n	752	539
No. of movements	1.41	4.31
No. of sites	2.07	3.74
Total distance	1.52	5.58
Extent	1.18	3.98
% FOC - Total	60.00 (18.33)	40.00 (18.33)
% FOC - Females	67.92 (14.30)	32.08 (14.30)
% FOC - Males	55.59 (19.07)	44.41 (19.07)

Daily salmon movement metrics (mean) and frequency of occurrence (FOC) by movement type and sex.

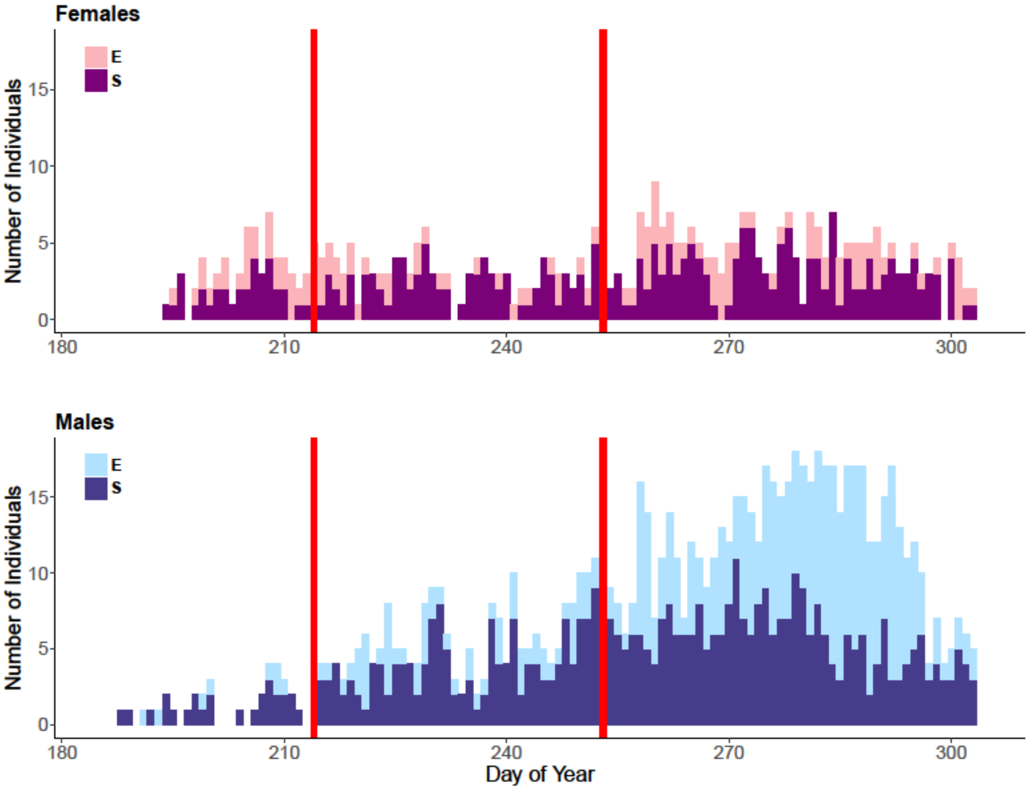


Figure 7.6 : Frequency of movement type by day

Number of females (upper panel) and males (lower panel) that exhibited exploratory (E) or sedentary (S) movement patterns each day for 2014, 2015, and 2016 combined. Red lines are included for reference and indicate 1 August and 10 September, where 10 September represents the breakpoint between "summer" and "autumn" seasons.

Because only two movement types were identified and an individual salmon only exhibited one movement type per day, we used a binomial mixed GLM to assess the effects of explanatory variables on the probability of expressing the sedentary movement type. The response variable was "1" if an individual expressed sedentary movement and "0" if it expressed exploratory movement on a given day. The covariates retained in the selected model were temperature, discharge, and the interactions between sex and temperature and between sex and discharge (Table 7.4). Using the methods of Royston and Altman (1994), we determined that a linear function was appropriate to define the relationship between the response variable and both temperature and discharge. The area under the ROC was 0.72, indicative of acceptable discrimination (Hosmer et al. 2013) Correlation between observations made one-day apart was very low (0.26), thus temporal autocorrelation was not considered to be problematic. Neither temperature nor discharge influenced the probability that a female was sedentary. That is, females were more likely to be sedentary regardless of the river temperature or discharge. The significant interactions between temperature and sex and temperature and discharge indicate that males were more likely to be sedentary at high temperature and high discharge. The variance attributed to the random effect of individual was very low (0.39).

Table 7.4 : Estimated model coefficients predicting probability of sedentary movement type

Fixed effects	Estimate	Std. Error	z value	Pr(>|z|)
Intercept	0.86	0.21	4.08	< 0.0001
Tst	0.06	0.11	0.56	0.58
Qst	-0.13	0.13	-1.04	0.30
SexM	-0.56	0.26	-2.17	0.03
Tst:SexM	0.54	0.14	3.87	0.00
Qst:SexM	0.41	0.15	2.74	0.01

Random effect	Variance	Std.Dev.
Fish ID	0.39	0.62

Model coefficients for the binomial GLM predicting probability of expressing the sedentary movement type, presented with associated standard error (fixed effects) or variance and standard deviation (random effect). Qst = standardized mean daily discharge and Tst = standardized mean daily temperature.

Salmon exhibited a predominantly crepuscular movement pattern. The number of movements initiated during dawn and dusk was greater than expected and the number of movements initiated during daylight hours was less than expected for both males ($X^2 = 479$, df = 3, p = 0.01) and females ($X^2 = 536$, df = 3, p = 0.01). Males initiated more movements at night than expected, whereas females initiated slightly fewer movements at night than expected.

7.5.4 Habitat Use

Pools in the colonization habitat ranged substantially in size (Annex 8). The smallest pool (U8) had a surface area of 1176 m^2 and maximum depth of 2.9 m. The shallowest pool (U1) had a maximum depth of 1.25 m, but was the third largest in terms of surface area (8714.03 m^2). Expansion factor, another measure of pool size, ranged from 0.54 (pool U1) to 3.48 (pool U7). Pool U7 was the most frequently used pool, with 867 residences that were ≥ 1 h in duration, whereas pool U1 was least frequently used (only 7 residences ≥ 1 h in duration). The total number of hours that fish were present in pools (residences ≥ 1 h in duration) ranged from 27.7 (U1) to 15201.5 (U7). Sub-surface cold seeps were identified in three pools during the August 2017 ground survey (pools U3, U6, and U7). Surface-intersecting cold water patches were previously identified by Frechette et al. (2018) in these three pools by thermal infrared imagery, where pool U6 (this study) was referred to as pool U7 and pool U7 (this study) was referred to as U8 by Frechette et al. (2018).

With the optimal number of variables randomly sampled as candidates at each split set at 5, (the value which minimized RMSE), the random forest regression (500 trees) explained 53.3% of the variance in pool use, where pool use was defined as the frequency of residences ≥ 1 hr. Mean daily discharge was associated with the greatest increase in percent mean squared error (%MSE), indicating that this variable had the greatest importance in predicting pool use, followed by day of year and mean daily temperature (Table 7.5). Examination of partial dependence plots indicate that pool use was greatest at river discharge less than 10 m^3s^{-1} and stabilized at discharges greater than 20 m^3s^{-1} (Fig. 7.7). Pool use increased steadily until mid-September and decreased as the spawning season approached. Pools were used less frequently when river temperature was less than 11°C and most frequently at the highest river temperatures (≥ 20°C).

For the periods when tagged salmon were available in the novel habitat, discharge ≥ 20 m^3s^{-1} was recorded primarily during the autumn spawning period and following isolated summer rainfall events, except in 2015, when discharge routinely exceeded 20 m^3s^{-1} throughout the summer (Fig. 4). During 2015, mean daily discharge was ≤ 20 m^3s^{-1} on only 43% of days when fish were available for tracking (48 of 113), whereas mean discharge was ≤ 20 m^3s^{-1} on 62% of days during 2014 (58 of 94 days) and 2016 (78 of 125 days). High temperature events (≥ 20°C) were restricted to August (Fig. 7.4), and correspond to periods when salmon were not moving (Fig. 7.5) or were engaged in sedentary behavior (Fig. 6). The greatest number of days with mean daily temperature ≥ 20°C occurred during 2014 (7.4% of days, or 7 of 94). Mean daily temperature exceeded 20°C on 4.4% of days during 2015 (5 of 113) and 4.8% of days during 2016 (6 of 125). River temperature did not drop below 11°C until after 10 September during all years, which corresponds with the overall increased movement exhibited by tagged salmon and the increase in exploratory behavior exhibited by males.

Surface area was the physical pool characteristic associated with the greatest increase in %MSE (Table 7.5), followed by maximum depth. Specifically, pools with surface areas < 15000 m^2 or maximum depth < 4 m were used less than pools exceeding these size thresholds (Fig. 7.7). Expansion factor (EF) was associated with a relatively low increase in %MSE and the partial dependence plot demonstrated a step-wise form: pools with EF <1 were rarely used and pools with EF > 2.5 were most frequently used, whereas pools with intermediate EF values (1.5 - 2.5) had moderate use. The presence of a cold refuge was associated an increase in %MSE of only 6.28, however, pools with cold refuges were more frequently used than pools without cold refuges. The least important variable was the proximity to spawning sites. Pools that were < 3 km from spawning sites were used more than pools that were further away, however, there was an increase in use of pools that were ≥ 5 km away from pools, relative to those that were at intermediate distances to spawning sites.

Table 7.5 : Importance of variables used to predicting probability of pool use.

Variable	% Increase in MSE	Increase in node purity
Mean daily discharge	37.07	1461.84
Day of year	29.68	1283.65
Mean daily temperature	25.86	1224.12
Surface area	21.14	442.39
Maximum depth	15.44	328.96
Expansion Factor	10.88	173.55
Presence of cold refuge	6.28	22.35
Mean distance to spawning sites	5.25	50.51

Importance of physical variables included in the random forest analysis for predicting probability of pool use as expressed by percent increase in mean squared error and increase in node purity.

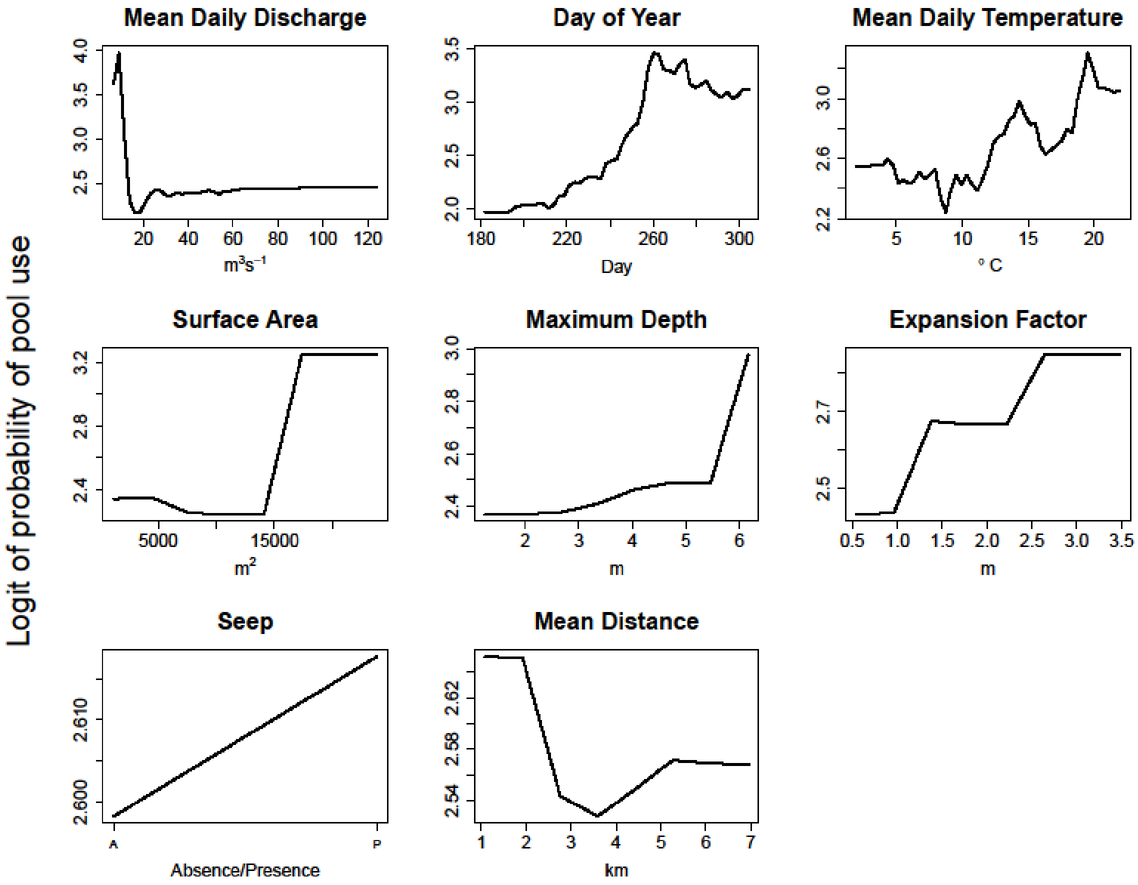


Figure 7.7 : Partial dependence plots

Partial dependence plots for the relationship between the logit of the probability of pool use, and each variable included in the random forest analysis, with pool use was defined as the frequency of residences ≥ 1 hr. Note the different axes.

The most heavily used pool during the summer months was U7 (Fig. 7.8), which was the largest pool in the novel habitat in terms of surface area and depth, and contained a cold refuge. Use of pool U7 decreased during the autumn as the spawning season approached, river temperature cooled, and greater river discharge was recorded. As autumn progressed, the frequency of residences in pool U6 increased, which was closer than pool U7 to known spawning sites. The increase in use of pools other than U7 after mid-September corresponds with the general increase in exploratory movements that we described previously.

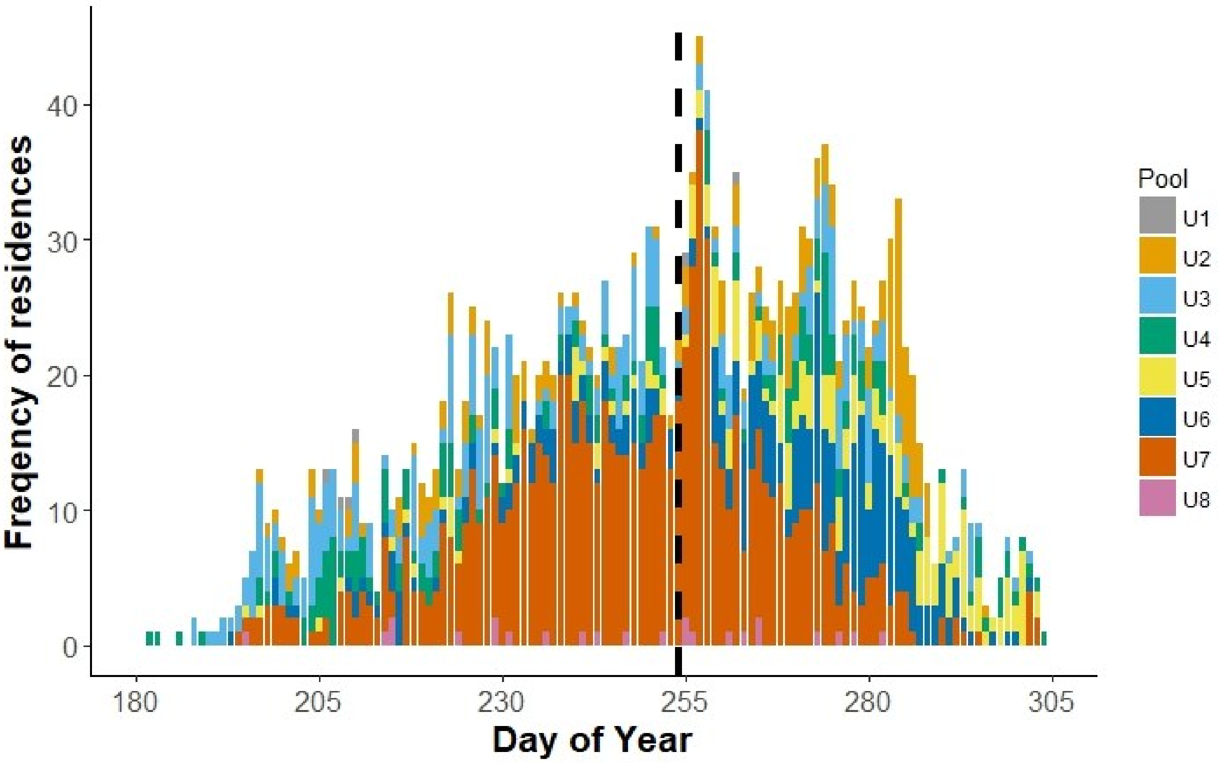


Figure 7.8 : Frequency of pool use

Frequency of pool use, (defined as the frequency of residences ≥ 1 hr) by day of the year (x-axis) for 2014, 2015, and 2016 combined, where color denotes individual pools. The vertical dashed line falls is placed at day 253.5, corresponding to 10 September (the breakpoint between "summer" and "autumn" seasons).

7.6 Discussion

Our study provides a detailed picture of the movement patterns and habitat use by adult Atlantic salmon during the colonization of a pristine, unregulated river in relation to biotic and abiotic variables at a high spatial and temporal resolution. Overall, salmon had a lower probability of movement during the summer, which means that individuals spent more days resident in pools during summer than during autumn. The probability of movement increased as the spawning season approached, suggesting that individuals began to move between holding pools and spawning sites. River temperature and discharge influenced salmon movements, with the nature of an individual's response dependent on fish sex, but not on fish size. Pool size was the most important physical characteristic identifying "suitable" holding pools for Atlantic salmon during in-river residence. However, river temperature, discharge, and day of year were also extremely influential in predicting whether salmon were likely to use pools.

In general, male salmon moved more and engaged in more exploratory behavior than females, however, males moved less as river temperature increased, (i.e. the probability of movement was lower and the probability of being sedentary was greater at elevated river temperature). Increased pool use by males as temperature increased was further reflected in the random forest analysis of habitat use: pool use was greatest when river temperature exceeded 20˚C. Temperatures exceeding 20˚C were only recorded in the Nord-Est during July and August, which coincided with expression of increased sedentary behavior and lower probability for movement by males. The energy expenditure by male and female Atlantic salmon during migration and spawning are similar (c. 59% of total energy reserves), however males are less likely than females to survive spawning, possibly because of intense male-male competition (Fleming 1998). It should be evolutionally beneficial, therefore, for males to maximize their within-season (as opposed to among-season) reproductive success. Holding in pools during stressful summer heat events could allow males to maximize: 1) survival to spawning, 2) energy available to search for females and engage in male-male competition for mates, and 3) reproductive success (Fleming 1996, 1998). Male Atlantic salmon maximize reproductive success by spawning with multiple females (Hawkins and Smith 1986, Fleming 1996). Consequently, the greater incidence of exploratory behavior exhibited by males may be explained by active search for females to increase mating success, which is supported by the observed increase in exploratory movements from mid-September as river temperature cooled and spawning season approached.

Contrary to what we observed in males, river temperature did not affect the probability of females to move. Females, however, moved more as discharge increased and they exhibited more sedentary than exploratory movements, regardless of river temperature and discharge. The increased probability of movement exhibited by females at greater discharge likely indicates movement to and from redd sites during the spawning season. Baglinière et al. (1990) also observed that an increase in discharge corresponded to movement of female salmon to spawning grounds in a tributary of the Selune River (France). Female Atlantic salmon produce a finite number of eggs each year and have a greater probability of repeat-spawning than males (Fleming 1996, 1998). High movement rates can reduce energy stores needed for egg development, redd digging, and egg laying or by increasing post-spawning mortality that prevents females from spawning during subsequent years (Thorstad et al. 2008). It may be evolutionarily more advantageous for females to move less during the pre-spawning period (even at temperatures when males were highly active) so as to conserve energy to increase not only within-season reproductive effort, but also the chance of repeat spawning, which would increase life-time reproductive success (Hawkins and Smith 1986, Fleming 1996, 1998).

Interestingly, although plots of post-transport migration revealed that many 1SW males made numerous upstream and downstream movements, fish size was not retained in either the model for the probability of movement or the model of movement type. Smaller (1SW) males are less capable of defending mates and so may move more extensively among different spawning grounds to find mates and increase their chances of spawning successfully (Fleming 1996). In the Selune River (France), 1SW males made more upstream and downstream movements and had a greater amplitude of movement than larger males (Baglinière et al. 1991). In the same river, daily distance moved by female salmon was inversely correlated with fish size, (Baglinière et al. 1990). We had, therefore, expected smaller individuals would move more than large salmon. Our sample size was relatively small and was comprised primarily of MSW males (N = 12) and females (N = 15) with similar length and mass, whereas 1SW salmon comprised only one-third of the tagged individuals (N = 15), which may have reduced our ability to resolve any differences in movement patterns according to size.

During colonization in the Nord-Est, the majority of MSW salmon and some 1SW salmon exhibited a three-phase migratory pattern similar to that previously described in the Escoumins River (Richard et al. 2014). This migratory pattern consisted of: 1) directed, stepwise migration followed by 2) a holding period, then 3) a search phase with movements centered on spawning areas. This pattern differs from that observed in the freely-flowing, subarctic Tana and Lærdalselva rivers of Norway. As observed in the Nord-Est and Escoumins rivers, salmon migration was first characterized by directed upstream movements (migratory phase), however, in the Norwegian rivers, the migratory phase was followed by a search phase, in which salmon made erratic movements around future spawning areas. The "holding" phase, occurred after the search phase and lasted until the onset of spawning (Økland et al. 2001, Finstad et al. 2005). The pattern described in the Tana and Lærdalselva rivers has come to be considered the "normal" migration pattern for Atlantic salmon in unregulated rivers; deviations from this pattern have been classified as aberrant behavior associated with stress from handling fish during tagging or catch and release (Thorstad et al. 2003, Havn et al. 2015). In the Escoumins River, however, both salmon that had experienced catch and release (C&R) angling and control fish that had not experienced C&R exhibited the same migratory pattern that we observed in the Nord-Est. It is possible that the migratory pattern observed in the Nord-Est could be attributed to the fact that salmon were transported via truck, surgically tagged, and released into novel habitat where they had no prior experience. However, given the similarity to the migratory pattern observed in the Escoumins River, we suggest that habitat availability and environmental conditions may drive the difference in migration patterns between the Quebec rivers (Nord-Est and Escoumins) and the Norwegian rivers (Tana and Lærdalselva).

Richard et al. (2014) hypothesized that suitable holding pools may be scarce in small rivers like the Escoumins relative to larger rivers like the Tana, causing fish to direct migration to over-summering habitat. The Lærdalselva River, however, is smaller than the Escoumins River, so availability of holding pools alone may not explain the difference in migration patterns. The Tana and Lærdalselva are subarctic rivers that have cooler water temperature than the Escoumins and the Nord-Est. Water temperature in the Tana River during migration was 9-13˚C, whereas temperatures ranged from 14-23˚C in the Nord-Est and Escoumins rivers (Økland et al. 2001, Richard et al. 2014, this study). Further, the alternative pattern observed in the Escoumins and Nord-Est also was also observed in more southerly rivers of the United Kingdom, France, and New Brunswick, Canada (Hawkins and Smith 1986, Bardonnet and Bagliniere 2000, Mitchell and Cunjak 2007). These rivers span a range of catchment size and discharge regimes, leading us to suggest that migratory patterns are influenced by the effects of both discharge and temperature on the availability of pools for holding during in-river residence.

Assessing availability of holding pools requires an understanding of the factors that influence suitability of habitat for this function, a subject that has received little attention (Bardonnet and Bagliniere 2000). Our telemetry array facilitated not only detailed assessment of salmon movements, but also the frequency with which pools were used throughout the pre-spawn period, which allowed us to assess factors influencing use of individual pools over time. Of the physical features measured, pool size was the most important habitat feature defining a suitable holding pool, with larger and deeper pools being used more often. Pool use was modified by temperature, discharge, and timing within the pre-spawn period. Specifically, pool use increased throughout the summer as more salmon entered the colonizing population, peaked in mid-September, and then decreased slightly as the spawning season approached and salmon became more active. Pool use was greatest at low discharge (< 10 m^3s^{-1}) and high temperature ($\geq 20°C$), which occurred during the summer. Only one pool was consistently used for long-term holding during the three years of this study (U7), suggesting that suitable holding pools likely are scarce in the Nord-Est, as Richard et al. (2014) suggested was the case for the Escoumins River.

Pool temperature and pool depth have previously been identified as influencing carrying capacity of holding pools (Moreau and Moring 1993). The largest pool in the colonization habitat (pool U7) was the only pool used for long-term holding. Although pool size was more influential than presence of a cool seep in predicting pool use, the three largest pools also contained cold seeps (pools U3, U6, U7). In a study of thermal refuge use in the Nord-Est, pool U7 (referred to as pool "U8" by Frechette et al. 2018) was found to become thermally stratified during summer heat events, and was the only pool consistently used for behavioral thermoregulation (Frechette et al. 2018). Cold seeps in pool U6 (referred to as U7 by Frechette et al. 2018) and pool U3 were smaller than the area affected by thermal stratification in pool U7, so they likely had lower carrying capacity for use as thermal refuges, in addition to having lower carrying capacity in general because of their smaller area and shallower depth.

Distance to spawning grounds was the least influential variable in predicting pool use, which may stem from the predominant use of pool U7 as over-summering habitat. The use of small pools closer to spawning sites increased during autumn concurrent with the decrease in river temperature, increase in river discharge, and increase in probability of movement. In addition to over-summering habitat, salmon require suitable habitat to rest between spawning attempts (Bardonnet and Bagliniere 2000). Our results suggest that as discharge increased and temperature decreased, pools that were not suitable for holding during the warm, dry summer months became suitable for resting during the spawning season, allowing salmon to use pools closer to spawning sites. These results also support the suggestion made by Richard et al. (2014) that the holding phase preceded the search phase in the Escoumins River because salmon must reach suitable holding pools to over-summer and wait for fall freshets to enable them to resume migration to more distant spawning grounds. Consequently, in rivers where low discharge and high temperature co-occur, larger pools with high carrying capacity that allow salmon to find thermal and hydraulic refuge are likely more important for over-summer holding than are pools that are closest to spawning grounds. A wider range of pools may be suitable for over-summer holding in cooler rivers like the Tana and Lærdalselva, where temperatures do not become stressful during migration (i.e. temperature remains < 20˚C). This would allow salmon to search for holding pools near spawning sites before entering the holding phase of the migration, and explain the differences in migratory patterns between salmon in Norwegian rivers and those in more southerly rivers of Canada, the United Kingdom, and France (Bardonnet and Bagliniere 2000, Økland et al. 2001, Finstad et al. 2005, Richard et al. 2014)

Initiation of movement by translated salmon was concentrated during dawn and dusk. Although salmon moved during daylight hours, fewer movements were initiated than expected by individuals of both sexes. Reviews of previous studies indicate that Atlantic salmon migrate predominantly from dusk until dawn, although passage of obstacles may be concentrated during the day (Hawkins and Smith 1986, Jonsson

1991, Thorstad et al. 2008). Movement between dusk and dawn has been considered an evolutionarily adaptive mechanism to avoid visual predators that are active predominantly during the day (Hansen and Jonsson 1986, Thorstad et al. 2008), whereas daytime passage of obstacles may represent a tradeoff between the need for light to visually navigate obstacles and use of dark for predator avoidance (Thorstad et al. 2008). The colonization habitat is free of obstacles to migration, so we expected that individuals would be least active during daylight hours. The salmon translocated into novel habitat did not deviate from this expectation. Use of low light conditions to avoid visual predators may be so well conserved a trait that salmon exhibit crepuscular and nocturnal behavior even in systems like the Nord-Est where species large enough to prey on adult salmon are rare or absent. Given that water temperature was generally coolest during the night and early morning (Frechette et al. 2018), movement between dawn and dusk could alternatively be explained by use of cooler water temperatures to reduce the energetic costs of swimming.

Combining multiple daily movement metrics (number, sites visited, distance, and extent) into discrete movement patterns allowed us to maximize the information used to examine the effects of environmental variables and fish characteristics on movement. Previous studies relying on telemetry have produced conflicting results regarding the relationship between environmental conditions and upstream migration by salmonids. Most studies, however, used rate of movement, or migration speed as the response variable describing salmon movement. Migration speed has been observed to increase, stop, or show no response to increasing discharge (Hawkins and Smith 1986, Hawkins 1989, Erkinaro et al. 1999, Karppinen et al. 2004). Movement rates have been shown to both increase and decrease with increasing temperature, or be greatest at intermediate temperatures (Alabaster 1990, Erkinaro et al. 1999, Karppinen et al. 2004, Hasler et al. 2012, Strange 2012). Recently, Martin et al. (2015) used a novel application of exercise physiology to demonstrate that differences among studies in the response of salmon movement rates to temperature and discharge was context-specific and resulted from the way each variable modified the effect of the other. That is, migration speed was driven by temperature at low water velocities, but discharge became more important than temperature in influencing migration speed at high water velocities (Martin et al. 2015). The development of such discrete movement patterns based on multi-dimensional measures of movement may improve among-river comparisons of how salmon respond to environmental conditions relative to comparisons based solely on movement rates or plots of migratory tracks.

Thorough understanding of how salmon colonize novel habitat will be a direct asset for optimizing future reintroduction and assisted migration programs. Specifically, our findings provide additional support for the importance of pools where salmon can rest during upstream migration (Økland et al. 2001, Finstad et al. 2005, Richard et al. 2014). Consequently, in selecting drainages or river reaches for release of adult salmon, priority should be placed on those that contain an adequate number of deep pools to support the number of adults to be introduced. In temperate rivers where summertime temperatures exceed the tolerance range, release of adults should occur in systems or river reaches containing thermal refuge habitat within adequately-sized pools. If thermal refuge habitat is lacking, release of adults should occur later in the season, when the risk of exposure to high heat events is reduced. Because the ability for salmon to ascend challenging obstacles is limited at low temperatures (Gerlier & Roche 1998), release must also occur before temperatures drop too low to allow salmon to reach spawning areas. Timing of release must also take local discharge regimes into consideration, as release when river discharge is too low could prevent salmon from accessing thermal refuges or spawning habitat.

Our findings may also provide insight into the adaptive advantages of premature migration by Atlantic salmon. Holding in pools was associated with river temperatures generally considered stressful to Atlantic salmon (> 19˚C; Shepard 1995; Wilke et al. 1997, Breau 2013, Frechette et al. 2018). If salmon are exposed to stressful temperatures for prolonged periods and holding areas with a source of cool water are not available for recovery, individuals may die (Elliott and Elliott 2010). Pool use was least frequent at temperatures less than 11˚C, which has been associated with limited swimming capacity and decreased ability to ascend obstacles (Gerlier & Roche 1998). Further, females moved more at high discharge, and pool use was greatest at low discharge (c. 10 m^3s^{-1}). Low discharge can limit the ability of salmon (especially large individuals) to access holding and spawning areas (Mitchell and Cunjak 2007). In some years, river discharge may remain low right up until the onset of the spawning season in the autumn. Consequently, low discharge and temperatures that are either too high or too low can serve as barriers to upstream migration and prevent adults from accessing spawning areas at the correct time to ensure that timing of egg deposition is optimal for embryo survival, emergence, and initial foraging by offspring (Alabaster 1990, Fleming 1998, Torgersen et al. 1999; Hasler et al. 2012). Salmon translocated into the novel habitat in the Nord-Est exhibited movement patterns and habitat use that was consistent with the evolutionary strategies expected to maximize reproductive success. These strategies reflect the differences in reproductive capacity of males and females, are designed to ensure that spawning occurs at the right time to maximize offspring survival, and are highly conserved among populations (Fleming 1998). Premature migration, therefore, may be a mechanism that allows salmon to reach suitable holding areas before the onset of high temperature and low discharge conditions, while also allowing them to ascend challenging river reaches (rapids, waterfalls) before low temperatures reduce swimming capacity, ensuring that individuals are present in spawning habitat at the correct time to maximize offspring survival and reproductive fitness.

7.7 Acknowledgements

Funding for this work was provided by the Programme de mise en valeur des habitats du saumon de la Côte-Nord of the Fédération Québécoise du Saumon Atlantique, and the Atlantic Salmon Conservation Foundation. Financial support for D. Frechette was provided by the Fonds de recherche du Québec - Nature et technologies (FRQNT) Merit Scholarship Program for Foreign Students. We would like to thank the Ministère de la Faune, des Forêt, et des Parcs du Québec, the Association de la Rivière Sainte-Marguerite, and the Corporation de Pêche Ste-Marguerite for their vital collaboration and support of this research. We thank Gaétan Daigle (Université Laval) for invaluable statistical advice and editing for the movement analyses, and Jon Lefcheck for statistical advice for the random forest analysis. This research program could not have been accomplished without an army of individuals who helped get this program up and running, deployed and recovered acoustic receivers, and safely transported and tagged salmon. In particular, we wish to thank the following people for their invaluable field and logistical support: A. Boivin, V. Maltais, F. Caron, M. Valentine, V. Cauchon, S. Gravel, M. Murdock, R. Gagnon, J.B. Toteroto, J. Isabelle, J. Carrier, M. St-Amour, I. Bergeron, and T. Suskiewicz.

8 BIBLIOGRAPHIE – CHAPITRE 7

Agafonkin, V., Thieurmel, B. (2018). suncalc: Compute Sun Position, Sunlight Phases, Moon Position and Lunar Phase. R package version 0.4. https://CRAN.R-project.org/package=suncalc

Akaike, H. 1974. A new look at the statistical model identification. IEEE Transactions on Automatic Control 19:716-723.

Alabaster, J. S. 1990. The temperature requirements of adult Atlantic salmon, *Salmo salar* L., during their upstream migration in the River Dee. Journal of Fish Biology 37:659-661.

Anderson, J. H., G. R. Pess, R. W. Carmichael, M. J. Ford, T. D. Cooney, C. M. Baldwin, and M. M. McClure. 2014. Planning Pacific Salmon and Steelhead Reintroductions Aimed at Long-Term Viability and Recovery. North American Journal of Fisheries Management 34:72-93.

Askling, O. 2015. A telemetry study for reintroducing wild Atlantic salmon (*Salmo salar* L.) in the Daugava and Ogre Rivers, Latvia. M.S. Karlstad University, Karlstad, Sweden.

Baglinière, J. L., G. Maisse, and A. Nihouarn. 1990. Migratory and reproductive behaviour of female adult Atlantic salmon, Salmo salar L., in a spawning stream. Journal of Fish Biology 36:511-520.

Baglinière, J. L., G. Maisse, and A. Nihouarn. 1991. Radio-tracking of male adult Atlantic salmon, *Salmo salar* L., during the last phase of spawning migration in a spawning stream (Brittany, France). Aquatic Living Resources 4:161-167.

Bardonnet, A., and J. L. Baglinière. 2000. Freshwater habitat of Atlantic Salmon (*Salmo salar*). Canadian Journal of Fisheries and Aquatic Sciences 57:497-506.

Bates, D., M. Maechler, B. Bolker, and S. Walker. 2015. Fitting Linear Mixed-Effects Models Using lme4. Journal of Statistical Software 67:1-48.

Bendall, B., A. Moore, D. Maxwell, P. Davison, N. Edmonds, D. Archer, D. Solomon, V. Greest, R. Wyatt, and K. Broad. 2012. Modelling the migratory behaviour of salmonids in relation to environmental and physiological parameters using telemetry data. Fisheries Management and Ecology 19:475-483.

Bett, N. N., and S. G. Hinch. 2015. Attraction of migrating adult sockeye salmon to conspecifics in the absence of natal chemical cues. Behavioral Ecology 26:1180-1187.

Boyer, C., St-Hilaire, A., Bergeron, N.E., Daigle, A., Curry, R.A., and Caissie, D. 2016. RivTemp: A water temperature network for Atlantic salmon rivers in eastern Canada. Water News. **35**: 10–15.

Breau, C. 2013. Knowledge of fish physiology used to set water temperature thresholds for in-season closures of Atlantic salmon (*Salmo salar*) recreational fisheries.in D. o. F. a. Oceans, editor. Canadian Science Advisory Secretariat, Moncton, N.B.

Breiman, L. 2001. Random Forests. Machine Learning, 45 45:5–32.

Bryant, M. D., B. J. Frenette, and S. J. McCurdy. 1999. Colonization of a watershed by anadromous salmonids following the installation of a fish ladder in Margaret Creek, Southeast Alaska. North American Journal of Fisheries Management 19:1129-1136.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodal inference: A practical information-theoretic approach. 2 edition. Springer-Verlag, New York, NY.

Campbell, H. A., Watts, M.E., Dwyer, R.G., Franklin, C.E. 2012. . V-Track: software for analysing and visualising animal movement from acoustic telemetry detections. Marine and Freshwater Research 63:815–820.

Charrad, M., N. Ghazzali, V. Boiteau, and A. Niknafs. 2014. NbClust: An R Package for Determining the Relevant Number of Clusters in a Data Set. Journal of Statistical Software 61:1-36.

COSEWIC. 2010. COSEWIC assessment and status report on the Atlantic Salmon **Salmo salar** (Nunavik population, Labrador population, Northeast Newfoundland population, South Newfoundland population, Southwest Newfoundland population, Northwest Newfoundland population, Quebec Eastern North Shore population, Quebec Western North Shore population, Anticosti Island population, Inner St. Lawrence population, Lake Ontario population, Gaspé-Southern Gulf of St. Lawrence population, Eastern Cape Breton population, Nova Scotia Southern Upland population, Inner Bay of Fundy population, Outer Bay of Fundy population) in Canada. Committee on the Status of Endangered Wildlife in Canada. Ottawa. xlvii + 136 pp.

Cutler, D. R., J. Edwards, Thomas C., K. H. Beard, A. Cutler, K. T. Hess, J. Gibson, and J. J. Lawler. 2007. Random Forests for Classification in Ecology. Ecology 88:2783-2792.

Dahl, J., J. Dannewitz, L. Karlsson, E. Petersson, A. Löf, and B. Ragnarsson. 2004. The timing of spawning migration: implications of environmental variation, life history, and sex. Canadian Journal of Zoology 82:1864-1870.

DFO. 1998. Atlantic Salmon Eastern Canada Overview 1998. Stock Status Report D0-01. Department of Fisheries and Oceans. Ottowa, Ontario.

Dugdale, S.J., Bergeron, N.E., and St-Hilaire, A. 2013. Temporal variability of thermal refuges and water temperature patterns in an Atlantic salmon river. Remote Sens. Environ. **136:** 358–373. doi:10.1016/j.rse.2013.05.018.

Dunham, J., K. Gallo, D. Shively, C. Allen, and B. Goehring. 2011. Assessing the feasibility of native fish reintroductions: a framework applied to threatened Bull trout. North American Journal of Fisheries Management 31:106-115.

Elliott, J. M., and Elliott, J.A. 2010. . 2010. Temperature requirements of Atlantic salmon *Salmo salar*, brown trout Salmo trutta and Arctic charr *Salvelinus alpinus*: predicting the effects of climate change. Journal of Fish Biology 77.

Erkinaro, J., F. Okland, K. Moen, E. Niemelä, and M. Rahiala. 1999. Return migration of Atlantic salmon in the River Tana: the role of environmental factors. Journal of Fish Biology 55:506–516.

Everitt, B. S., and T. Hothorn. 2009. A Handbook of Statistical Analyses Using R, Second Edition. Chapman & Hall/CRC, Boca Raton, FL.

Finstad, A. G., F. Økland, E. B. Thorstad, and T. C. Heggberget. 2005. Comparing upriver spawning migration of Atlantic salmon *Salmo salar* and sea trout *Salmo trutta*. Journal of Fish Biology 67:919–930.

Fleming, I. A. 1996. Reproductive strategies of Atlantic salmon: ecology and evolution. Reviews in Fish Biology and Fisheries 6:379-416.

Fleming, I. A. 1998. Pattern and variability in the breeding system of Atlantic salmon (*Salmo salar*), with comparisons to other salmonids. Canadian Journal of Fisheries and Aquatic Sciences 55:59-76.

Frechette, D. M., S. J. Dugdale, J. J. Dodson, and N. E. Bergeron. 2018. Understanding summertime thermal refuge use by adult Atlantic salmon using remote sensing, river temperature monitoring, and acoustic telemetry. Canadian Journal of Fisheries and Aquatic Sciences.

Gerlier, M., and P. Roche. 1998. A radio telemetry study of the migration of Atlantic salmon (*Salmo salar L.*) and sea trout (Salmo trutta trutta L.) in the upper Rhine. Hydrobiologia 371/372:283–293.

Gustafson, R. G., R. S. Waples, J. M. Myers, L. A. Weitkamp, G. J. Bryant, O. W. Johnson, and J. J. Hard. 2007. Pacific salmon extinctions: quantifying lost and remaining diversity. Conservation Biology 21:1009-1020.

Hasler, C. T., B. Mossop, D. A. Patterson, S. G. Hinch, and S. J. Cooke. 2012. Swimming activity of migrating Chinook salmon in a regulated river. Aquatic Biology 17:47-56.

Hawkins, A. D., and G. W. Smith. Radio-tracking observations on Atlantic salmon ascending the Aberdeenshire Dee. Scottish Fisheries Research Report 36:1-24.

Hewitt, N., N. Klenk, A. L. Smith, D. R. Bazely, N. Yan, S. Wood, J. I. MacLellan, C. Lipsig-Mumme, and I. Henriques. 2011. Taking stock of the assisted migration debate. Biological Conservation 144:2560-2572.

Hosmer Jr., D. W., S. Lemeshow, and R. X. Sturdivant. 2013. Applied Logistic Regression, Third Edition. John Wiley & Sons, Inc, Hoboken, New Jersey.

ICES. 2018. Report of the Working Group on North Atlantic Salmon (WGNAS), 4–13 April 2018, Woods Hole, MA, USA. ICES CM 2018/ACOM:21. 386 pp.

Izzo, L. K., G. A. Maynard, and J. Zydlewski. 2016. Upstream Movements of Atlantic Salmon in the Lower Penobscot River, Maine Following Two Dam Removals and Fish Passage Modifications. Marine and Coastal Fisheries 8:448-461.

Jokikokko, E., I. Kallio-Nyberg, and E. Jutila. 2004. The timing, sex and age composition of the wild and reared Atlantic salmon ascending the Simojoki River, northern Finland. Journal of Applied Ichthyology 20:37-42.

Jonsson, B., and N. Jonsson. 2011. Ecology of Atlantic Salmon and Brown Trout: Habitat as a Template for Life Histories. Springer, New York, NY.

Jonsson B., Jonsson N., and H. L. P. Does juvenile experience affect migration and spawning of adult Atlantic salmon? Behavioral Ecology and Sociobiology 26:225–230.

Jonsson, N. 1991. Influence of Water Flow, Water Temperature and Light on Fish Migration in Rivers. Nordic Journal of Freshwater Research 66:20-35.

Karppinen, P., J. Erkinaro, E. Niemelä, K. Moen, and F. Okland. 2004. Return migration of one-sea-winter Atlantic salmon in the River Tana. Journal of Fish Biology 64:1179–1192.

Kennedy, R. J., and M. Allen. 2016. The pre-spawning migratory behaviour of Atlantic salmon *Salmo salar* in a large lacustrine catchment. Journal of Fish Biology 89:1651-1665.

Klemetsen, A., P.-A. Amundsen, J. B. Dempson, B. Jonsson, N. Jonsson, M. F. O'Connell, and E. Mortensen. 2003. Atlantic salmon *Salmo salar* L., brown trout *Salmo trutta* L. and Arctic charr *Salvelinus alpinus* (L.): a review of aspects of their life histories. Ecology of Freshwater Fish 12:1-59.

Kuhn, M. 2008. Caret package. Journal of Statistical Software 28:1-26.Liaw, A., and M. Wiener. 2002. Classification and Regression by randomForest. R News 2:18-22.

Maechler, M., Rousseeuw, P., Struyf, A., Hubert, M., Hornik, K. (2018). cluster: Cluster Analysis Basics and Extensions. R package version 2.0.7-1.

Martin, B. T., R. M. Nisbet, A. Pike, C. J. Michel, and E. M. Danner. 2015. Sport science for salmon and other species: ecological consequences of metabolic power constraints. Ecology Letters 18:535-544.

Milner, N. J., D. J. Solomon, and G. W. Smith. 2012. The role of river flow in the migration of adult Atlantic salmon, *Salmo salar*, through estuaries and rivers. Fisheries Management and Ecology 19:537-547.

Mitchell, S. C., and R. A. Cunjak. 2007. Relationship of upstream migrating adult Atlantic salmon (*Salmo salar*) and stream discharge within Catamaran Brook, New Brunswick. Canadian Journal of Fisheries and Aquatic Sciences 64:563-573.

National Research Council. 1996. Upstream: salmon and society in the Pacific Northwest. National Academy Press, Washington, D.C.

Økland, F., J. Erkinaro, K. Moen, E. Niemelä, P. Fiske, R. S. McKinley, and E. B. Thorstad. 2001. Return migration of Atlantic salmon in the River Tana: phases of migratory behaviour. Journal of Fish Biology 59:862-874.

Okland, F., T. C. Heggberget, and B. Jonsson. 1995. Migratory behaviour of wild and farmed Atlantic salmon (*Salmo salar*) during spawning. Journal of Fish Biology 46:1-7.

Pess, G. R., R. Hilborn, K. Kloehn, T. P. Quinn, and M. Bradford. 2012. The influence of population dynamics and environmental conditions on pink salmon (*Oncorhynchus gorbuscha*) recolonization after barrier removal in the Fraser River, British Columbia, Canada. Canadian Journal of Fisheries and Aquatic Sciences 69:970-982.

Pess, G. R., P. M. Kiffney, M. C. Liermann, T. R. Bennett, J. H. Anderson, and T. P. Quinn. 2011. The Influences of Body Size, Habitat Quality, and Competition on the Movement and Survival of Juvenile Coho Salmon during the Early Stages of Stream Recolonization. Transactions of the American Fisheries Society 140:883-897.

Power, G. 1981. Stock Characteristics and Catches of Atlantic Salmon (Salmo solar) in Quebec, and Newfoundland and Labrador in Relation to Environmental Variables. Canadian Journal of Fisheries and Aquatic Sciences 38:1601-1611.

Quinn TP, Brannon EL, Whitman RP (1983) Pheromones and the water source preferences of adult coho salmon Oncorhynchus kisutch Walbaum. J Fish Biol 22:677–684

Richard, A., L. Bernatchez, E. Valiquette, M. Dionne, and B. Jonsson. 2014. Telemetry reveals how catch and release affects prespawning migration in Atlantic salmon (*Salmo salar*). Canadian Journal of Fisheries and Aquatic Sciences 71:1730-1739.

Roy, M. L., A. G. Roy, J. W. A. Grant, N. E. Bergeron, and I. Fleming. 2013. Individual variability in the movement behaviour of juvenile Atlantic salmon. Canadian Journal of Fisheries and Aquatic Sciences 70:339-347.

Royston, P., and D. G. Altman. 1994. Regression Using Fractional Polynomials of Continuous Covariates: Parsimonious Parametric Modelling. Journal of the Royal Statistical Society. Series C (Applied Statistics) 43:429-467.

Schoen, E. R., M. S. Wipfli, E. J. Trammell, D. J. Rinella, A. L. Floyd, J. Grunblatt, M. D. McCarthy, B. E. Meyer, J. M. Morton, J. E. Powell, A. Prakash, M. N. Reimer, S. L. Stuefer, H. Toniolo, B. M. Wells, and F. D. W. Witmer. 2017. Future of Pacific Salmon in the Face of Environmental Change: Lessons from One of the World's Remaining Productive Salmon Regions. Fisheries 42:538-553.

Scott, W.B and Scott, M.G. 1988. Atlantic fishes of Canada. Canadian Bulletin of Fisheries and Aquatic Sciences. 219: 731 p.

Seddon, P. J., D. P. Armstrong, and R. F. Maloney. 2007. Developing the science of reintroduction biology. Conservation Biology21:303-312.

Stabell O.B. 1984. Homing and olfaction in salmonids: a critical review with special references to the Atlantic salmon. Biological Review 59: 333-388,

Thomas, C. D. 2011. Translocation of species, climate change, and the end of trying to recreate past ecological communities. Trends Ecology and Evolution 26:216-221.

Thorstad, E. B., P. Fiske, K. Aarestrup, N. A. Hvidsten, T. G. Hårsaker, T. C. Heggberget, and F. Okland. 2003. Upstream migration of Atlantic salmon in three regulated rivers. Pages 111–121 in Aquatic telemetry: advances and applications. FAO/COISPA, Ustica, Italy.

Thorstad, E. B., F. Økland, K. Aarestrup, and T. G. Heggberget. 2008. Factors affecting the within-river spawning migration of Atlantic salmon, with emphasis on human impacts. Reviews in Fish Biology and Fisheries 18:345-371.

Thorstad, E. B., F. Okland, and A. G. Finstad. 2000. Effects of telemetry transmitters on swimming performance of adult Atlantic salmon. Journal of Fish Biology 57:531-535.

Thorstad, E. B., F. Whoriskey, A. H. Rikardsen, and K. Aarestrup. 2011. Aquatic Nomads: The Life and Migrations of the Atlantic Salmon. Pages 1-23 in O. Aas, E. S., A. Klemesten, and J. Skurdal, editors. Atlantic Salmon Ecology. John Wiley & Sons Ltd, Chichester, West Sussex, PO19 8SQ, United Kingdom.

Trépanier, S., M. A. Rodriguez, and P. Magnan. 1996. Spawning migrations in landlocked Atlantic salmon: time series modelling of river discharge and water temperature effects. Journal of Fish Biology 48:925–936.

Venables, W. N., and B. D. Ripley. 2002. Modern Applied Statistics with S. Fourth Edition. Springer, New York.

Wilkie, M. P., M. A. Brobbel, K. Davidson, L. Forsyth, and B. L. Tufts. 1997. Influences of temperature upon the postexercise physiology of Atlantic salmon (Salmo salar). Canadian Journal of Fisheries and Aquatic Sciences 54:503–511.

Wolf, C. M., B. Griffith, C. Reed, and S. A. Temple. 1996. Avian and mammalian translocations: update and reanalysis of 1987 survey data. Conservation Biology10:1142-1154.

Zuur, A. F., A. A. Saveliev, E. N. Ieno, and G. M. Smith. 2009. Mixed effects models and extensions in ecology with R. Springer, New York, NY.

9 DISCUSSION GÉNÉRALE ET CONCLUSION

9.1 General discussion and conclusions

Taken together, the three chapters of this thesis provide a detailed description of how adult Atlantic salmon use habitat during the colonization of a pristine, unregulated river in relation to biotic and abiotic variables at a high spatial and temporal resolution. The findings presented herein will be a direct asset for optimizing future reintroduction and colonization programs in unregulated river systems, and may be applied to regulated systems as well.

The results presented in Chapter 1 indicate a strong propensity for salmon to remain in novel habitat, thereby confirming that translocation of adults is a viable strategy for rehabilitating or re-establishing Atlantic salmon populations. Although the findings of this study are of primary importance for local managers, they also have more far-reaching implications, as they may be useful for setting initial transport targets when implementing similar programmes in other free-flowing systems.

Transported individuals were exposed to a wide range of river discharge and temperature conditions, however, the propensity to fallback was not linked to the environmental conditions at the time of transport. Conditions experienced by salmon during transport were held to a narrow range to reduce the chance of inducing a stress response. Since transport conditions did not appear to influence the propensity to fallback, therefore, it is likely that the efforts to reduce stress during handling and transport were successful. Although not included in the time-to-event analysis, the direction a fish initially moved following release into novel habitat may be a good indicator of whether an individual will exhibit fallback, as the majority of salmon that fell back initially moved in the downstream direction after release, whereas 70% salmon that remained upstream initially moved upstream after release. Consequently, in programs where costs prohibit as exhaustive of a telemetry approach as was employed in this study, deployment of acoustic or radio-telemetry receivers immediately upstream or downstream of a release site may provide an indication of the number of salmon that remain in a novel habitat following release.

In our study, fish length appeared to be the strongest driver of fallback after transport, suggesting that transport of small and average-sized salmon would result in lower fallback rates than transport of large (> 780 mm) individuals. The estimate that 30% of average-sized salmon exhibit fallback within 7 days of transport suggests that to meet the program target for colonization of the novel habitat on the Nord-Est, it may be necessary to increase the number of individuals transported by approximately 30%. Although this suggestion may result in the desire to transport only salmon with the lowest risk of fallback (i.e. smaller salmon), intentionally selecting salmon for transport based on size may result in artificial selection for smaller bodied individuals or those that initiate spawning migration after fewer years at sea. Not all large individuals exhibited fallback, and some studies have indicated that larger salmon (with the exception of repeat spawners) may have greater reproductive success than smaller individuals (Fleming 1996; Garant et al. 2001, 2003; Berntson et al. 2011), therefore, intentionally choosing individuals for transport based on size is generally not recommended. Given that four of five salmon greater than 90 cm FL (all female) exhibited fallback, however, suggests that a size cut-off of 90 cm could be beneficial to ensure that the larger females are not removed from the spawning population and are able to contribute offspring to subsequent generations.

The results presented in Chapter 2 highlight the importance of combining aerial and ground-based methods to identify thermal refuges that are suitable for use by adult salmon.

The use of thermal refuges for behavioral thermoregulation at lower temperatures than previously recorded for this species, combined with the fact that individuals were less active at high temperature and low discharge highlights the importance of thermal refuge habitat for adult salmon during summer, in-river residence, especially in rivers where low discharge and high temperature co-occur. Maintaining access to large, stable refuges may be crucial for persistence of Atlantic salmon within their North American range given current climate change scenarios that predict warmer, drier summers.

The previously unreported use of warm water patches during summer by migrating adult salmon that was observed in the Nord-Est could allow adults to remain within an optimal temperature range to balance energy conservation with gamete maturation (Berman and Quinn 1991; Newell and Quin 2005; Hasler et al. 2012). Use of cool and warm patch in the Nord-Est may suggest that adults have a narrow optimal temperature range similar to that previously described to optimize growth in juvenile Atlantic salmon, i.e. approximately 16-20°C (Elliott 1991; Jonsson and Jonsson 2009). Consequently, in selecting drainages or river reaches for colonization by adult salmon, priority should be placed on those that contain an adequate number of deep pools with thermal refuges to support the number of adults to be introduced. If thermal refuge habitat is lacking, release of adults could occur later in the season, when the risk of exposure to high heat events is reduced, but before temperatures drop low enough to prevent salmon from ascending obstacles. Timing of release must also take local discharge regimes into consideration, as release when river discharge is too low could prevent salmon from accessing thermal refuges or spawning habitat.

The results presented in Chapter 3 provide a detailed picture of the movement patterns and habitat use by adult Atlantic salmon during the colonization of a pristine, unregulated river in relation to biotic and abiotic variables at a high spatial and temporal resolution. Thorough understanding of how salmon colonize novel habitat will be a direct asset for optimizing future reintroduction and colonization programs. The findings of this study support the results of Chapter 2 by further highlighting the importance of pools where salmon can rest during upstream migration (Økland et al. 2001, Finstad et al. 2005, Richard et al. 2014). The behavioral patterns observed may reflect the different evolutionary strategies exhibited by males and females for maximizing fitness. Male Atlantic salmon maximize reproductive success by spawning with multiple females (Fleming 1996). The greater incidence of exploratory behavior exhibited by males may be explained by their actively searching for females to increase mating success, which is supported by the observed increase in exploratory movements from mid-September as river temperature cooled and spawning season approached. The greater incidence of sedentary behavior exhibited by females may reflect the need to conserve energy stores necessary for egg development, redd digging, and egg laying to maximize reproductive success (Fleming 1996, 1998).

Although this study was conducted using transported individuals in a novel habitat, spawning behavior is highly conserved in salmon, such that spawning occurs at the right time to maximize offspring survival (Fleming 1998). It is possible, therefore, that the movement patterns observed in the Nord-Est may be broadly applicable across systems and used to predict how Atlantic salmon will react to novel habitat during reintroduction, assisted migration, or range expansion.

9.2 On-going research and future considerations

The general endpoint used to measure the success of a colonization program is the establishment of a self-sustaining population (Griffith et al. 1989, Pess et al. 2012). The colonization program initiated in the Nord-Est Sainte-Marguerite River in 1982 via installation of the fish ladder at Chute Blanche has led to a self-sustaining population that reproduces annually between Chute Blanche and the impassible Chute du 16 Miles, and can be deemed successful based on this metric. The colonization of novel habitat upstream of the impassible falls, however, will never yield a self-sustaining population because salmon can only access the novel habitat through continuation of the trap and haul program. Thus, a different metric is necessary to evaluate the success of the translocation program on the Nord-Est.

The ultimate goal of the translocation program on the Nord-Est is to provide a demographic boost in terms of the numbers of adults returning to the river to spawn in future years. Specifically, increasing juvenile rearing habitat is expected to increase smolt production to mitigate the effects of poor marine survival on adult returns. There are two primary pathways by which the translocation program on the Nord-Est may enhance smolt production. First, if translocation results in reduced juvenile rearing density in the novel habitat, survival to the smolt stage may be greater than in accessible (high-density) habitat. Consequently, more smolts may be produced per spawner in the novel versus accessible habitat, which could translate to an increase in overall smolt production for the river. Secondly, increasing the juvenile growth rate via reduced juvenile rearing density may result in younger age at smolt outmigration (Fleming 1998).

The true success of the translocation program cannot be evaluated in the number of adults that remained upstream, or how they used the habitat, but in how the use of this additional habitat translates into increased production of out-migrating smolts that become spawning adults. The success of the translocation program in the Nord-Est, measured in terms of increased smolt production, will depend on whether reducing adult spawner abundance translates to reduced juvenile rearing densities to the point that offspring are released from the negative effects of density-dependence. The distribution of spawning habitat, spawning site selection by adults, and the proximity to quality rearing habitat for offspring will all influence subsequent juvenile density and the success of the translocation program to increase smolt production (e.g. Einum et al. 2006, Finstad et al. 2009, Foldvik et al. 2010).

Although it is beyond the scope of the current dissertation because of on-going data collection, we also conducted spawning surveys to assess redd density, electro-fishing to estimate parr density, and smolt trapping to estimate smolt abundance in both the colonization habitat and in the previously colonized habitat between Chute Blanche and Chute du 16. Redd surveys were conducted during late October in 2015 and 2016 (high river flows prevented surveys during 2014). Electro-fishing was conducted during 2016 and 2017 to estimate juvenile density at the end of the summer growing season in late August/early September. Scales collected during electro-fishing were used to determine size-at-age for 0+ and 1+ parr. Finally, smolt trapping was conducted during 2017 and 2018 to compare size and age at outmigration (via scale analysis) between the colonization habitat and the downstream, previously colonized habitat. Because 2016 was the final year of adult transport, two-year-old smolts produced by the 2016 spawning are expected to outmigrate in 2019, so a third and final year of smolts trapping will occur in 2019. Once those data are collected and scales are analyzed, then we will have a better understanding of how the increased habitat translated to juvenile production. Preliminary results are presented here.

Adult abundance was considerably lower upstream of Chute du 16 (7 in 2014, 18 in 2015, and 22 in 2016) than between Chute Blanche and Chute du 16 (135 in 2014, 71 in 2015, and 190 in 2016). The reduced adult abundance upstream of Chute du 18 translated into lower redd density: mean redd density in the surveyed habitat during 2016 was 2 redds per site upstream of Chute du 18 Sector and 8 redds per site between Chute Blanche and Chute du 16. Relative juvenile density was lower in upstream, low-redd-density sites (2016 = 0.02 parr/m^2; 2017 = 0.04 parr/m^2) than in the high-redd density sites downstream of Chute du 16 (2016 = 0.75 parr/m^2; 2017 = 0.1 parr/m^2). Parr were significantly larger for their age at low density sites than at high density sites. During 2016, median fork length of age-0+ parr was 62 mm at low-density sites and 47 mm at high-density sites (Kruskal-Wallis test, $p < 0.01$). Age 0+ parr were again significantly larger in low density habitat (median FL = 60 mm) than age 0+ parr in high density habitat (median FL = 47 mm). Age 1+ parr were also significantly larger in the low-density habitat upstream of Chute du 18 (median FL = 108 mm) than age 1+ parr captured in the high-density habitat downstream of Chute du 16 (median FL = 77 mm; Kruskal-Wallis test, $p < 0.01$).

One of the conditions that must be satisfied before the use of colonization of unoccupied habitat for population enhancement is approved is that no sensitive species are present in the targeted river or river reaches (MFFP 2016). Prior to the initiation of the transport program on the Nord-Est, electro-fishing surveys were conducted upstream of Chute due 18 by a consulting firm (AECOM 2014). The only species present was Brook trout (*Salvelinas fontinalis*). It was beyond the scope of the current study to assess interactions between the offspring of transported adult Atlantic salmon. Brook trout and Atlantic salmon are sympatric, native species in the Province of Quebec, with relatively low niche overlap (Thibault and Dodson 2013). During electro-fishing surveys, brook trout were also captured. The habitat at site-of-capture was recorded for the two species and will be analyzed in the future. In general, however, Brook trout were found in slow moving water near the stream margin and in tributaries, whereas Atlantic salmon parr were captured in swifter moving water and further from stream margins. Further, these two species do co-occur in accessible parts of the Nord-Est, and although it is possible that Atlantic salmon parr may have caused some displacement of Brook Trout into less favorable habitat, the low abundance of salmon parr is unlikely to have substantial impacts on the resident Brook trout population in upstream of Chute du 18.

Sub-optimal placement of a rotary screw-trap in the high-density habitat prevented estimation of smolt abundance in 2017 and resulted in very wide confidence intervals around the 2018 estimate (4583 smolts; 95% CI: 542 – 8623). Recapture rates for smolts captured in low density habitat were substantially better and resulted in smolt abundance estimates of 440 smolts (95% CI: 208-1006) in 2017 and 2581 smolts (95% CI: 1338 - 3823) in 2018 produced using the modification of the Peterson method (FSA package for R, Ogle et al. 2019). Based on scale analysis, all smolts captured during 2017 were age 2+ and were offspring of the one female that spawned during 2014. Three smolt age classes were identified during 2017 in the high density habitat: age 1+, age 2+, and age 3+. Age-2+ smolts captured upstream of Chute du 18 were significantly larger (median FL = 147 mm) than age-2+ smolts captured downstream of Chute Blanche (median FL = 117 mm; Kruskal-Wallis test, $p < 0.01$). Age-determination of the 2018 smolt scales is on-going, however, smolts were again larger upstream of Chute du 18 (median FL = 140 mm) than downstream of Chute Blanche (median FL = 121 mm).

Overall, transporting adult Atlantic salmon into novel habitat resulted in reduced spawning and rearing density and increased size-at-age for 0+ and 1+ parr. Smolts produced in the low density habitat were both larger younger than smolts produced in the high-density habitat. It is uncertain whether the faster growth and greater smolt size that resulted from low-density rearing will translate to increased marine survival and greater adult returns. Detection of passive integrated transponders deployed in smolts at both trapping locations in 2018 may provide an initial indication of marine survival, but sample size may limit the ability to interpret any observed trends. If patterns in scale growth differ between salmon from the high- and low-density habitats, it may be possible in future years to capture returning adults in the Chute Blanche fish ladder and collect scales to assess relative marine survival between the two rearing habitats. Such analyses would provide the final measure of success for the transport program on the Riviere Sainte-Marguerite Nord-Est.

10 BIBLIOGRAPHIE – CHAPITRE 9

AECOM. 2014. *Réfection de la passe migratoire de la rivière Sainte-Marguerite Nord-Est et colonisation du secteur amont des chutes du Dix-Huit. Rapport technique décrivant les interventions réalisées en 2012 - 2013.* Présenté au programme de mise en valeur des habitats du saumon atlantique de la Côte-Nord. 35 pages et annexes.

Berman CH, Quinn TP (1991) Behavioural thermoregulation and homing by spring chinook salmon, *Oncorhynchus tshawytscha* (Walbaum), in the Yakima River. *Journal of Fish Biology* 39: 301-312.

Berntson EA., Carmichael RW, Flesher MW, Ward EJ, Moran P (2011) Diminished Reproductive Success of Steelhead from a Hatchery Supplementation Program (Little Sheep Creek, Imnaha Basin, Oregon). *Transactions of the American Fisheries Society* 140: 685-698.

Einum S, Sundt-Hansen L, Nislow KH (2006) The partitioning of density-dependent dispersal, growth and survival throughout ontogeny in a highly fecund organism. *Oikos* 113:489-496.

Elliott JM (1991). Tolerance and resitance to thermal stress in juvenile Atlantic salmon, *Salmo salar*. *Freshwater Biol*ogy 25:61-70.

Finstad AG, Einum S, Ugedal O, Forseth T (2009) Spatial Distribution of Limited Resources and Local Density Regulation in Juvenile Atlantic Salmon. *Journal of Animal Ecology* 78:226-235.

Finstad, AG, Okland F, Thorstad EB, Heggberget TG (2005) Comparing upriver spawning migration of Atlantic salmon *Salmo salar* and sea trout *Salmo trutta*. *Journal of Fish Biology* 67:919-930.

Fleming, IA (1996) Reproductive strategies of Atlantic salmon: ecology and evolution. *Reviews in Fish Biology and Fisheries* 6:379-416.

Fleming, IA (1998) Pattern and variability in the breeding system of Atlantic salmon (Salmo salar), with comparisons to other salmonids. *Canadian Journal of Fisheries and Aquatic Sciences* 55:59–76.

Foldvik, A., A. G. Finstad, and S. Einum. 2010. Relating juvenile spatial distribution to breeding patterns in anadromous salmonid populations. J Anim Ecol **79**:501-509.

Garant D, Bernatchez L, Dodson J (2001) A genetic evaluation of mating system and determinants of individual reproductive success in Atlantic salmon (*Salmo salar* L.). *The Journal of Heredity* 92:137-145.

Garant D, Bernatchez L, Dodson J (2003) Differential reproductive success and hereitability of alternative reproductive tactics in wild Atlantic salmon (*Salmo salar* L.). *Evolution:* 57:1133- 1141.

Griffith, B, Scott, JM, Carpenter, JW, Reed C (1989) Translocations as a species conservation tool: status and strategy. *Science* 245**:**477-480.

Hasler CT, Cooke SJ, Hinch SG, Guimond E, Donaldson MR, Mossop B, Patterson DA (2012) Thermal biology and bioenergetics of different upriver migration strategies in a stock of summer-run Chinook salmon. *Journal of Thermal Biology* 37:265–272.

Jonsson, B, Jonsson N (2009) A review of the likely effects of climate change on anadromous Atlantic salmon Salmo salar and brown trout Salmo trutta, with particular reference to water temperature and flow. *Journal of Fish Biology* 75: 2381–2447.

Newell JC, Quinn TP (2005) Behavioral thermoregulation by maturing adult sockeye salmon (*Oncorhynchus nerka*) in a stratified lake prior to spawning. *Canadian Journal of Zoology* 83: 1232-1239.

Ogle DH, Wheeler P, Dinno A (2019). FSA: Fisheries Stock Analysis. R package version 0.8.23, https://github.com/droglenc/FSA.

Pess, GR, Hilborn R, Kloehn K, Quinn, TP (2012) The influence of population dynamics and environmental conditions on pink salmon (Oncorhynchus gorbuscha) recolonization after barrier removal in the Fraser River, British Columbia. *Canadian Journal of Fisheries and Aquatic Science*s 69: 970-982.

Richard A, Bernatchez L, Valiquette E, Dionne M, Jonsson B (2014) Telemetry reveals how catch and release affects prespawning migration in Atlantic salmon (Salmo salar). Canadian Journal of Fisheries and Aquatic Sciences 71:1730-1739.

Thibault I, Dodson J (2013). Impacts of exotic rainbow trout on habitat use by native juvenile salmonid species at an early invasive stage. *Transactions of the American Fisheries Society* 142:1141-1150.

ANNEXE I

Six-point classification used to score injury type.

Injury Score	Description
0	No visible external injury
1	Light to mild descaling
2	Torn fins OR heavy descaling OR superficial marks to head
3	Small cuts on head OR bruising to head or body
4	Open wounds on body
5	Catch and release: hook injury to mouth/face/gills

ANNEXE II

Identity, release date, sex, and fork length (FL) of adult salmon transported by year and fallback type.

Year	Type	Tag ID	Date	Sex	FL
2014	Complete	19176	27/Jul/14	M	585
	Partial	19170	22/Jul/14	F	780
		19172	24/Jul/14	M	545
		19175	26/Jul/14	M	560
	Pre-Spawn (partial)	19174	26/Jul/14	M	745
	No Fallback	19171	24/Jul/14	F	875
		19173	26/Jul/14	M	545
		19195	27/Jul/14	M	820
		19177	27/Jul/14	M	560
		19178	27/Jul/14	M	580
		19180	5/Sep/14	M	600
		19179	5/Sep/14	F	750
2015	Complete	19187	16/Jul/15	F	755
		19189	18/Jul/15	M	770
	Pre-Spawn (complete)	19184	15/Jul/15	F	780
		19193	2/Aug/15	M	560
	Partial	19181	30/Jun/15	F	930
		19183	8/Jul/15	F	950
		19192	1/Aug/15	F	750
	Post-spawn	19188	16/Jul/15	F	750
	No Fallback	19182	7/Jul/15	M	810
		19185	15/Jul/15	F	930
		19186	15/Jul/15	M	790
		19190	31/Jul/15	M	585
		19191	31/Jul/15	F	685
		19194	3/Aug/15	M	835
		19196	4/Aug/15	F	780
		19197	5/Aug/15	M	560
		19198	6/Aug/15	M	780
		19199	6/Aug/15	M	580
		19983	9/Aug/15	M	580
		19984	9/Aug/15	M	520
		19985	14/Aug/15	F	770
		19986	14/Aug/15	F	775
		19987	15/Aug/15	M	600
		37369	17/Aug/15	F	770
		37370	24/Aug/15	M	600

Year	Type	Tag ID	Date	Sex	FL
2016	Complete	2910	13/Jul/16	M	790
		2909	13/Jul/16	F	780
		37366	22/Jul/16	F	740
		37363	23/Jul/16	F	810
		2908	3/Aug/16	F	920
	Partial	2915	29/Jun/16	F	720
		2916	1/Jul/16	F	975
		37364	19/Jul/16	M	790
		37368	22/Jul/16	M	860
		2900	18/Aug/16	F	780
	Post-spawn	2918	12/Jul/16	F	740
		2913	12/Jul/16	M	770
		37372	14/Jul/16	F	770
		37365	20/Jul/16	F	895
		37357	3/Aug/16	M	540
		2901	18/Aug/16	M	750
	No Fallback	2914	29/Jun/16	M	820
		2917	10/Jul/16	F	720
		2912	12/Jul/16	M	820
		2911	13/Jul/16	F	770
		37371	14/Jul/16	F	810
		37373	14/Jul/16	F	720
		37367	22/Jul/16	M	765
		37362	23/Jul/16	M	545
		37361	24/Jul/16	M	570
		37360	26/Jul/16	F	760
		37358	3/Aug/16	M	560
		37359	3/Aug/16	M	580
		2902	11/Aug/16	M	830
		2903	11/Aug/16	M	680
		2899	22/Aug/16	M	630

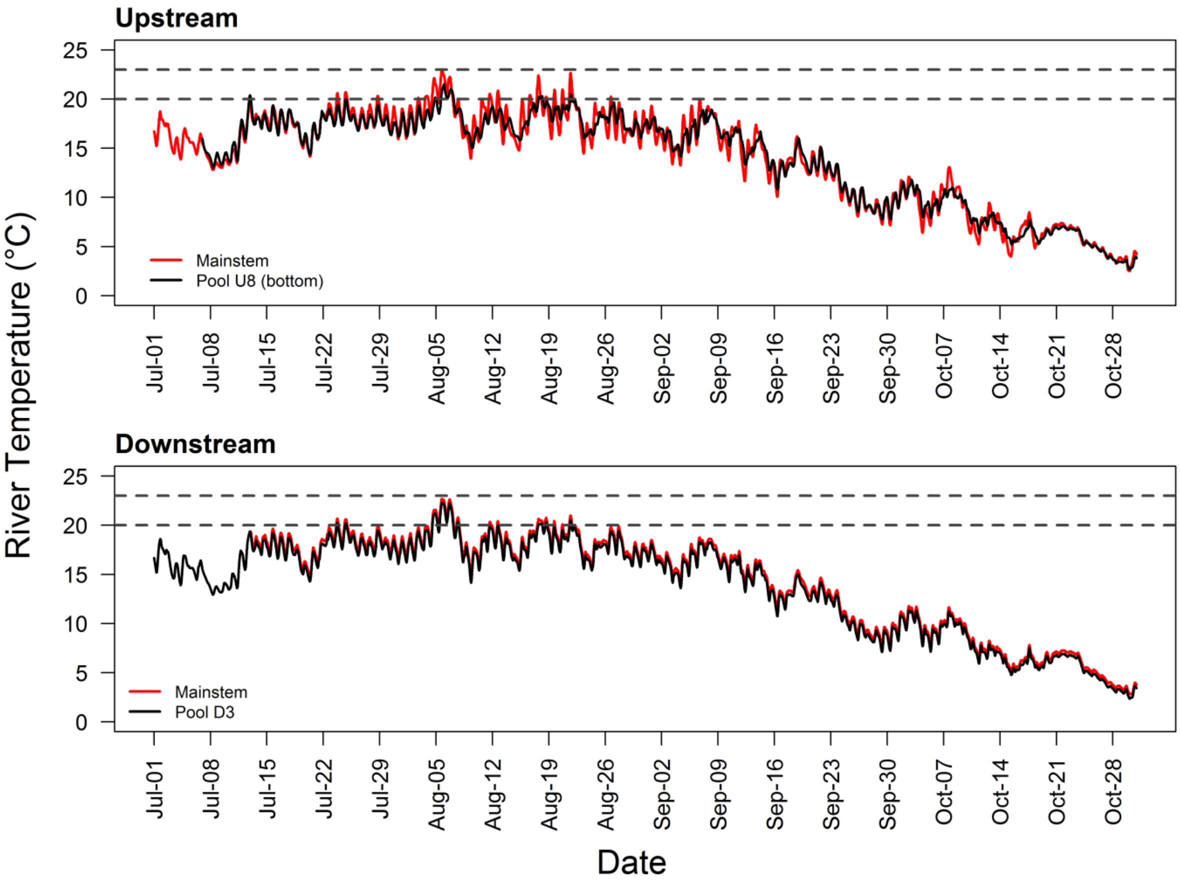
ANNEXE III

Summary statistics for continuous variables that were measured but not included as explanatory variables in the time-to-event analysis. Sample size (N) used to compute each metric (number of transports and number of individual salmon) is also presented.

	Mean	SD	Min	Max	N (transports/fish)
Air T (°C)	17.0	3.0	9.0	24.0	35/50
River T: arrival (°C)	17.6	1.4	14.0	19.9	43/68
Tank T: departure (°C)	18.1	1.5	14.6	20.5	42/66
Tank T: Arrival (°C)	18.1	1.5	14.6	20.5	40/61
Tank T - Ladder T: departure (°C)	0.6	0.4	-0.6	1.5	42/66
Tank T - River T: arrival (°C)	0.6	0.6	-1.0	2.2	40/61
O_2 saturation at departure (%)	115	21	88	180	37/55
O_2 saturation at arrival (%)	112	16	88	175	37/55

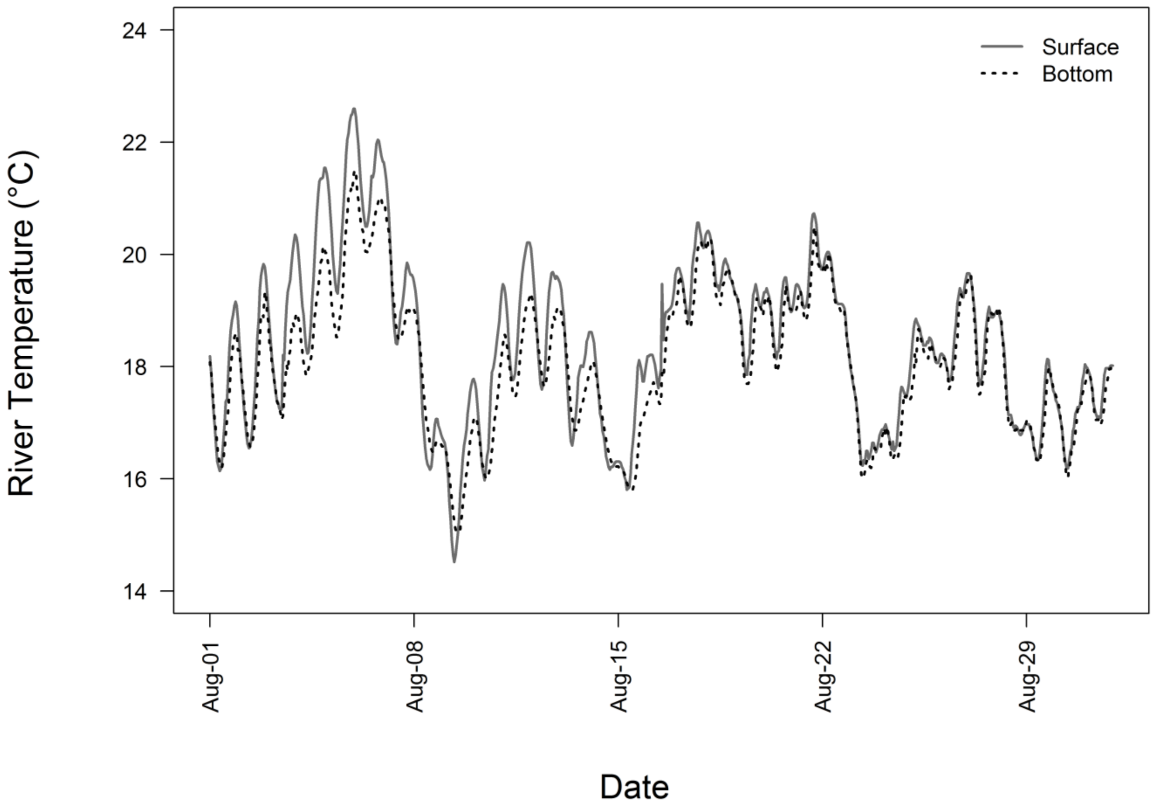
ANNEXE IV

River temperature measured in the Rivière Sainte-Marguerite Nord-Est during 2016 at rkm 45 and at the bottom of pool U8 in the upstream sector and at rkm 30 and at the bottom of pool D3 in the downstream sector.



ANNEXE V

Temperature logged 10 cm below the surface and 10 cm above the substrate in pool U8, indicating presence of thermal stratification in the pool during August 2016.



ANNEXE VI

Characteristics of tagged Atlantic salmon included in movement analysis (Chapter 7). Transmitter ID corresponds to Tag ID in Annex II, and are a subset of the individuals included in the analysis of fallback (Chapter 3).

Year	Fish ID	Transmitter ID	Date Tagged	Sex	FL (cm)
2014	2014-M-01	19173	26-Jul-14	M	54.5
	2014-M-02	19195	27-Jul-14	M	82
	2014-M-03	19177	27-Jul-14	M	56
	2014-M-04	19178	27-Jul-14	M	58
	2014-M-05	19180	05-Sep-14	M	60
	2014-F-06	19179	05-Sep-14	F	75
2015	2015-M-01	19182	07-Jul-15	M	81
	2015-F-02	19185	15-Jul-15	F	93
	2015-M-03	19186	15-Jul-15	M	79
	2015-F-04	19188	16-Jul-15	F	75
	2015-M-05	19190	31-Jul-15	M	58.5
	2015-F-06	19191	31-Jul-15	F	68.5
	2015-M-07	19197	05-Aug-15	M	56
	2015-M-08	19198	06-Aug-15	M	78
	2015-M-09	19199	06-Aug-15	M	58
	2015-M-10	19983	09-Aug-15	M	58
	2015-M-11	19984	09-Aug-15	M	52
	2015-F-12	19985	14-Aug-15	F	77
	2015-F-13	19986	14-Aug-15	F	77.5
	2015-M-14	19987	15-Aug-15	M	60
	2015-F-15	37369	17-Aug-15	F	77
	2015-M-16	37370	24-Aug-15	M	60
2016	2016-M-01	2914	29-Jun-16	M	82
	2016-F-02	2917	10-Jul-16	F	72
	2016-F-03	2918	12-Jul-16	F	74
	2016-M-04	2913	12-Jul-16	M	77
	2016-M-05	2912	12-Jul-16	M	82
	2016-F-06	2911	13-Jul-16	F	77
	2016-F-07	37371	14-Jul-16	F	81
	2016-F-08	37372	14-Jul-16	F	77
	2016-F-09	37373	14-Jul-16	F	72
	2016-F-10	37365	20-Jul-16	F	89.5
	2016-M-11	37367	22-Jul-16	M	76.5
	2016-M-12	37361	24-Jul-16	M	57
	2016-F-13	37360	26-Jul-16	F	76
	2016-M-14	37357	03-Aug-16	M	54
	2016-M-15	37358	03-Aug-16	M	56
	2016-M-16	37359	03-Aug-16	M	58
	2016-M-17	2902	11-Aug-16	M	83
	2016-M-18	2903	11-Aug-16	M	68
	2016-M-19	2901	18-Aug-16	M	75
	2016-M-20	2899	22-Aug-16	M	63

ANNEXE VII

Summary statistics for daily temperature and discharge for the period when tagged salmon were available in the colonization habitat upstream of Chute du 18 each year of the study.

Year	No. of Days	Mean	Median	Min	Max
			Temperature (°C)		
2014	94	14.24	15.63	5.24	22.23
2015	113	15.12	16.82	1.95	21.56
2016	125	14.48	16.27	3.49	21.93
			Discharge (m^3s^{-1})		
2014	94	27.65	17.59	6.74	167.31
2015	113	24.91	21.65	8.98	78.95
2016	125	20.10	15.35	8.09	112.60

ANNEXE VIII

Measured pool characteristics. Measurements in bold were included in the random forest analysis of habitat use. Measurements in italics were used to calculate the expansion factor.

	Pool Use		**Pool surface area (m^2)**	**Max. pool depth (m)**	*Max. pool width (m)*	*Upstream channel width (m)*	**Expansion factor**	**Mean distance to spawning sites (km)**	**Cold seep**
Receiver	**Frequency**	Hours							
U1	**7**	27.7	8714.0	1.3	*68.3*	*44.8*	1.5	6.9	P
U8	**24**	140.2	1176.7	2.9	*25.1*	*46.2*	0.5	3.3	A
U5	**180**	1433.6	6743.8	2.4	*56.1*	*47.5*	1.2	1.1	A
U4	**189**	2124.3	7770.7	3.3	*51.2*	*57.3*	0.9	3.3	P
U2	**197**	2097.1	9169.4	5.3	*40.0*	*48.1*	0.8	6.0	A
U3	**290**	2959.7	7710.8	4.0	*64.0*	*46.6*	1.4	4.3	P
U6	**309**	3627.2	5901.7	3.0	*42.0*	*36.5*	1.2	1.2	P
U7	**867**	15201.5	23800.9	6.2	*134.5*	*38.7*	3.5	2.7	P