ISABEL THIBAULT

INVASION DE LA TRUITE ARC-EN-CIEL (*ONCORHYNCHUS MYKISS*) DANS L'EST DU QUÉBEC

Thèse présentée
à la Faculté des études supérieures de l'Université Laval
dans le cadre du programme de doctorat en biologie
pour l'obtention du grade de Philosophiae doctor (Ph.D.)

DÉPARTEMENT DE BIOLOGIE
FACULTÉ DES SCIENCES ET GÉNIE
UNIVERSITÉ LAVAL
QUÉBEC

2010

Résumé

Les invasions biologiques constituent l'une des plus grandes menaces pour la biodiversité. La truite arc-en-ciel, un salmonidé originaire de la côte ouest de l'Amérique du Nord, en est un bon exemple. Introduite dans près de cent pays pour des raisons essentiellement récréatives, elle a eu d'importants impacts négatifs sur la faune et les écosystèmes indigènes. Au Québec, son introduction remonte à la fin du XIX^{e} siècle. Bien que son ensemencement soit restreint aux régions situées dans la portion sud-ouest de la province, on dénombre de plus en plus de captures et d'événements de reproduction dans les rivières de l'Est du Québec, où elle pourrait entrer en compétition avec deux salmonidés indigènes : le saumon atlantique et l'omble de fontaine. La présente étude avait pour objectif principal d'évaluer la capacité de la truite arc-en-ciel à franchir différents filtres hiérarchiques qui limitent le succès des invasions, soit la pression d'introduction, la résistance abiotique, la résistance biotique et la capacité de dispersion. Nous avons démontré que les populations naturalisées suite aux ensemencements dans les lacs Ontario et Memphrémagog étaient les principales sources de l'invasion de l'espèce dans l'Est du Québec. Elles ont notamment mené à l'établissement d'une population dans la région de Charlevoix, qui contribue désormais elle-aussi fortement au processus d'invasion. La présence de l'espèce exotique dans les rivières à saumon semble principalement associée à la présence de tributaires, qui fourniraient un refuge contre les fluctuations de débit, notamment contre les crues printanières qui surviennent durant la période d'éclosion des œufs et d'émergence des alevins. Une relation positive a également été observée entre l'occurrence de l'espèce et la température moyenne durant la saison de croissance, laissant présager une intensification de l'invasion parallèlement au réchauffement climatique. Au stade juvénile, nous avons observé que la présence des deux compétiteurs indigènes, malgré une taille supérieure au début de la première année de vie, n'affectait pas la croissance de la truite arc-en-ciel. Au contraire, l'espèce exotique, malgré de faibles densités, les obligerait à utiliser des habitats moins préférentiels et à partager plus intensément les ressources disponibles. Finalement, nous avons observé que la présence d'un phénotype anadrome favorisait grandement la dispersion de l'espèce vers les rivières de l'Est du Québec.

Abstract

Biological invasions are threatening biodiversity. One good example is the rainbow trout, a salmonid from the North American west coast. Introduced in about one hundred countries, mainly for recreational purposes, it had important detrimental impacts on native fauna and ecosystems. Its introduction in Quebec watersheds started at the end of the XIXth century. Even if its stocking is restricted to the south-western part of the province, captures and reproduction events are more and more frequent in Eastern Quebec streams, where it could compete with two indigenous salmonids: Atlantic salmon and brook charr. This study first aimed to evaluate rainbow trout capacity to surpass a series of hierarchical filters impeding invasion success, that are introduction pressure, abiotic resistance, biotic resistance, and dispersion capacity. We demonstrated that naturalized populations following stocking programs in Lakes Ontario and Memphremagog constitute the main origin of the invasion towards Eastern Quebec. They moreover contributed to the establishment of a new population in Charlevoix region, which now also strongly participates to the invasion process. The presence of the exotic species in salmon rivers seems to be significantly related to the presence of tributaries, that might provide a refuge against flow variations, especially against spring floods occurring during the period of eggs' hatching and emergence of fry. A positive relationship was also found between the species occurrence and mean temperature during the growing season, suggesting an increase of the invasion progress with the climate warming. At juvenile stage, we observed that the presence of the two native competitors, despite their greater size at the beginning of age-0, did not affect the growth of the rainbow trout. On the contrary, the exotic species, despite being found in low densities, forced them to use less preferred habitats and to share more intensively the resources available. Finally, we found that the presence of an anadromous phenotype promoted greatly the dispersion of the species towards Eastern Quebec streams.

Avant-Propos

Cette thèse de doctorat se divise en six sections. Les chapitres 1 et 6 constituent respectivement l'introduction et la conclusion de la thèse. Les chapitres 2 à 5 présentent les résultats de l'étude et ont été rédigés en anglais dans un format d'article scientifique. Les chapitres 2, 3 et 5 ont déjà été acceptés pour publication dans une revue scientifique. Le chapitre 4 sera soumis à une revue en écologie aquatique. Voici la référence des quatre chapitres rédigés en anglais :

Chapitre 2 : **Thibault, I.**, Bernatchez, L. & Dodson, J.J. 2009. The contribution of newly established populations to the dynamics of range expansion in a one-dimensional fluvial-estuarine system: rainbow trout (*Oncorhynchus mykiss*) in Eastern Quebec. Diversity and Distributions, 15 : 1060-1072. doi: 10.1111/j.1472-4642.2009.00606.x

Chapitre 3 : **Thibault, I.**, Hedger, R.D., Crépeau, H., Audet, C. & Dodson, J.J. 2010. Abiotic variables accounting for presence of the exotic rainbow trout (*Oncorhynchus mykiss*) in Eastern Quebec Rivers. Knowledge and Management of Aquatic Ecosystems, 398 : publié en ligne le 14 octobre. doi: 10.1051/kmae/2010025

Chapitre 4 : **Thibault, I.** & Dodson, J.J. Biotic resistance as fact or fiction; interspecific competition between introduced and native juvenile salmonid species at an early invasive stage.

Chapitre 5 : **Thibault, I.**, Hedger, R.D., Dodson, J.J., Shiao, J.C., Iizuka, Y. & Tzeng, W.N. 2010. Anadromy and the dispersal of an invasive fish species (*Oncorhynchus mykiss*) in Eastern Quebec, as revealed by otolith microchemistry. Ecology of Freshwater Fish, 19 : 348-360. doi: 10.1111/j.1600-0633.2010.00417.x

Il est à noter qu'une digression a été faite lors de l'insertion du 5^{e} chapitre dans la thèse. Dans la version publiée, une section des résultats a été raccourcie et déplacée en annexe à la demande de l'éditeur. Toutefois, c'est la version non abrégée des résultats qui figure dans le présent document.

I.T. est chercheure principale, a réalisé la totalité ou la majeure partie des analyses, l'ensemble des figures et des tableaux, et est auteure principale de tous les chapitres. J.J.D., professeur titulaire en biologie à l'Université Laval, est le directeur de thèse d'I.T. et co-auteur des chapitres 2 à 5. L.B., professeur titulaire en biologie à l'Université Laval, est co-auteur du chapitre 2. R.D.H., étudiant post-doctoral à l'Université Laval et à NINA (Norwegian Institute for Nature Research), a réalisé une partie des analyses et des figures, et est co-auteur des chapitres 3 et 5. H.C., statisticienne à l'Université Laval, a participé aux analyses et est co-auteure du chapitre 3. C.A., professeure titulaire à l'Université du Québec à Rimouski, est co-auteure du chapitre 3. W.-N.T., professeur à la National Taiwan University, de même que Y.I et J.-C.S., chercheurs à l'Academia Sinica (Taiwan), ont collaboré à une portion des analyses et sont co-auteurs du chapitre 5.

I.T., J.J.D. et ce projet de doctorat ont reçu le support logistique et financier des organismes suivants : le Conseil de recherche en Science Naturelle et de Génie du Canada (CRSNG), le Centre Interuniversitaire de Recherche sur le Saumon Atlantique (CIRSA), le Ministère des Ressources naturelles et de la Faune (MRNF), Québec-Océan, le Réseau Aquaculture Québec (RAQ), la Fédération Québécoise de la Faune (FQF) et sa Fondation Héritage Faune.

Les résultats du projet de recherche ont été présentées à plusieurs reprises dans le cadre de congrès, d'assemblées générales annuelles et de rencontres gouvernementales :

- Congrès annuel du CIRSA (Québec) : 2010-2009-2008-2007
- Congrès annuel de la Fédération des gestionnaires de rivières à saumon du Québec (Rimouski et Rivière-du-Loup) : 2010-2008
- Atelier de la Fédération québécoise pour le saumon atlantique à l'occasion du Forum des moucheurs de Granby (Granby) : 2010-2008
- Canadian Conference for Fisheries Research (Ottawa) : 2009
- Atelier sur la Faune Aquatique, MRNF (Québec) : 2008
- Réunion annuelle de la Table Saumon, MRNF (Québec) : 2008
- Conférence à l'Université de Turku, sur l'invitation du Dr Craig Primmer (Finlande) : 2007
- Congrès annuel de la Fédération québécoise pour le saumon atlantique (Drummondville) : 2007

Remerciements

Prendre la décision d'entreprendre des études doctorales n'est pas une mince affaire et je dois avouer qu'à la fin de ma maîtrise, mon ambition était de me retrouver le plus rapidement possible sur le marché du travail. Lorsque mon directeur, Dr Julian Dodson, m'a offert la possibilité de poursuivre mes études graduées dans son laboratoire, mon hésitation était grande. Mais Julian a toujours eu un don pour déceler ce qui anime ses étudiants et il savait bien que je ne pourrais refuser le projet qu'il me proposait : étudier les divers aspects de l'invasion d'un poisson exotique qui pouvait affecter des espèces bien de chez nous, à la demande des utilisateurs et gestionnaires de la ressource, pour qui c'était un sujet d'inquiétude. Un projet donc qui se ferait en collaboration directe avec le Ministère des Ressources naturelles et de la Faune (MRNF) – mon *partenaire* de maîtrise – et avec les pêcheurs sportifs. Un véritable travail de recherche aux répercussions des plus concrètes. Il ne m'en fallait pas pour pour dire oui! Alors mes premiers remerciements vont à toi Julian, d'abord pour m'avoir offert un si beau projet, et surtout pour avoir eu suffisamment foi en mes compétences pour poursuivre l'aventure quelques années de plus. Merci aussi d'avoir accepté sans broncher mes idées de fou (vive les pièges étagés!), ainsi que toutes mes exigences et contraintes qui ont ralenti ma progression : mon séjour de quelques mois en Europe, mon congé de maternité, mon retour à temps partiel et finalement, mon contrat à temps plein au MRNF alors que ma thèse n'était pas encore terminée. Ce fut un honneur pour moi d'avoir cheminé au sein de ton équipe au cours de ces 6½ dernières années (et oui, déjà!). J'y ai appris grandement, tant sur le plan académique, professionnel que personnel. Encore merci!

Évidemment, partager quotidiennement son bureau avec d'autres étudiants, ça crée nécessairement des liens et forge de solides amitiés. Pour tous ces moments partagés ensembles, merci à vous tous, chers collègues et amis. Avec le temps, le laboratoire Dodson s'est vidé tranquillement de ses membres, mais le souvenir des moments partagés demeure intact. Je quitte donc à mon tour avec une pensée pour vous, qui avez partagé mes bonheurs et mes déboires : Catherine, Marie-Andrée, David, Gabriel, Emmanuel, Véronique, François, Françoise et Simon. Un merci tout spécial à Marc-Antoine qui est demeuré avec moi (bien involontairement!) jusqu'à la toute fin, avec qui j'ai eu de longues discussions sur à peu près tout, et qui a écouté sans se tanner, tous mes commentaires extasiés de nouvelle maman! Bonne chance dans ta nouvelle vie de Biologiste M.Sc. sur le marché du travail!

Je tiens également à remercier le Dr Louis Bernatchez et toute son équipe, notamment Lucie Papillon et Vicky Albert, mais aussi Mélanie, Vincent, Guillaume, Marika, Nathalie et tous les autres, pour toute l'assistance qui m'a été offerte durant mes manipulations et analyses génétiques. C'est un domaine qui m'était complètement inconnu et j'ai grandement apprécié vos conseils, votre expertise, votre aide et surtout votre compagnie lors de mon passage dans le laboratoire.

Un projet de doctorat comme le mien n'aurait pas été possible sans un gros travail de terrain. À ce sujet, je tiens à remercier du fond du cœur tous ceux et celles qui m'ont accompagnée lors de mes échantillonnages et qui ont fait un travail incommensurable dans des conditions souvent très exigentes. Équipe 2006 : Catherine Brisson-Bonenfant, André Boivin, Alain Lehoux (MRNF-Gaspé), François Barnard (MRNF-Sept-Îles), René Isabel (MRNF-Rimouski), Martin Arvisais (MRNF-Québec), Jean-Guy Frenette (MRNF-Québec), Alain Vallière (MRNF-Québec) et Pierre-Yves Collin (MRNF-Charny). Équipe 2007 : Geneviève Ouellet-Cauchon, Jessie Motard-Côté, Marion Trudel et sa sœur Mélanie, Julien Forestier, François Colas, Rémy Pouliot, Jean-Guy Frenette (MRNF) et Pierre-Yves Collin (MRNF). Équipe 2008 : Julie Faure-Lacroix, Marie Chantal Émond, Marc-Antoine Couillard et Rémy Pouliot. Sachez qu'une grande part de ce travail vous revient.

Durant deux ans, j'ai sollicité la collaboration des pêcheurs sportifs et commerciaux, des associations de pêcheurs, des gestionnaires de zecs-saumon et pourvoiries, de la Sépaq, de l'Aquarium de Québec, des différents organismes et intervenants du milieu de la pêche, de même que le personnel du MRNF pour m'aider dans ma cueillette de spécimens. Je tiens à vous exprimer toute ma gratitude, car votre participation enthousiaste à mon projet de recherche a été des plus précieuses. Merci également aux biologistes, techniciens et pisciculteurs du Québec, de l'Ontario, du Vermont (É-U) et des Maritimes de m'avoir fourni les échantillons des populations sources pour mes analyses génétiques.

Je m'en voudrais de passer sous silence certains collaborateurs qui m'ont énormément aidé avec mes analyses, notamment Pierre Duchesne avec son logiciel FLOCK, Richard Hedger, mon complice depuis la maîtrise pour toutes les analyses nécessitant de la modélisation, de même que l'équipe de Taiwan, Jay, Yoshi et Dr Tzeng, qui ont encore une fois accepté de procéder aux analyses microchimiques de mes otolithes. Merci à vous tous!

En 2007, j'ai eu l'opportunité de séjourner quelques temps en Europe. Durant ce périple qui m'a menée notamment en Estonie et Finlande, j'ai fait la rencontre de grands biologistes : Dr Anti Vasemagi, Dr Riho Gross, Dr Tiit Paaver et Dr Craig Primmer. Merci de m'avoir accueillie dans vos laboratoires et d'avoir accepté de partager avec moi votre savoir. Vos conseils éclairés ont été grandement appréciés.

Depuis plusieurs mois déjà, j'ai la chance de travailler au sein du Service de la faune aquatique au Ministère des Ressources naturelles et de la Faune à Québec. J'y ai découvert une équipe dynamique et passionnée. Merci à vous tous, Martin, Jessy, Véronique, Michel, Yves, Daniel, Henri et tous les autres, j'apprécie énormément travailler à vos côtés. Vos encouragements et votre sollicitude m'ont aidé à franchir les derniers milles qui me séparaient du fil d'arrivée.

Toutes ces années de dur labeur n'auraient pas été possibles sans le soutien de ma famille, belle-famille et amis. Vous avez été présents à chaque coup dur comme dans les bons moments. Vous avez fait preuve d'une grande compréhension quand mes études empiétaient sur ma vie de famille et sociale, et n'avez jamais hésité à m'offrir votre aide. Votre support et vos encouragements m'ont été inestimables. À toi Rémy, mon compagnon de vie, mon amoureux, mon ami, merci de ta présence, de ta patience, de ton aide et de tes conseils avisés. Comme le dit un vieil adage, à deux, ça va deux fois mieux! Merci pour TOUT. Et mon beau Thomas, toi qui illumine nos vies depuis bientôt deux ans, ne t'en fais, maman a enfin terminé, désormais, mes soirées et fins de semaine seront entièrement pour toi et papa.

Et finalement, à vous, Julian, Pierre, Ladd et Stéphane, imminents membres de mon jury de thèse, je tiens à vous remercier d'avoir accepté de siéger sur mon comité. J'espère que vous avez apprécié la lecture de ce document autant que j'ai aimé à le produire.

À Rémy et Thomas

Table des matières

Liste des tableaux

Liste des figures

Liste des annexes

CHAPITRE 1. INTRODUCTION

1.1. LES INVASIONS BIOLOGIQUES

L'accroissement du nombre d'invasions biologiques est l'une des conséquences majeures de l'activité humaine et constitue une menace pour l'intégrité biologique de plusieurs écosystèmes (García-Berthou 2007; Kolar & Lodge 2001). Par définition, une invasion biologique survient lorsqu'un organisme arrive dans un endroit situé au-delà de son aire de distribution originale et s'y établit (Hengeveld 1989; Shigesada & Kawasaki 1997; Williamson 1996). Il existe plusieurs invasions biologiques dites *naturelles*, comme l'échange de la faune mammalienne entre l'Amérique du Nord et l'Amérique du Sud et l'évolution subséquente des espèces, rendu possible par les mouvements tectoniques. Mais la plupart du temps, les invasions biologiques sont le résultat d'une intervention humaine, volontaire ou non. C'est notamment le cas pour les organismes marins qui sont transportés d'un pays à l'autre via les eaux de ballaste des bateaux commerciaux (Elton 1958; Williamson 1996).

On définit trois stades aux invasions biologiques (Theoharides & Dukes 2007; Williamson 1996) :

1) Introduction : lorsqu'un organisme **importé** d'un environnement étranger s'échappe hors des barrières imposées par l'importation, ou en est volontairement libéré, pour s'**introduire** dans un nouvel environnement.

2) Établissement : lorsqu'un organisme qui s'est **introduit** dans un nouvel environnement s'y **établit**, i.e. qu'il y survit et s'y reproduit avec succès. Le stade d'établissement comprend une phase de dispersion de l'espèce dans son nouvel environnement. Cette dispersion se fait via la croissance de la population et la diffusion des individus, qui peut alors prendre plusieurs formes : aléatoire (par voisinage), par sauts (longue-distance) ou stratifiée (hiérarchique) (Hengeveld 1989).

3) Nuisance : lorsqu'un organisme **établi** dans un nouvel environnement devient une **nuisance**. La définition d'espèce nuisible est très anthropomorphique, variable et peut mener à une interprétation subjective (Colautti & MacIsaac 2004).

De façon générale, on considère qu'il y a environ 10% des espèces importées qui s'introduisent dans la nature, 10% des espèces introduites qui s'établissent avec succès et 10% de celles-ci qui deviennent nuisibles (Ricciardi & Kipp 2008; Williamson 1996). C'est ce qu'on appelle la *règle du 10%.*

1.1.1. Les conditions nécessaires au succès des invasions biologiques

Plusieurs chercheurs ont tenté d'identifier les facteurs qui influencent le succès des invasions biologiques pour être en mesure de prédire quelles espèces et dans quelles conditions les risques d'invasion sont les plus élevés (pour des revues exhaustives : García-Berthou 2007; Jeschke & Strayer 2008; Kolar & Lodge 2001; Korsu et al. 2008) (Tableau 1.1). Ces nombreuses études ont généré une multitude d'hypothèses, concepts et théories, parfois contradictoires et souvent caractérisés par plusieurs exceptions (ex. : Fausch 2008). Ces concepts ne sont pas mutuellement exclusifs et, lorsque considérés individuellement, n'expliquent pas de façon satisfaisante l'ensemble des situations où une invasion biologique peut subvenir. Leur implication dans le succès des invasions peut également varier selon le stade du processus d'invasion et selon le type d'organisme étudié (García-Berthou 2007; Hayes & Barry 2008; Jeschke & Strayer 2008; Ricciardi & Mottiar 2006).

L'approche par filtres hiérarchiques, utilisée depuis le début du siècle (Colautti & MacIsaac 2004; Colautti et al. 2004; Kolar & Lodge 2001; Moyle & Marchetti 2006; Quist et al. 2005; Theoharides & Dukes 2007), a l'avantage d'intégrer ces différents concepts (Tableau 1.1) en une approche plus englobante. On distingue généralement cinq filtres hiérarchiques principaux qui peuvent entraîner une mortalité importante des espèces exotiques entre les différents stades de l'invasion : le transport, la pression d'introduction, la résistance abiotique, la résistance biotique et la capacité de dispersion. Les deux premiers filtres sont associés à la capacité d'une espèce à s'introduire dans un nouvel environnement. Les deux filtres suivants déterminent la capacité d'une espèce à s'y établir. Finalement, le dernier filtre à la réussite des invasions biologiques concerne les espèces envahissantes elles-mêmes et leur capacité à accroître leurs populations et à se diffuser dans le nouvel environnement. Le succès des invasions biologiques dépend de la capacité des espèces à franchir ces différents filtres (Figure 1.1).

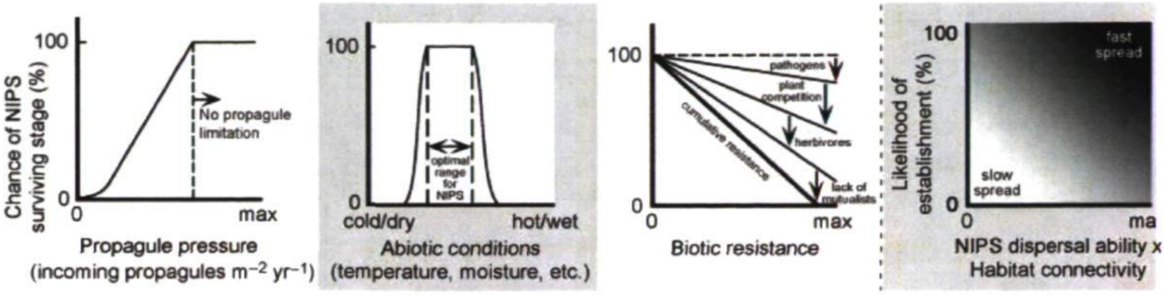

Figure 1.1 Schéma tiré de Theoharides & Dukes (2007, Figure 1) illustrant les chances de survie et d'établissement des espèces de plante non-indigènes (NIPS) selon quatre des cinq filtres hiérarchiques (de gauche à droite) : la pression de propagules, les conditions abiotiques, la résistance biotique et la capacité de dispersion.

Le transport. Les espèces doivent en premier lieu être captées par un vecteur et être en mesure de survivre au transport entre leur habitat d'origine et leur nouvel environnement. Plusieurs organismes meurent durant le transit (Kolar & Lodge 2001). Les espèces qui présentent une tolérance physiologique élevée (e.g. capacité à tolérer une grande gamme de températures) performent généralement mieux (Moyle & Marchetti 2006).

La pression d'introduction (ou pression de propagules). Cette pression fait référence au nombre d'événements d'introduction, d'individus introduits et de foyers d'introduction. La pression de propagule est l'un des facteurs les plus importants dans le succès des invasions (Colautti & MacIsaac 2004; Moyle & Marchetti 2006). Plus le nombre d'individus introduits et le nombre d'événements d'introduction sont élevés, plus la probabilité d'établissement est grande (Colautti et al. 2006; Kolar & Lodge 2001; Williamson 1996). De même, des introductions multiples diluent l'effet fondateur, souvent caractéristique des introductions, en augmentant la diversité génétique (Hänfling 2007).

Tableau 1.1 Caractéristiques associées positivement au succès des invasions selon différentes études et principaux filtres hiérachiques auxquels ils peuvent être reliés (1: pression d'introduction, 2: résistance abiotique, 3: résistance biotique et 4: capacité de dispersion).

Description	Filtres	Exemples de références supportant ces concepts
Propriétés intrinsèques des espèces exotiques		
herbivorie	3	[10]
diète généraliste	3	[10]
taille élevée des oeufs	3, 4	[10]
existence de soins parentaux	3, 4	[10]
stratégie-r	3, 4	[13], [15]
fort taux de dispersion	4	[15]
fort taux de croissance	3, 4	[13]
reproduction asexuée	3, 4	[11], [15]
variabilité génétique élevée	2, 3, 4	[15]
historique d'invasion	1, 2, 3, 4	[11], [18]
ampleur de la distribution géographique native	2, 3, 4	[10], [15]
Caractéristiques de l'habitat envahi		
connectivité des habitats	2, 4	[1]
habitat perturbé	1, 2, 3	[12], [13], [15], [17], [18], [21]
présence de niches vacantes	3	[16], [20]
faible richesse spécifique	3	[7], [13], [15], [21], [23]
peu d'ennemis	3	[3], [13], [15]
similaire à l'habitat natif	2	[8], [15], [18], [24]
espèces présentes non apparentées	3	[15], [19]
espèces présentes apparentées	3	[15]
disponibilité des ressources	2, 3	[6], [13], [22]
Proximité humaine		
pression de propagule	1	[2], [4], [5], [9], [10], [11], [18], [24]
association avec l'homme	1, 2, 3, 4	[9], [10], [13], [14], [15]

[1] Benjamin et al. 2007
[2] Colautti & MacIsaac 2004
[3] Colautti et al. 2004
[4] Colautti et al. 2006
[5] Copp et al. 2007
[6] Davis et al. 2000
[7] Elton 1958
[8] Hayes & Barry 2008
[9] Jeschke & Strayer 2006
[10] Jeschke & Strayer 2008
[11] Kolar & Lodge 2001
[12] Laurenson & Hocutt 1985
[13] Laurenson et al. 1989
[14] Leprieur et al. 2008
[15] Lodge 1993
[16] Moles et al. 2008
[17] Moyle & Light 1996
[18] Moyle & Marchetti 2006
[19] Ricciardi & Atkinson 2004
[20] Shea et Chesson 2002
[21] Simberloff 1996
[22] Stohlgren et al. 1999
[23] Tilman 1982
[24] Williamson 1996

La résistance abiotique. L'espèce envahissante doit être en mesure de survivre et de proliférer en fonction du climat et des gradients de conditions physiques présents dans le nouvel habitat. Il semble que les environnements instables, perturbés par l'homme et présentant une grande variété d'habitats soient les plus propices à l'invasion (Laurenson & Hocutt 1985; Moyle & Marchetti 2006). De plus, les environnements qui sont semblables à l'habitat d'origine des espèces envahissantes offriraient une moins grande résistance à l'invasion (Moyle & Marchetti 2006; Williamson 1996). Selon Moyle et Light (1996), si les conditions abiotiques du nouvel environnement sont appropriées, l'espèce envahissante a de fortes chances de s'y établir, peu importe la résistance biotique du milieu (voir prochain filtre), de sorte que le filtre environnemental serait le filtre le plus important (sauf dans les premiers stades de l'invasion où le nombre d'individus est petit).

La résistance biotique. Les interactions avec la faune native peuvent affecter la capacité d'une espèce envahissante à s'établir. Les invasions réussissent généralement davantage lorsque le nouvel environnement présente peu de prédateurs, de parasites et de maladies et une faune native appauvrie (Laurenson & Hocutt 1985). Plusieurs études suggèrent que les habitats ayant une faible richesse spécifique sont plus susceptibles d'être envahis par des espèces exotiques et que les communautés diversifiées sont plus résistantes à l'invasion (Elton 1958). Cependant, des travaux menés à différentes échelles spatiales semblent démontrer que même des environnements avec une grande richesse spécifique peuvent être envahis, particulièrement à l'échelle du paysage ou du biome (Levine 2000; Moyle & Marchetti 2006; Stohlgren et al. 1999). Ce paradoxe s'explique en partie par le fait que si à l'échelle locale, où l'environnement est stable, la présence de nombreuses espèces natives réduit les niches disponibles pour les espèces envahissantes, à grande échelle, les variations de l'environnement qui favorisent une augmentation de la diversité native ont le même effet sur les espèces exotiques et permettent ainsi à des biomes fort diversifiés d'être envahis (Shea & Chesson 2002). Le paradoxe peut également être expliqué par la disponibilité des ressources, en termes d'approvisionnement et de libération (Stohlgren et al. 1999). Selon Davis et al. (2000), c'est la fluctuation dans la disponibilité des ressources qui est le facteur clé contrôlant la susceptibilité d'un environnement à être envahi par des espèces non-résidentes : une communauté végétale devient plus susceptible à l'invasion s'il y a augmentation de la quantité de ressources non utilisées. Les communautés très diversifiées, contrairement aux communautés pauvres en espèces, réussissent généralement à utiliser la quasi-totalité des ressources disponibles, nuisant ainsi à l'établissement de nouvelles espèces (Tilman 1982). Cependant, ce n'est pas toujours le cas : des communautés peu diversifiées peuvent être en mesure d'utiliser efficacement l'ensemble des ressources et des communautés très riches peuvent présenter une grande quantité de ressources non utilisées. Il est également probable qu'une communauté diversifiée contienne des espèces (natives ou non) qui pourraient faciliter l'invasion d'une espèce exotique (Bruno et al. 2003; Ricciardi 2005; Sax et al. 2005; Simberloff & Von Holle 1999). Ainsi, la diversité biotique n'est pas toujours indicatrice de la résistance d'une communauté aux invasions. Pour qu'une espèce puisse envahir une nouvelle communauté, il doit non seulement y avoir des ressources disponibles, mais l'espèce doit également présenter un R^* (quantité de ressources qui permet la persistance d'une espèce) plus faible que celui des espèces natives (Grover 1997; Morin 1999; Tilman 1982). La présence d'ennemis naturels dans le nouvel environnement constitue également une barrière biotique. Il existe une hypothèse selon laquelle les prédateurs, les maladies et les parasites sont moins abondants ou moins efficaces contre les espèces exotiques dans les habitats envahis (Colautti et al. 2004). Cependant, une espèce envahissante peut s'avérer une proie ou un hôte « naïf » pour ces *nouveaux* ennemis, ou encore faire preuve d'une moins grande résistance aux maladies suite à une perte de diversité génétique durant le processus d'invasion (e.g. effet de Allee) (Colautti et al. 2004). De plus, les espèces envahissantes qui sont fonctionnellement similaires (apparentées) aux espèces indigènes sont plus susceptibles de rencontrer des ennemis qui pourraient affecter leur abondance (Ricciardi & Atkinson 2004).

Capacités reproductrices et dispersives. Les espèces exotiques qui ont une fécondité élevée, un mode de reproduction asexué, un taux de croissance rapide, une reproduction hâtive, une petite taille, un mode de dispersion efficace et qui font preuve de plasticité phénotypique ont généralement, mais pas toujours (Moyle & Marchetti 2006), davantage de chances de succès (Colautti et al. 2006; Kolar & Lodge 2001; Laurenson & Hocutt 1985; Richards et al. 2006). Les probabilités de succès sont souvent plus importantes lorsque l'espèce a un historique d'invasions réussies et/ou des espèces apparentées invasives (Kolar

& Lodge 2001; Moyle & Marchetti 2006; Ricciardi 2003; Williamson & Fitter 1996), mais ce n'est pas une règle absolue (Williamson 1996).

1.1.2. Impacts des invasions biologiques

Une espèce exotique qui réussit à franchir l'ensemble de ces filtres et à envahir un nouvel environnement peut avoir des impacts considérables sur les communautés natives. Ces impacts peuvent être d'ordre écologique ou évolutif.

Un impact écologique majeur des invasions biologiques est la réduction de l'abondance des espèces natives via la prédation, la compétition et l'introduction de maladies (Byström et al. 2007; Kohler & Courtenay 1986; Ojaveer et al. 2002; Williamson 1996). Parce que les espèces natives et envahissantes n'ont pas évolué en sympatrie, la sélection naturelle n'a pu mener à l'évolution d'une utilisation différentielle des ressources, ce qui entraîne une forte compétition pour des ressources limitées (Fausch 1988). Même si la compétition interspécifique est généralement la conséquence la plus importante de toutes les invasions biologiques (Williamson 1996), ce sont les espèces envahissantes prédatrices qui ont les effets les plus dramatiques, car elles peuvent causer l'extinction totale et irrévocable des espèces natives (Mooney & Cleland 2001). Outre la réduction d'abondance, on retrouve également parmi les impacts écologiques l'altération de l'habitat, du réseau trophique et des processus écosystémiques, comme le cycle de l'eau, la productivité du milieu ou le cycle de l'azote (Byström et al. 2007; Dodson 2000; Kohler & Courtenay 1986; Ojaveer et al. 2002; Welcomme 1984; Williamson 1996). Ce dernier type d'impact est notamment fréquent chez les plantes envahissantes.

Les conséquences évolutives des invasions biologiques sont également nombreuses. En s'hybridant avec les espèces natives, les espèces exotiques peuvent causer de l'introgression (Gross et al. 2004). En réduisant la taille effective des populations natives, les espèces envahissantes peuvent également entraîner une hausse de la dérive génétique (perte d'allèles) et de la consanguinité (Dodson 2000; Kohler & Courtenay 1986; Williamson 1996). Finalement, suite à la compétition interspécifique, il peut y avoir un déplacement de caractères et de niches, de même qu'une spéciation chez les espèces indigènes (Hutchinson 1959; MacArthur & Levins 1964; Mooney & Cleland 2001).

Au final, les invasions biologiques entraînent l'homogénisation du biota global et la perte de biodiversité (Olden & Rooney 2006). Les impacts d'une invasion biologique peuvent ne pas être perçus immédiatement s'il y a un *effet de décalage*, i.e. si l'espèce introduite présente une petite taille de population pendant plusieurs années avant d'exploser en nombre (Mooney & Cleland 2001). L'effet de décalage peut être le résultat d'une augmentation normale de la taille et de la distribution d'une population, d'une période d'adaptation au nouvel environnement ou d'un effet de Allee.

1.1.3. Des invasions biologiques dans tout le règne animal

L'activité humaine et l'ouverture du commerce international ont grandement augmenté le nombre d'invasions biologiques à travers le monde. On estime qu'au cours des 500 dernières années, les espèces envahissantes en sont venues à dominer 3% de la surface libre de glace de la Terre (Mooney & Cleland 2001). On retrouve dans la littérature des exemples bien détaillés d'invasions biologiques chez différents groupes d'organismes, notamment les plantes, les insectes et les oiseaux. Chez les mammifères, l'expansion du rat musqué (*Ondatra zibethica*) en Europe est l'un des premiers cas documentés. Natif d'Amérique du Nord, il a été introduit en Europe pour le commerce de la fourrure. En 1905, cinq individus s'échappaient d'une ferme près de Prague. En cinquante ans, l'espèce s'est répandue de façon fulgurante dans toute l'Europe, aidée par d'autres échappements locaux. Considéré comme une espèce nuisible, on n'a réussi à l'éradiquer que dans les îles (ex. Angleterre), vers 1930. Aujourd'hui, on en retrouve des millions sur le vieux continent (Shigesada & Kawasaki 1997; Williamson 1996).

Les invasions biologiques en milieux aquatiques sont également nombreuses, tant chez les invertébrés (ex. : moule zébrée : Griffiths et al. 1991; Mellina & Rasmussen 1994; Ricciardi 2003), les plantes aquatiques (ex. : jacinthe d'eau : Jacot Guillarmod 1979), que les poissons (ex. : Casal 2006; Copp et al. 2005; Goren & Galil 2005; Laurenson & Hocutt 1985). Plusieurs organismes planctoniques et larvaires profitent du transport maritime pour étendre leur distribution (Elton 1958; MacIsaac et al. 2001). Par exemple, dans les Grands Lacs, les eaux de ballaste sont responsables de 65% de toutes les invasions enregistrées depuis l'ouverture de la voie maritime du Saint-Laurent en 1959 (Ricciardi 2006; Ricciardi & MacIsaac 2000). Les Grands Lacs sont d'ailleurs l'un des écosystèmes aquatiques ayant le plus haut taux d'invasions : au moins 182 espèces envahissantes au total et une nouvelle espèce est découverte aux 28 semaines (Ricciardi 2006). Au Canada, les espèces aquatiques envahissantes, principalement introduites pour la pêche sportive, constituent la deuxième plus grande menace pour les poissons d'eau douce jugés à risque selon le COSEWIC[1] (Dextrase & Mandrak 2006).

Contrairement au transport accidentel d'organismes par les eaux de ballastes, les invasions piscicoles sont fortement associées aux introductions volontaires. Les raisons pour introduire une nouvelle espèce de poisson dans un habitat sont nombreuses : augmenter l'intérêt pour la pêche sportive, permettre l'élevage pour la table, exercer un contrôle biologique d'espèces indésirables, faire des manipulations écologiques (remplacer une espèce indésirable, combler une niche apparemment vide) ou décorer (jardins d'eau) (Courtenay & Taylor 1982; Crossman 1991; McCann 1984; Welcomme 1984). Selon la *FishBase*, il y aurait eu 3072 introductions inter-pays de poissons dans le monde, la majorité en eau douce (Figure 1.2), totalisant 568 espèces et 104 familles. Plus de la moitié (59%) de ces introductions auraient mené à l'établissement des espèces (Casal 2006).

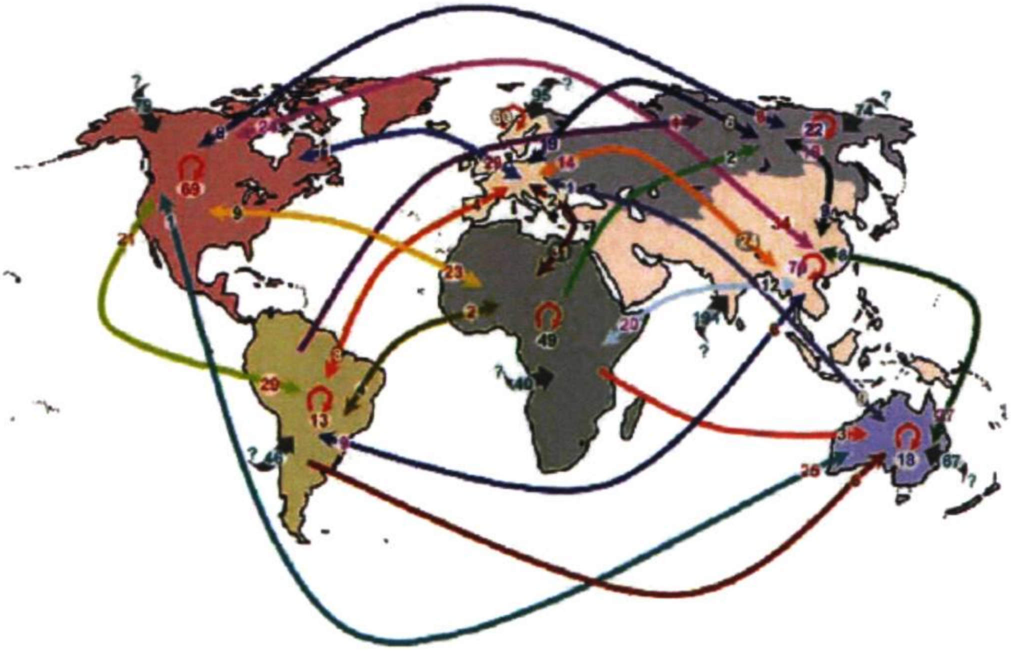

Figure 1.2 Introductions mondiales de poissons en eau douce. Tirée de Casal (2006, Figure 1)

---

[1] Committee on the Status of Species at Risk in Canada

Juste aux États-Unis, on dénombre près d'une centaine d'espèces exotiques, provenant d'autres pays ou États (Courtenay & Taylor 1982), alors qu'au Canada, on estimait en 1989 à 92 le nombre d'espèces de poisson introduites, dont 16 avaient réussi à s'établir (Crossman 1991). Leprieur et al. (2008) ont démontré l'existence de six points chauds où les espèces exotiques contribuent pour plus du quart des espèces de poissons dans les bassins hydrologiques : la Côte Pacifique des Amériques Centrale et du Nord, le sud de l'Amérique du Sud, l'ouest et le sud de l'Europe, le centre de l'Eurasie, l'Afrique du Sud et Madagascar, le sud de l'Australie et la Nouvelle-Zélande (Figure 1.3). Ces six régions comprennent également le plus grand nombre d'espèces piscicoles en danger. Si les échappements accidentels de quelques individus reproducteurs peuvent être à l'origine de certaines invasions, ce sont surtout les ensemencements répétés qui ont mené à ces résultats (Stauffer 1984).

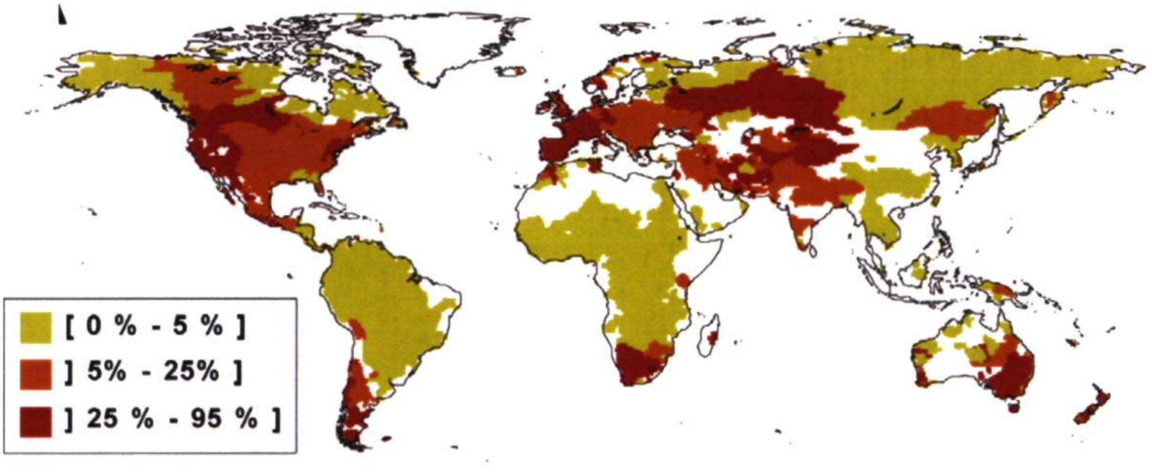

Figure 1.3 Le pourcentage d'espèces de poisson non indigènes par bassin (i.e. ratio d'espèces non-natives/richesse spécifique totale). Tirée de Leprieur et al. (2008, Figure 1A).

1.2. LA TRUITE ARC-EN-CIEL, UNE ESPÈCE ENVAHISSANTE PAR EXCELLENCE

Dans bien des cas, l'introduction de poissons exotiques a été néfaste pour l'écosystème. Les ensemencements les plus dommageables jamais enregistrés sont ceux des salmonidés, particulièrement ceux de la truite arc-en-ciel (*Oncorhynchus mykiss*) en raison de sa distribution mondiale (Korsu et al. 2008; Welcomme 1984).

1.2.1. Introduction de la truite arc-en-ciel dans le monde

La truite arc-en-ciel est un salmonidé natif de la côte ouest de l'Amérique du Nord. À l'origine, sa distribution était restreinte à l'océan Pacifique et au bassin de drainage côtier s'étendant de l'Alaska au Mexique (MacCrimmon 1971). Aujourd'hui, elle s'étend à la grandeur du globe (Figure 1.4). L'histoire de son introduction remonte à 1874, alors que 7 800 œufs de la rivière McCloud, au nord de la Californie, étaient transférés dans une pisciculture privée à Caledonia, New-York (MacCrimmon 1971; MacCrimmon & Gots 1972). Ces œufs, qui ont servi à produire les premières lignées domestiques, auraient été constitués d'un mélange d'individus anadromes et résidents (Needham & Behnke 1962). Depuis, la truite arc-en-ciel a été introduite sur tous les continents, à l'exception de l'Antarctique, principalement pour favoriser la pêche sportive. On estime qu'au moins 82 pays en auraient fait l'introduction (Cambray 2003a, b). Il s'agit désormais de l'espèce d'eau douce froide la plus répandue au monde (Crowl et al. 1992). Le nombre de truite arc-en-ciel introduit figure parmi les plus élevés chez les vertébrés (Fausch 2007), pouvant atteindre entre 10^5 à 10^7 individus annuellement dans certaines régions du monde (Fausch et al. 2001).

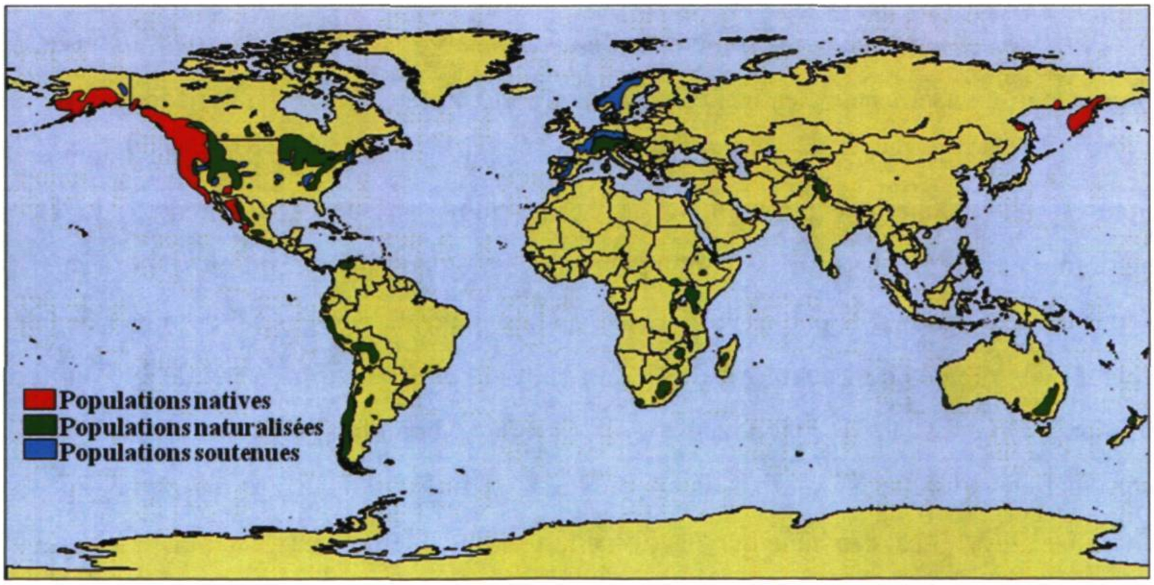

Figure 1.4 Distribution de la truite arc-en-ciel (*Oncorhynchus mykiss*) dans le monde (d'après MacCrimmon 1971)

1.2.2. Introduction de la truite arc-en-ciel dans l'est du Canada

Les cours d'eau de l'est canadien l'ont accueilli dès 1876; tout d'abord dans les Grands Lacs suite à l'intervention des États-Unis, puis dans le lac Saint-Clair en 1881 par le gouvernement canadien (MacCrimmon 1971; MacCrimmon & Gots 1972). La truite arc-en-ciel est aujourd'hui considérée comme une espèce naturalisée en Ontario (Kerr & Lasenby 2000). L'introduction dans les provinces maritimes se fera ensuite graduellement, entre 1887 et 1894 (MacCrimmon 1971). C'est en 1893-94 qu'avait lieu la première importation d'œufs au Québec. Mais il faudra attendre jusqu'en 1916 pour que ne débutent l'élevage et l'ensemencement de la truite arc-en-ciel par le gouvernement provincial, particulièrement dans les Cantons de l'Est et le lac Memphrémagog (Legendre et al. 1980; MacCrimmon 1971). C'est à partir de 1966, devant le succès des ensemencements de la truite brune, que le gouvernement entreprend des ensemencements soutenus de truite arc-en-ciel dans les eaux de la Plaine de Montréal afin de favoriser la pêche sportive (Mongeau et al. 1980a). Les rivières Richelieu et Châteauguay font également l'objet d'ensemencements réguliers (Dumont 1991). De 1967 à 1973, la truite arc-en-ciel était déjà capturée dans plusieurs cours d'eau de la région de Montréal et dans les rivières Richelieu, Châteauguay et Yamaska (Mongeau et al. 1974; Mongeau et al. 1980b). Toutefois, le succès de ces ensemencements n'a été réellement observé qu'à partir de 1974, alors qu'on commençait à ensemencer des truites de plus grande taille (Dumont 1991; Mongeau et al. 1980a, b). Ce succès s'est rapidement fait sentir plus en aval, alors que le nombre de captures à la pêcherie expérimentale de l'Aquarium de Québec augmentait de façon fulgurante en 1975, passant de 3 captures en moyenne par année jusqu'en 1974, à près de 36 par la suite (Robitaille et al. 1987). On soupçonne la truite arc-en-ciel de frayer dans les secteurs des rapides de Lachine, de l'Île aux Hérons, de Coteau-du-lac et de la Pointe du Buisson (Dumont 1991; Mongeau et al. 1980a). Toutefois, la contribution de la reproduction naturelle au soutien des populations semble faible, voire même négligeable (Dumont 1991). Il est probable que les juvéniles, moins tolérants aux eaux chaudes que les adultes, ne rencontrent pas de conditions favorables à leur développement (Dumont 1991). Il est aussi possible que les juvéniles subissent une prédation excessive (Dumont 1991). Le programme de soutien dans les eaux de la Plaine de Montréal s'est achevé en 2004 et depuis, les captures sportives ont considérablement diminué dans ce secteur (P. Dumont, MRNF, comm. pers.). Les ensemencements se poursuivent toutefois dans les autres régions (Figure 1.5).

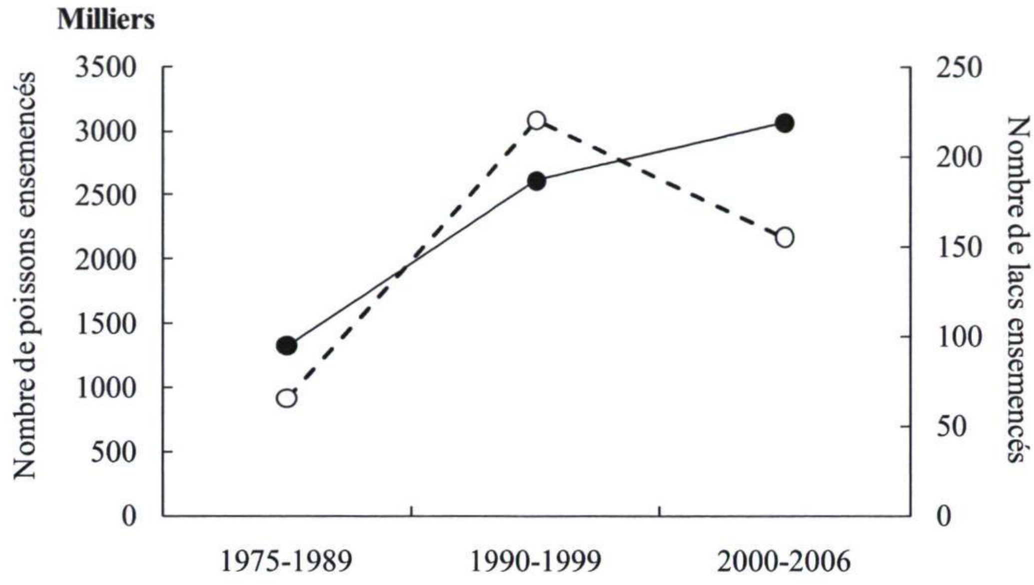

Figure 1.5 Évolution temporelle des ensemencements de la truite arc-en-ciel au Québec (excluant la région de Chaudière-Appalaches) et dans le lac Ontario. Cercles noirs : nombre total d'individus ensemencés. Cercles blancs : nombre de plans d'eau ensemencés au Québec. Données tirées de la base de données des ensemencements du MRNF. Aucune information disponible avant 1990 pour le lac Ontario.

1.2.3. Des signes d'une invasion dans l'Est du Québec

Les régions où il est permis d'ensemencer ou d'élever la truite arc-en-ciel sont restreintes à la portion sud-ouest du Québec. Sur la rive nord du fleuve Saint-Laurent, la limite est du zonage piscicole se situe aux environs de Beaupré, tandis qu'elle se prolonge jusqu'aux environs de La Pocatière sur la rive sud (Figure 1.6). Pourtant, très tôt après le début des ensemencements massifs dans la région de Montréal, la présence de truite arc-en-ciel était rapportée à l'extérieur du zonage permis. Dès 1973, les premières captures de truite arc-en-ciel étaient enregistrées dans plusieurs tributaires du Fleuve Saint-Laurent et dans les eaux saumâtres et salées de son estuaire (Dumont et al. 1988; Whoriskey Jr. et al. 1981). Un tel débordement vers l'aval des secteurs ensemencés n'est pas surprenant puisque la truite arc-en-ciel manifeste un fort comportement migrateur. Sur 653 individus recapturés après leur ensemencement dans la région de Montréal, 3,2% s'étaient déplacés de plusieurs kilomètres en aval du lieu de relâche. Un spécimen s'était même rendu jusqu'à Trois-Pistoles, à 500 km de son lieu d'ensemencement (Dumont 1991; Mongeau & Brisebois 1982). Dans le but de réduire les risques potentiels d'établissement et de compétition avec les salmonidés indigènes, le gouvernement provincial a décidé dès 1993 de n'utiliser que des truite arc-en-ciel stériles pour ses ensemencements dans les eaux de la Plaine de Montréal (Bouthillier 1995). Cependant, bien qu'efficace, la technique de production d'individus stériles n'est pas sûre à 100% (jusqu'à 15% d'erreurs, Dubé et al. 1991) et le gouvernement a abandonné la méthode après 2003 (Y. Guillemette, MRNF, comm. pers.).

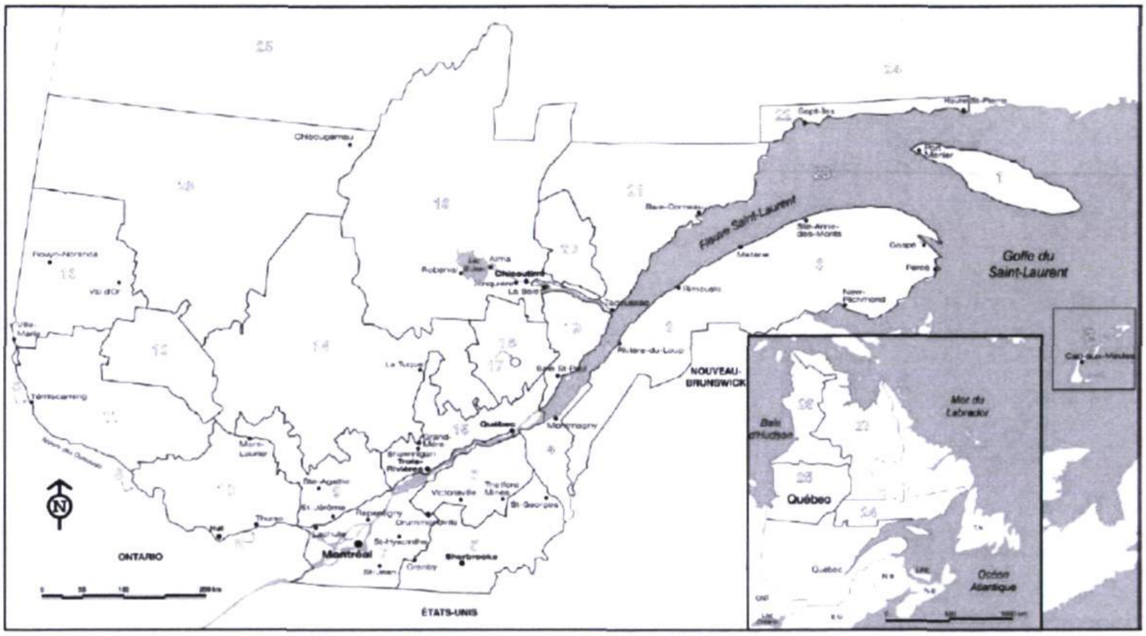

Figure 1.6 Les zones piscicoles du Québec. Il est interdit de garder, de produire, d'élever, de transporter (sauf en zone 12) et d'ensemencer la truite arc-en-ciel dans les zones 1 à 3, 11 à 12, 14 et 16 à 28 (tirée du Ministère de l'Agriculture, des Pêcheries et de l'Alimentation du Québec, février 2002)

1.2.4. Son cycle vital en bref

On retrouve chez *O. mykiss* une plasticité phénotypique qui s'illustre par des formes de vie différentes (Burgner *et al.* 1992). On exprime généralement cette plasticité en terme de *variétés* de truite arc-en-ciel, chacune présentant un cycle vital particulier (MacCrimmon & Gots 1972; Scott & Crossman 1974). Certaines variétés résident toute leur vie en eau douce, soit en rivière (truite arc-en-ciel commune) ou en lac (truite arc-en-ciel Kamloops). D'autres présentent plutôt un mode de vie anadrome, avec une croissance en eau salée (truite arc-en-ciel *steelhead*). Chez les truites anadromes, la migration vers la mer survient généralement vers 2 ou 3 ans, lorsque le poisson atteint une taille d'environ 100 à 200 mm (Burgner et al. 1992; Scott & Crossman 1974). La durée du séjour en eau salée, allant de 2 à 4 saisons de croissance (étés), varie grandement d'une région à l'autre (Burgner et al. 1992). Le moment du retour en rivière peut également varier; il y a des truites à montaison estivale (migration hâtive) qui vont séjourner 3 à 4 mois en rivière et des truites à montaison hivernale (migration tardive) qui passent de 9 à 12 mois en eau douce.

Dans son aire de distribution native, la truite arc-en-ciel fraie généralement au printemps, mais certaines populations se reproduisent plutôt à l'automne. Certaines truites vont même frayer deux fois par année. Au Québec toutefois, la fraie n'aurait lieu qu'une fois au printemps (mi-avril à juin) (Mongeau et al. 1980a). La frayère est constituée d'un lit de gravier fin situé dans un rapide en amont d'une fosse, où l'eau est bien oxygénée. La température idéale pour la fraie se situe généralement entre 10,0°C et 15,5°C. L'éclosion des œufs survient 4 à 7 semaines après la fertilisation (entre 583 à 661 degrés-jours (Burgner et al. 1992)), selon la région, et la résorption du sac vitellin a lieu généralement 3 à 7 jours plus tard. La période d'alevinage s'étend de quelques mois à 4 ans (Scott & Crossman 1974). L'âge à maturité serait de 3 à 5 ans, un an plus tôt chez les mâles. Les truites résidentes ont généralement une durée de vie de 3 ou 4 ans, alors que certaines truites anadromes peuvent vivre de 6 à 8 ans. La survie de la truite arc-en-ciel adulte est optimale dans des habitats où la température est de 21°C ou légèrement inférieure, quoiqu'elle puisse survivre dans des eaux beaucoup plus chaudes, pourvu qu'il y ait des refuges plus frais et bien oxygénés (Scott & Crossman 1974).

1.2.5. Impacts de l'invasion de la truite arc-en-ciel

On dénombre une grande quantité d'études établissant les impacts négatifs de son introduction à travers le monde, que ce soit sur la faune piscicole (Baxter et al. 2007; Cambray 2003a; Coghlan Jr et al. 2007; Korsu et al. 2008; Larson & Moore 1985; Moore et al. 1986; Moore et al. 1983; Soto et al. 2006), les invertébrés aquatiques (Buria et al. 2007; Cambray 2003a; sauf Englund & Polhemus 2001) ou les amphibiens (Cambray 2003a; Orizaola & Brana 2006). La truite arc-en-ciel a notamment été impliquée dans le déclin de l'omble de fontaine (*Salvelinus fontinalis*) dans les Appalaches aux États-Unis (Larson & Moore 1985), de galaxidés endémiques et de *Prototroctes oxyrhynchus* en Nouvelle-Zélande, de salmonidés endémiques en Yougoslavie, du *Oreodaemion quathlambae* au Lesotho et du *Trichomycterus* sp. en Colombie (Welcomme 1984), pour ne nommer que quelques exemples. Ce n'est donc pas sans raison que la truite arc-en-ciel figure parmi les 100 espèces exotiques envahissantes les plus néfastes au monde (Lowe et al. 2007).

Au Québec plus spécifiquement, la présence de la truite arc-en-ciel risque d'affecter les salmonidés indigènes, comme le saumon atlantique (*Salmo salar*) et l'omble de fontaine (*Salvelinus fontinalis*), de diverses façons (Dumont 1991; Dumont et al. 1988; et révisés par Kerr & Lasenby 2000; Krueger & May 1991). La truite arc-en-ciel est une espèce opportuniste, généralement piscivore, qui s'alimente sur plusieurs espèces de poissons dont les salmonidés (Kerr & Lasenby 2000). Elle pourrait donc exercer une pression de prédation importante sur les jeunes stades de vie (œufs et juvéniles) des espèces indigènes (Dodson 2000). On sait également qu'elle peut altérer le matériel génétique des populations natives par hybridation et introgression (Busack & Gall 1981; Hitt et al. 2003; Ostberg & Rodriguez 2006), quoique ce risque soit pour le moment limité étant donné la ségrégation temporelle des périodes de fraie. En effet, la truite arc-en-ciel fraierait principalement au printemps dans les rivières de la province, alors que les salmonidés natifs se reproduisent à l'automne. Néanmoins, comme les trois espèces utilisent le même type d'habitat pour la fraie (fond de gravier en eau peu profonde, en aval des fosses, où le courant est rapide), la truite arc-en-ciel pourrait altérer, recouvrir ou balayer les nids des espèces natives, nuisant ainsi à la survie des œufs et au développement des alevins (Dodson 2000; Scott & Irvine 2000). Pouvant être infestée par une grande variété de parasites (Scott & Crossman 1974), l'arrivée de la truite arc-en-ciel dans un nouvel écosystème pourrait également s'accompagner de l'introduction de diverses maladies et parasites auxquels les espèces natives sont vulnérables (Dumont et al. 1988; Kiesecker et al. 2001).

Finalement, les impacts les plus importants de la truite arc-en-ciel sur les salmonidés du Québec seraient probablement associés à la compétition interspécifique puisqu'elle utilise des habitats similaires à ceux du saumon atlantique (Fausch 1988; Gibson 1981; Hearn & Kynard 1986) et de l'omble de fontaine (Larson & Moore 1985; Magoulick & Wilzbach 1998; Rose 1986, sauf Cunjak & Green 1983). De plus, la truite arc-en-ciel étant reconnue pour être plus tolérante que les autres salmonidés à une plus grande variété de conditions, comme des températures plus chaudes (14°C à 20°C, 22°C maximum), un pH plus élevé et une augmentation de la salinité (Kerr & Lasenby 2000), la dégradation de l'habitat ou une élévation des températures pourraient la favoriser au détriment des espèces natives.

1.3. PROBLÉMATIQUE

Les risques d'une invasion de la truite arc-en-ciel sont bien réels et soulèvent depuis quelques années déjà des inquiétudes quant aux impacts potentiels sur les salmonidés indigènes dans l'est du Québec (Dumont et al. 1988). Cependant, il semblerait que les capacités d'établissement de cette espèce en dehors de son aire de distribution native soient relativement limitées, comme l'indiquent les nombreuses tentatives d'introduction qui ont échoué à travers le monde (Fausch 1988; MacCrimmon 1971).

Ce projet de recherche a été réalisé dans le but d'établir dans quelle mesure la truite arc-en-ciel était en mesure de franchir les différents filtres hiérarchiques aux invasions biologiques dans l'Est du Québec. Puisque que la barrière du transport n'était pas un obstacle à la réussite de son invasion (ensemencement volontaire, donc survie optimisée durant le transit), la présente étude s'est intéressée aux filtres subséquents, chacun ayant fait l'objet d'un chapitre distinct : la pression d'introduction (Chapitre 2), la résistance abiotique (Chapitre 3), la résistance biotique (Chapitre 4) et les capacités de dispersion (Chapitre 5). L'hypothèse principale de l'étude était que certains filtres, notamment ceux associés à la résistance abiotique ou biotique, limitent la capacité de la truite arc-en-ciel à s'implanter avec succès dans les eaux du Québec.

CHAPITRE 2. THE CONTRIBUTION OF NEWLY-ESTABLISHED POPULATIONS TO THE DYNAMICS OF RANGE EXPANSION IN A ONE-DIMENSIONAL FLUVIAL-ESTUARINE SYSTEM: RAINBOW TROUT (*ONCORHYNCHUS MYKISS*) IN EASTERN QUEBEC

Thibault, I., Bernatchez, L. & Dodson, J.J. 2009. Diversity and Distributions, 15 : 1060-1072.

2.1. ABSTRACT

Rainbow trout (*Oncorhynchus mykiss*, Walbaum 1792) is an exotic salmonid invading eastern Canada. First introduced for recreational fishing in Ontario, Quebec and the Maritime provinces, the species is now spreading in salmon rivers located in Eastern Quebec, where its stocking is strictly forbidden. Newly established populations have been found along the St. Lawrence Estuary. To effectively mitigate the potential threat the invasion poses to native salmonids, we aimed to document the invasion's origin and progress in the St. Lawrence River and estuary. We first determined genetic origins among several potential wild and cultured source populations, found at the upstream and downstream extremities of the St. Lawrence system. Thereafter, we studied the range expansion, predicting that the invasion process conforms to a one-dimensional stepping-stone dispersion model. The study area was the recently invaded salmon rivers that flow into the Estuary and Gulf of St. Lawrence in Quebec, and watercourses supporting naturalized populations (Lake Ontario, Lake Memphremagog and Prince-Edward-Island rivers). Rainbow trout from ten potential source populations (wild and domestic strains) and 243 specimens captured in salmon rivers were genotyped at ten microsatellite loci. Genetic origins of specimens and relationship between colonies were assessed using assignment analyses based on individuals and clusters. Invasion of rainbow trout in Eastern Quebec is directed downstream, driven by migrants from upstream naturalized populations, found in the Ganaraska River (Lake Ontario), and, to a lesser extent, in Lake Memphremagog. Populations from the Maritime provinces and domestic strains do not contribute to the colonisation process. A recently established population in Charlevoix (Eastern Quebec) supplies other downstream colonies. Rainbow trout is spreading from Lake Ontario downstream to Eastern Quebec using the St. Lawrence River system as an invasion corridor. Range expansion in a downstream direction is driven by a more complex stepping-stone dispersion model than predicted. Management options to protect native salmonids include reducing the effective size of the Charlevoix population, impeding reproduction in recently colonized rivers, halting the upstream migration of anadromous spawners, and curtailing stocking events inside the stocking area.

2.2. RÉSUMÉ

La contribution des populations nouvellement établies à la dynamique d'expansion dans un système fluvial-estuarien à une dimension : la truite arc-en-ciel (*Oncorhynchus mykiss*) dans l'Est du Québec

La truite arc-en-ciel (*Oncorhynchus mykiss*) est un salmonidé exotique qui envahit l'est du Canada. D'abord introduite pour la pêche récréative en Ontario, au Québec et dans les provinces maritimes, l'espèce colonise désormais les rivières à saumon de l'Est du Québec où son ensemencement est strictement interdit. On a découvert des populations récemment établies le long de l'estuaire du St-Laurent. Pour évaluer adéquatement l'impact potentiel que cette invasion pose pour les salmonidés natifs, nous avons voulu documenter l'origine de l'invasion et sa progression dans le Fleuve St-Laurent et son estuaire. Nous avons d'abord déterminé l'origine génétique des spécimens à partir de populations sources potentielles sauvages et d'élevage, que l'on retrouve en amont et en aval du système du St-Laurent. Nous avons ensuite étudié le processus d'expansion, prédisant que l'invasion allait se conformer à un modèle de dispersion à une dimension de type *stepping-stone*. L'aire d'étude comprenait les rivières à saumon récemment envahies se déversant dans l'estuaire et le golfe du St-Laurent (Québec) et les plans d'eau supportant des populations naturalisées (lac Ontario, lac Memphrémagog et rivières de l'Île-du-Prince-Édouard). Dix populations sources potentielles (lignées sauvages et domestiques) et 243 spécimens capturés dans les rivières à saumon ont été génotypés à dix microsatellites. L'origine génétique des spécimens et les relations entre colonies ont été déterminées par des analyses d'assignations basées sur des individus et des groupes d'individus. L'invasion de la truite arc-en-ciel dans l'Est du Québec suit un mouvement amont-aval et est dirigée par des migrants provenant des populations naturalisées en amont, i.e. dans la rivière Ganaraska (lac Ontario), dans une moindre mesure, dans le lac Memphrémagog. Les populations des provinces Maritimes et les lignées domestiques ne contribuent pas au processus de colonisation. Une population récemment établie dans la région de Charlevoix (Est du Québec) alimente désormais d'autres colonies en aval. La truite arc-en-ciel se disperse du lac Ontario vers l'Est du Québec en utilisant le système du Fleuve St-Laurent comme corridor d'invasion. Son expansion vers l'aval suit un modèle de dispersion *stepping-stone* plus complexe qu'attendu. Les options de gestion envisageables pour la protection des salmonidés indigènes incluent de réduire la taille effective de la population de Charlevoix, d'empêcher la reproduction dans les rivières nouvellement colonisées, de freiner la migration vers l'amont des reproducteurs anadromes et de réduire les ensemencements.

2.3. INTRODUCTION

The dynamics of species' range expansions, particularly those of exotic species invading new habitats, is of considerable fundamental and applied importance in wildlife ecology. The study of invaders' range expansion is of particular interest as the invasion success and their impact on native fauna and flora relies in part on the rate and extent of spreading. Landscape spreading will depend on habitat connectivity, but also on the dispersion ability of the species which relies on many factors, including reproductive strategies and modes of dispersion. Good invaders are believed to be fast growing, to have high fecundity, to reproduce asexually and to have fast generation times and effective long and short distance dispersal (Colautti et al. 2006; Kolar & Lodge 2001; Laurenson & Hocutt 1985; Richards et al. 2006; Theoharides & Dukes 2007). Various efforts have been made to develop predictive numerical models of the invasion process. In the case of *continuum models,* space is represented by a continuous coordinate system and range expansion usually takes the form of reaction-diffusion equations (Kareiva 1990). These equations constitute the Fisher-Skellam theory and describe the temporal changes in population density according to the local population growth (r) and the diffusion coefficient (D). This theory implies that the rate of spread is a linear function of time and can be predicted quantitatively as a function of measurable life history traits affecting population growth and dispersal abilities (Hastings et al. 2005). Such models distinguish two kinds of diffusion: neighboring and long-distance diffusion. Neighboring diffusion results from individuals moving to adjacent areas over varying distances. Invasion dynamics are mainly driven by rare long-distance dispersers (Begon et al. 1996), that lead to the creation of daughter-populations or invasion foci. When dispersion is proceeding from several locations and implies several diffusion modes, spread follows a stratified (or hierarchical) diffusion. Stratified diffusion, usually observed in invasions, can be much faster than linear or exponential spread (Hengeveld 1989; Shigesada & Kawasaki 1997; Shigesada et al. 1995). Besides continuous systems, habitat can also be viewed as a series of patches or colonies. In *island models*, all patches are equally accessible as there is no specification about the distances between them (Kareiva 1990). Alternatively, *stepping-stone models* assume patches with fixed spatial coordinates and the exchange of individuals is restricted to adjacent colonies or populations. Such models allow studying the consequences of long-range versus short-range dispersal in terms of genotypic and phenotypic diversity (Kareiva 1990; Kimura & Weiss 1964). In cases where the distance between patches approaches zero, stepping-stone models can be interpreted as continuum models (Kimura & Weiss 1964).

Most studies of the spatial spread of invasions have used continuum models (see Kareiva (1990) and Hastings et al. (2005) for a review; Brown and Stepien (2009)), describing dispersal as waves of invasion involving simultaneous colonization on a large invasion front, with expansion being accelerated in good habitats, and slowed in poorer ones (Shigesada & Kawasaki 1997). However, when invasion involves freshwater fishes, stepping-stone or island models may be more appropriate as species are often habitat-specific (only found in lakes or rivers for example). Even if they are not completely isolated, watercourses can be geographically quite distant, supporting discrete colonies or populations. As an example, Boyer et al. (2008) demonstrated that populations of hybrids between native westslope cutthroat trout (*Oncorhynchus clarkii lewisi*, Girard 1856) and introduced rainbow trout (*O. mykiss*, Walbaum 1792) dispersed in the Flathead rivers (USA and Canada) according to a stepping-stone model. The authors found a reduction of rainbow trout admixture with upstream distance from a site containing a hybrid swarm where rainbow trout accounted for 92% of the genetic diversity.

Rainbow trout is one of the most widely introduced fish species in the world and its impact on native fish communities is of increasing concern. In eastern Canada, repeated and massive stockings have occurred since the end of the 1890s in the Great Lakes, in the south-western part of Quebec province, and in the Maritime provinces, leading to the establishment of some naturalized populations. In Quebec, stocking and farming of rainbow trout were restricted to specific zones, located upstream in the St. Lawrence River (Figure 2.1). Early in the 20th century, the naturalized populations were only found inside this area (such as in Lake Memphremagog, Lake Champlain and the St. Lawrence River near Montreal). However, since the 1970s, adult rainbow trout have frequently been captured by sport fishermen in the eastern part of Quebec in Atlantic salmon (*Salmo salar*, Linnaeus 1758) rivers that flow into the St. Lawrence Estuary, up to the eastern-most end of the Gaspe peninsula (Dumont et al. 1988; Whoriskey et al. 1981).

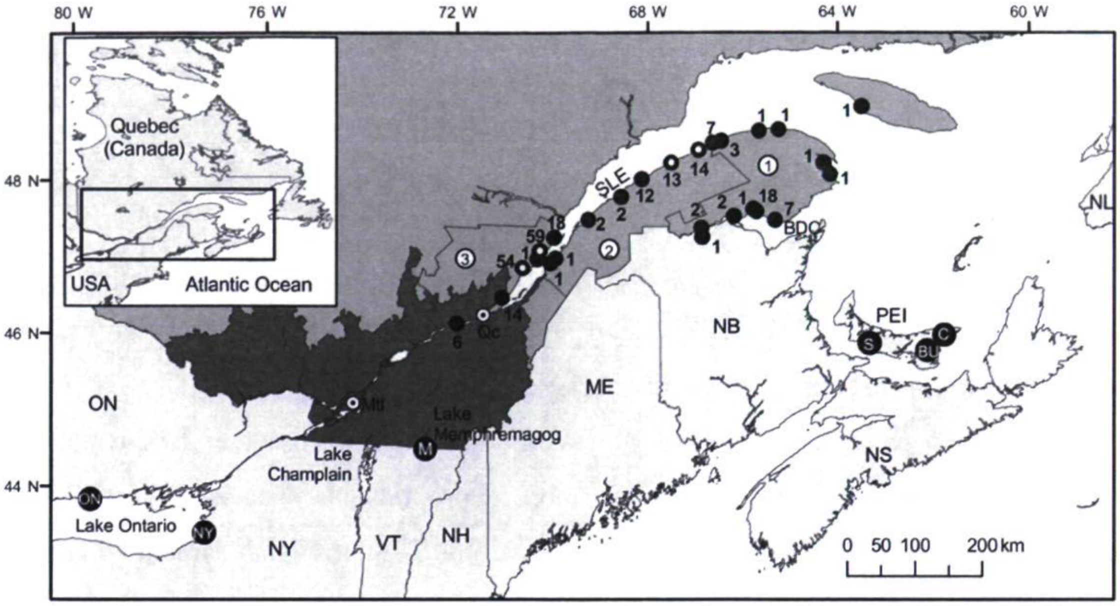

Figure 2.1 Map of the St. Lawrence River system from Lake Ontario to Maritime provinces (Canada). Area where stocking of rainbow trout is allowed is shown in dark grey. Large black circles identify the location of wild source populations: Ganaraska R. (ON), Salmon R. (NY), Lake Memphremagog (M), Cardigan R. (C), Brudenell R. (BU) and Summerside Harbor (S). Sites where rainbow trout were sampled in Eastern Quebec between 2005 and 2007 are identified by small black circles. Associated numbers indicated the sample size. Rivers supporting self sustaining populations are marked by a white spot. Main regions bording the St. Lawrence Estuary (SLE): Gaspesia (1), Bas-St-Laurent (2), and Capitale-Nationale (including Charlevoix region; 3). Qc: Quebec City, Mtl: Montreal, BDC: Baie-des-Chaleurs. Other Canadian provinces: New Brunswick (NB), Prince Edward Island (PEI), Nova Scotia (NS), Newfoundland (NL) and Ontario (ON). USA states: New York (NY), Vermont (VT), New Hampshire (NH) and Maine (ME).

Establishment of rainbow trout in salmon rivers might threaten native fishes, particularly other salmonid species, mainly by increasing competition and predation pressures. Conservation and management of the indigenous fish fauna thus requires better knowlegde of the origin and spreading mode of the invader. The main objective of this study was to establish the dynamics of range expansion by rainbow trout in Eastern Quebec waters, characterized by a large fluvial-estuarine system. This one-dimensional system dictates that the species expansion is constrained to a downstream and/or an upstream direction. We first aimed to establish if rainbow trout captured outside the stocking area originated from sources located upstream in the St. Lawrence system (up to Lake Ontario) and/or from sources located dowstream, in the Maritime provinces. Secondly, we aimed to establish if annual stocking programs in Quebec promote the invasion process by sustaining high propagule pressure. We thus determined if invading trout were derived from domesticated lineages currently used for stocking or from naturalized populations. Finally, we tested the hypothesis that the stepping-stone model best described the rainbow trout invasion process. To do so, we determined the relative importance of recently naturalized populations known to exist in Eastern Quebec waters relative to those existing in previously stocked areas to the east and/or to the west of the target area.

2.4. MATERIALS AND METHODS

To achieve our objectives, we performed population assignment analyses based on DNA microsatellite polymorphisms using several potential source populations (wild and domestic) and rainbow trout captured in 2005-2007 in Eastern Quebec waters.

2.4.1. Sampling

Source populations Ten source populations were selected for their potential contribution to the rainbow trout colonization in Eastern Quebec (Table 2.1). Two wild populations came from Lake Ontario, one reproducing in the Ganaraska River (ON, Canada), the other in the Salmon River (NY, United States). In Lake Ontario, rainbow trout has been stocked since 1878, both in Ontario (Canada) and New York (USA) (MacCrimmon 1971), and the species is now listed as a native species (Kerr & Lasenby 2000). Another wild population came from Lake Memphremagog, Vermont (USA). This lake was one of the first watercourses, with Lake Champlain, to be stocked (in the late 1800s) by both Quebec and Vermont agencies (L. Gerardi & K. Kelsey, Vermont Fish and Wildlife Department, pers. comm.). Lake Champlain was another potential source population. However, as this lake is stocked with rainbow trout from either Salmon River or Lake Memphremagog populations, we did not include this site among the source populations. In Lakes Ontario and Memphremagog, stocked juveniles are derived from wild populations (with egg fertilization and incubation in a hatchery), but also from domestic strains from USA and Canadian hatcheries. Historically, both anadromous (steelhead) and resident forms were stocked. In Lake Ontario, wild populations are known to be 'anadromous', even though they never have access to salt water, as fish migrate to the lake for growth and return in the tributaries for spawning (Scott & Crossman 1974).

Table 2.1 Origin and characteristics of ten potential rainbow trout (*Oncorhynchus mykiss*, Walbaum 1792) source populations.

Province/State	ID	Fish farm/water-body	N	Form	Strain characteristics
Quebec	M	Lake Memphremagog	50	steelhead	wild population[1]
	LDE	Lac-des-Écorces hatchery	47	resident	all-female
	JC	Jacques-Cartier hatchery	50	resident	all-female
Ontario	ON	Ganaraska R., Lake Ontario	50	steelhead	wild population[1]
NewYork (USA)	NY	Salmon R., Lake Ontario	50	steelhead	wild population[1]
Prince Edward Island	PEI	Ocean Trout Farms	50	steelhead	all-female
	PEI_C	Cardigan R.	27	steelhead	wild population
	PEI_BU	Brudenell R.	27	steelhead	wild population
	PEI_S	Dunk, Wilmot and Bradshaw rivers (Summerside Harbor)	50	steelhead	wild population
Nova Scotia	NS	Ocean Trout Farms	50	steelhead	both sexes

[1] supportive breeding with spawners from the same watercourse

In Quebec, rainbow trout is also periodically stocked in diverse watercourses by municipalities, fishing associations or private owners. Therefore, two cultured strains were sampled for their importance in annual local stockings: (i) a strain from *Pisciculture Lac-des-Écorces*, a governmental hatchery, and (ii) a strain from *Pisciculture Jacques-Cartier*, a private hatchery. The latter buys its eggs from *Troutlodge Inc.*, a commercial hatchery located in the United States that provides eggs and juveniles to many small hatcheries in the province.

The Maritime provinces have also conducted rainbow trout stockings since 1887 (MacCrimmon 1971), and some watersheds now support naturalized populations. Two cultured strains were obtained from the Atlantic provinces, one in Nova Scotia and one in Prince Edward Island. Wild populations were also sampled in five rivers in Prince Edward Island. No source population were obtained from Newfoundland as naturalized populations (mainly residents) are only found on the East Coast of the province (far from Quebec), and because rainbow trout cultured in marine cages (Bay d'Espoir) are all-female triploids (Chadwick & Bruce 1981; Mullins 2003; Porter 2000). We attempted to obtain fish from New Brunswick, but legislation now restricts rainbow trout stocking and farming to the southwest part of the province, which is very far from Quebec, and the only wild population, found in the Shepody River, is now almost extinct (G. Cline, Area Chief Fisheries and Aquaculture Management in New Brunswick, pers. comm.).

Fish of unknown origin In 2005, 2006 and 2007, sampling campaigns were organized with sport fishermen. They were invited to register their rainbow trout captures in one of the 70 registration centers, almost all located in the offices of fishing associations and government establishments. Electrofishing surveys in target streams and collaborations with commercial fishermen and governmental employees also provided additional samples. A total of 25 fish were collected in 2005, 220 in 2006, and 164 in 2007. The 409 fish were mainly captured in Eastern Quebec, but some also came from more western regions where stocking is allowed. For the purpose of this study, only diploid rainbow trout captured in salmon rivers were kept for the analyses (n = 243, Figure 2.1).

2.4.2. DNA extraction, amplification and sequencing

DNA was extracted using a modified salt-extraction protocol (Aljanabi & Martinez 1997). Briefly, a small piece of muscle or adipose fin tissue (conserved frozen or in 95% ethanol) was washed in distilled water and digested in 440 μL of salt homogenizing buffer [0.4 M NaCl; 10 mM Tris-HCl (pH 8.0); 2 mM ethylenediaminetetraacetic (EDTA, pH 8.0)] with 44 μL of 20% sodium dodecylsulphate (SDS) and 8 μL of 20 mg / mL proteinase K overnight at 37°C with gentle rocking. The digestion was extracted with 300 μL of 6 M NaCl. The supernatant (600 μL) was transferred to fresh tubes and DNA was precipitated with an equal volume of cold isopropanol. After incubation at -20°C for at least 1 h, the pellet was washed with 70% ethanol, dried and re-dissolved in 100 or 150 μL distilled water.

Variation at ten microsatellite loci was assessed (Table 2.2). Seven multiplex systems were used for PCR, adapted from those developed by Chris C. Wilson and colleagues (Trent University, Ontario). PCR included 1.0 μL of extracted DNA, 10 μM of each primer, 1.1 μL of the 10X reaction buffer [100 mM Tris-HCl; 15 mM / L $MgCl_2$; 1% Triton X-100; 500 mM KCl], 0.22 μL dNTPs (10 mM each), 1.1 μL of the 10X BSA, 1.0 U *Taq* DNA polymerase, and double-distilled H_2O to make up a total 11 μL reaction volume. The PCR conditions were a 11-min denature cycle (95°C), followed by 35 cycles of a 1-min denature step (94°C), a 1-min annealing step (59°C), and a 1-min extension cycle (72°C), followed by a final extension of 60°C for 45 minutes to ensures that the amplified alleles have the "+A" extension added on. The forward primers were fluorescently labelled and the resulting dye-labelled amplified fragments were run on a genetic analyzer (Applied Biosystems Model 3100) following manufacturer's protocols. Loci were combined in two groups of five microsatellites. Alleles were scored with GeneScan 3.7.1 and Genotyper 3.7 softwares (Applied Biosystems).

Table 2.2 Multiplex arrangement of ten microsatellites and locus-specific information based on 694 specimens: number of alleles, allelic richness (A_R), unbiased expected heterozygosity (H_E) and allelic range.

Locus	Multiplex	# alleles	A_R	H_E	Allelic range	Source
*Ots*3	A	15	14.897	0.645	[121-153]	Greig and Banks (1999)
*Ogo*4	A	12	11.995	0.777	[115-147]	Olson et al. (1998)
*Omy*1001	C	24	23.902	0.920	[169-235]	Spies et al. (2005)
*Omy*77	B	21	20.945	0.869	[79-139]	Morris et al. (1996)
*One*14	C	10	10.000	0.782	[148-166]	Scribner et al. (1996)
*One*8	D	16	15.945	0.684	[151-185]	Scribner et al. (1996)
*Omy*1011	E	21	20.900	0.887	[132-222]	Spies et al. (2005)
*Omy*27	F	10	9.894	0.556	[92-116]	Heath et al. (2001)
*Ssa*85	F	33	32.897	0.874	[92-180]	O'Reilly et al. (1996)
*One*2	G	25	24.988	0.910	[199-267]	Scribner et al. (1996)
Overall	-	18.7	18.636	0.790	[79-267]	-

2.4.3. Standard genetic analyses

Loci-specific and population-specific information, such as number of alleles, average number of alleles/locus, mean allelic richness, unbiased observed and expected heterozygosities (Nei 1987) and inbreeding coefficient (F_{IS}, Weir and Cockerham (1984)) were determined with FSTAT 2.9.3 (Goudet 1995) and EXCEL MICROSATELLITE TOOLKIT (Parks 2001). The number of distinct source populations was confirmed by clustering analyses using STRUCTURE 2.2 (Pritchard et al. 2000), based on maximum LLOD (Ln *P(D)*). Populations were tested individually and grouped (up to ten simultaneously). According to the number of populations tested in a same analysis, K varied from 1 to 15 (always three replicates). Burn-in period length and MCMC were set to either 100 000, 200 000 or 500 000 repetitions, adjusted according to K (increased with K) to ensure likelihood stationarity (Pritchard et al. 2000). All populations were considered as distinct, except for some Prince Edward Island wild populations. Results led us to pool all fish from the three rivers that flow into Summerside Harbor as only one source population (PEI_S). GENETIX 4.03 (Belkhir et al. 2004) and SMOGD (Crawford 2009) were used to determine the extent of genetic differentiation (θ estimate of F_{ST}, Weir and Cockerham (1984), and D_{est}, Jost (2008)) between source populations, based on 1 000 permutations. Hardy-Weinberg equilibrium on a per-locus basis and linkage disequilibrium between pairs of loci were tested with GENEPOP 1.2 (web version, Raymond and Rousset (1995)) for each source population. Markov chain parameters for both tests were set at 10 000 dememorizations, 1 000 batches and 10 000 iterations. Significance threshold (α) was fixed at 0.01.

2.4.5. Rainbow trout origins

The most probable genetic origin of individuals was determined using population assignment analyses performed in GENECLASS2 (Piry et al. 2004). This software determines to which population, among a specified set of potential source populations, an individual of unknown origin is most likely to belong. Parameters were set to 10 000 simulated individuals, and used the simulation algorithm (Monte Carlo) of Paetkau et al. (2004), and the criteria of Rannala and Mountain (1997). An individual was excluded from the assignment test (and thereafter considered as an unassigned fish) when its probability of belonging to any of the potential source populations was lower than 0.05 (α). The level of resolution of the test was determined with a re-assignment method (*leave-one-out*) based on individuals from source populations.

2.4.6. Rainbow trout dispersion mode

Common methods to document stepping-stone dispersal involve testing for isolation by distance, or by examining the correlation between geographic distance from *mother* populations and admixture found in *daughter* colonies (Boyer et al. 2008). However, as the rainbow trout invasion in Eastern Quebec is recent and ongoing, these methods cannot be used as there are only a small number of established populations and fish captured in other rivers are few and mainly consist of adult vagrants of various origins (see Results). Therefore, two alternative approaches involving different spatial scales were used in parallel to test the stepping-stone hypothesis. The first method exploited individual-level assignment and involved the addition to the assignment analyses of four new source populations recently naturalized in Eastern Quebec (Malbaie, Du Gouffre, Les Mechins, Matane), located both on the north and south shores of the St. Lawrence Estuary (Figure 2.1), in order to test for the presence of secondary invaders that could have contributed to the invasion process. The second approach involved a population-level analysis. We considered rivers as colonies (even in the absence of evidence for reproduction). Analyses consisted in determining the genetic relationships among colonies using clustering techniques.

Individual-based analyses It has been known since the 1980s that rainbow trout reproduces in Malbaie and Du Gouffre rivers, located in the Charlevoix region on the north shore of the St. Lawrence estuary. Analyses performed on fish captured in those rivers (n = 113) with STRUCTURE 2.2 revealed that they could be pooled and considered as only one population. We thus created a new source population, Charlevoix (CX), and added it to the population assignment analysis (GENECLASS2). Reproduction in Matane and Les Mechins rivers, located in the Matane region (Gaspe Peninsula), has also been reported since 2007. According to STRUCTURE 2.2, however, pooling these rivers was not justified. They were thus included in the analyses as two distinct populations, despite their small sample sizes (n = 13 and 14 respectively).

Population-based analyses In order to find clusters among the 26 colonies (rivers) in Eastern Quebec, we executed the program FLOCK (Duchesne & Turgeon 2009) with the number of requested partitions *k* varying from 2 to 9. For each *k*-value, *k* reference samples (*refs*) were built and all specimens within each sample were assigned to these reference samples. Samples comprising a majority of specimens assigned to a single *ref* were themselves assigned to that *ref* as samples. Thus the scale of the assignment operation was upgraded from specimen to sample. Samples assigned to the same *ref* within the same *k* run were grouped together within an *association list*. These association lists then served to calculate pairwise distances between samples based on the following rules. First, compute the co-occurrence index between A and B samples as follows: $CI_{AB} = 2^* (CO_{A,B})/(O_A + O_B)$, where $CO_{A,B}$ = number of times that A and B are found together within all association lists over all *k* values, and O_A or O_B = number of times that A or B is found within all association lists over all *k* values. The distance proper is: $D_{AB} = 1\text{-}CI_{AB}$. The rationale for this distance statistic is simply that, given samples A and B, the more closely related they are, the more likely they will be found within the same association list.

Several distance matrices, based on a random selection of association lists, were built from all pairwise sample distances and subsequently processed by the programs NEIGHBOR and DRAWTREE in PHYLIP 3.68 (Felsenstein 2004) to obtain sample clusters and their graphical representation (unrooted neighbor-joining tree). Eleven such graphs were built and only those clusters that consistently appeared in the various graphs were retained for further analysis. As a cross validation, another unrooted neighbor-joining tree was built in POPULATIONS 1.2.30 (Langella 1999), with the Cavalli-Sforza and Edwards chord distance method (Dc, based on allelic frequencies), with 10 000 bootstraps on individuals. To be clustered, rivers had to be grouped together in at least 50% of all replicated trees. For both methods, the minimum number of fish in each river was set to 5 individuals. Since the Dc measure does not correct for sample size bias and the number of specimens per population varied from 5 to 59, we conducted the same analysis on a modified dataset where we adjusted sample sizes (n = 5 to 7) by randomly removing specimens in populations with large sample size. We also performed clustering analyses using Bayesian genetic tools such as BAPS 5.2 (Corander et al. 2003) and STRUCTURE. As results were similar for all algorithms, we only present the clusters obtained with POPULATIONS and the complete dataset.

In order to investigate the relationship between clusters, specimens of each cluster were assigned to the set of samples comprising all other clusters and the most contributive source populations (see *Rainbow trout origins* section). Assignments were done according to Paetkau et al. (1995) based on the lowest LLOD threshold (LLOD = 0), i.e. each specimen was assigned to the target sample for which it showed the highest likelihood.

2.5. RESULTS

2.5.1. Standard genetic analyses

The total number of alleles per locus varied between ten and 33, with an overall mean allelic richness of 18.6 (Table 2.2). Among source populations, Hardy-Weinberg disequilibrium was observed at *One14* and *One2* loci (in 6 and 8 source populations respectively). These two loci were excluded from the population assignment analyses as HW equilibrium is required by algorithms used in GENECLASS2 (note that all loci were used with FLOCK which is less restrictive). Linkage disequilibrium ($p < 0.01$) was found in 29 pairs of loci out of 450 (0.06), as would be expected by chance alone. The source population PEI_S, which pools rainbow trout from three rivers, presented the highest rate with linkage disequilibrium observed at 11 pairs of loci (24%). When problematic loci were excluded, we observed heterozygosity values (range 0.528-0.833) similar to those expected under random mating (range 0.540-0.823) in almost all populations (Table 2.3). Significant F_{IS} values ($p < 0.05$) were observed for two cultured populations only (JC and PEI). Mean F_{ST} value was 0.14 and ranged from 0.04 to 0.25, whereas mean D_{est} value was 0.40 [0.16 – 0.58] (Table 2.4).

Table 2.3 Population-specific genetic information based on eight microsatellites: average number of alleles/locus (A), mean allelic richness (A_R), observed (H_O) and expected (H_E) heterozygosities and inbreeding coefficient (F_{IS}, $p < 0.05$ are indicated in bold).

Population	n	A	A_R	H_O	H_E	F_{IS}
ON	50	11.1	9.704	0.755	0.785	0.038
NY	50	10.4	9.097	0.747	0.772	0.033
M	50	11.9	10.743	0.833	0.823	-0.012
LDE	47	5.6	5.142	0.643	0.635	-0.013
JC	50	6.3	5.517	0.753	0.665	**-0.133**
PEI	50	6.9	6.190	0.723	0.622	**-0.163**
PEI_ BU	27	6.0	6.000	0.644	0.637	-0.010
PEI_C	27	5.1	5.125	0.528	0.540	0.023
PEI_S	50	6.6	5.989	0.663	0.656	-0.011
NS	50	5.5	4.978	0.576	0.557	-0.034

Table 2.4 Pairwise estimates of F_{ST} (above diagonal) and D_{est} (under diagonal) between source populations of rainbow trout (1 000 permutations), based on 8 microsatellites. Lowest differentiation values ($F_{ST} < 0.10$ and $D_{est} < 0.30$) are in bold.

	ON	NY	M	LDE	JC	PEI	PEI_BU	PEI_C	PEI_S	NS
ON	-	**0.05**	**0.04**	0.12	0.12	0.13	**0.09**	0.13	**0.08**	0.15
NY	**0.25**	-	**0.05**	**0.09**	0.14	0.16	0.11	0.15	**0.10**	0.20
M	**0.22**	**0.27**	-	0.12	0.13	0.15	0.11	0.14	**0.10**	0.17
LDE	0.41	0.32	0.45	-	0.20	0.22	0.14	0.19	0.14	0.25
JC	0.43	0.49	0.50	0.55	-	0.22	0.15	0.19	0.12	0.23
PEI	0.38	0.49	0.50	0.54	0.50	-	0.18	0.20	0.16	**0.09**
PEI_BU	**0.29**	0.44	0.38	0.42	0.40	0.46	-	**0.06**	**0.05**	0.17
PEI_C	0.40	0.47	0.41	0.58	0.47	0.42	**0.16**	-	**0.07**	0.16
PEI_S	0.30	0.39	0.36	0.47	0.32	0.37	**0.16**	**0.19**	-	0.15
NS	0.39	0.53	0.51	0.56	0.50	**0.17**	0.38	0.31	0.32	-

2.5.2. Origins of the invasion

The level of resolution obtained with the ten source populations was high (Table 2.5A). We obtained 82% of correct re-assignments, which reached 86% when α was set to 0.01 (data not shown). The majority of errors were found among locations from the Maritime provinces, and about half of them were re-assigned to another Maritime source population. Almost all the other errors involved re-assignment to the Ontario population (ON). The bias of incorrect re-assignments towards ON would be explained if that population were the principal founding population. No fish from a western source population was re-assigned to a Maritime source population.

Five source populations were identified (GENECLASS2, 10 000 simulated individuals, $\alpha = 0.05$), as contributing to the rainbow trout captured in Eastern Quebec: Ganaraska River (ON), Lake Memphremagog (M), Salmon River (NY), Brudenell River (PEI_BU) and Summerside Harbor (PEI_S) populations (Figure 2.2A). The great majority of the fish were assigned to either the Ganaraska River population (48%, thereafter referred to as the Lake Ontario population) or the Lake Memphremagog population (23%). Only 1% of fish were assigned to the Prince Edward Island populations. Sixty-four specimens (26%) could not be assigned to any of the source populations under the assignment criteria we applied. Interestingly, about half of these specimens were caught in one of the four rivers sustaining newly established populations, the Malbaie River.

2.5.3. Rainbow trout dispersion mode

Individual-based analyses (GENECLASS2) The level of resolution of the test was determined when Charlevoix (CX) was added as a source population (Table 2.5B). We obtained 79% of correct re-assignments, which reached 82% when α was set to 0.01 (data not shown). Twenty-one percent of Charlevoix individuals were re-assigned to the Ontario population, whereas 8% of Ontario fish were re-assigned to Charlevoix.

Table 2.5 Level of resolution analysis for source populations, based on eight microsatellites, according to the *leave-one-out* method (α = 0.05). A) Ten source populations used to determine rainbow trout origins. B) Eleven source populations, including Charlevoix, used to test the stepping-stone hypothesis. The proportions of correct assignments are in bold. Complete population names and characteristics are given in Table 2.1.”?” refers to un-assigned proportions.

			Re-assigned population											
	Origin	N	ON	NY	M	LDE	JC	PEI	PEI_BU	PEI_C	PEI_S	NS	CX	?
A)	ON	50	**0.82**	-	0.10	-	-	-	-	-	-	-		0.08
	NY	50	0.02	**0.86**	-	-	-	-	-	-	-	-		0.12
	M	50	-	-	**0.94**	-	-	-	-	-	-	-		0.06
	LDE	47	-	0.04	0.02	**0.92**	-	-	-	-	-	-		0.02
	JC	50	-	0.02	-	-	**0.96**	-	-	-	-	-		0.02
	PEI	50	0.04	-	-	-	-	**0.92**	-	-	-	0.02		0.02
	PEI_BU	27	0.04	-	0.07	-	-	-	**0.81**	-	-	-		0.07
	PEI_C	27	0.04	-	-	-	-	-	0.15	**0.59**	0.19	-		0.04
	PEI_S	50	0.20	0.02	-	-	-	-	0.08	-	**0.64**	-		0.06
	NS	50	0.12	-	0.02	-	-	0.18	-	-		**0.64**		0.04
B)	ON	50	**0.78**	-	0.08	-	-	-	-	-	-	-	0.08	0.06
	NY	50	0.02	**0.86**	-	-	-	-	-	-	-	-	-	0.12
	M	50	-	-	**0.94**	-	-	-	-	-	-	-	-	0.06
	LDE	47	-	0.04	0.02	**0.91**	-	-	-	-	-	-	-	0.02
	JC	50	-	0.02	-	-	**0.94**	-	-	-	-	-	0.02	0.02
	PEI	50	0.04	-	-	-	-	**0.88**	-	-	-	0.02	0.02	0.04
	PEI_BU	27	-	-	0.07	-	-	-	**0.78**	-	-	-	0.07	0.07
	PEI_C	27	-	-	-	-	-	-	0.11	**0.56**	0.19	-	0.11	0.04
	PEI_S	50	0.12	0.02	-	-	-	-	0.08	-	**0.62**	-	0.10	0.06
	NS	50	0.10	-	0.02	-	-	0.16	-	-	-	**0.62**	0.08	0.02
	CX	112	0.21	0.01	0.04	-	-	-	-	-	-	-	**0.72**	0.02

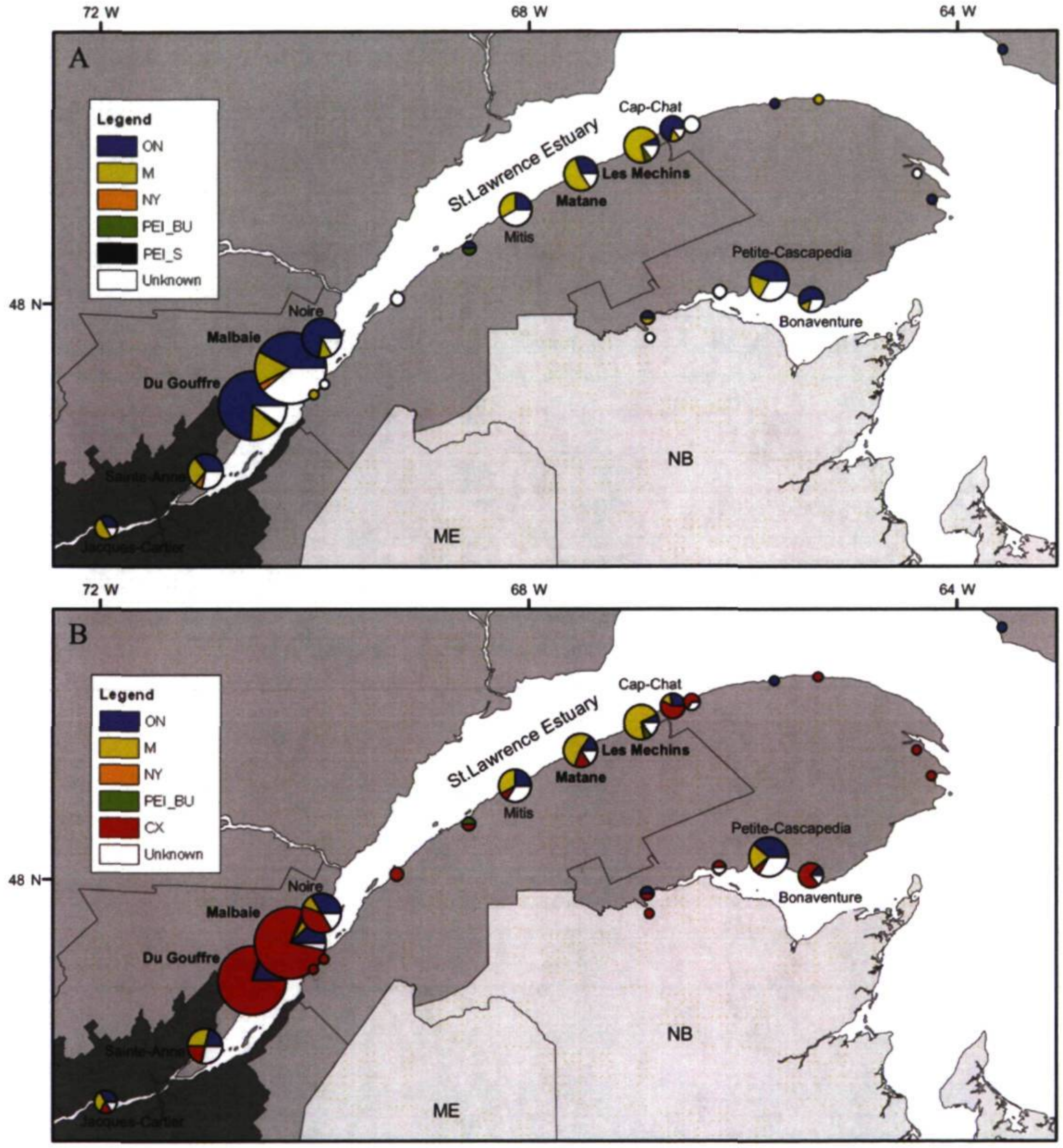

Figure 2.2 Genetic origin of 243 rainbow trout captured in salmon rivers located in Eastern Quebec between 2005 and 2007. Assignment analyses were performed with 8 microsatellites and A) ten source populations, or B) 11 source populations, including the newly established population of Charlevoix (Malbaie and Du Gouffre rivers). Stocking area is shown in dark grey. Rivers supporting self-sustaining populations are in bold. Circle size is proportional to sample size. Labelled rivers have more than five individuals. ON: Ganaraska River (Ontario), M: Lake Memphremagog, NY: Salmon River (New York), PEI_BU: Brudenell River (Prince Edward Island), PEI_S: Summerside Harbor (Prince Edward Island), CX: Charlevoix.

When Charlevoix was incorporated in the population assignment analysis as a new source population, 27 fish captured outside Malbaie and Du Gouffre rivers, initially mainly assigned to Lake Ontario, were assigned to Charlevoix (Figure 2.2B). Moreover, the number of fish previously un-assigned (excluding fish from Malbaie and Du Gouffre rivers) was reduced by 30% as 11 of them were revealed to belong to this population. The results also showed that although trout captured in Malbaie and Du Gouffre rivers were mainly assigned to the Charlevoix population, some fish were still re-assigned to the Ontario (n = 17) and Memphremagog (n = 4) populations with higher likelihood. The addition of populations from Les Mechins and Matane rivers did not change the assignment results as no fish caught elsewhere was assigned to either of these populations.

Population-based analyses (FLOCK & DC) According to the population trees built with fish captured in Eastern Quebec, three clusters were identified (Figure 2.3). A first group included Du Gouffre, Malbaie, Mare (large tributary of du Gouffre River[2]) and Noire rivers, all located in the Charlevoix region. Les Mechins and Matane rivers formed a second group. Finally, the last group comprised the Petite-Cascapedia and Bonaventure rivers, flowing into the Baie-des-Chaleurs. As there is no reproduction in that region, vagrants captured in both rivers presented a similar "origin profile". All three clusters were mainly assigned to Lake Ontario, followed by the Charlevoix population (Table 2.6). Percentage of assignment to any cluster other than Lake Ontario was always lower than 25%.

---

[2] Il est à noter qu'une coquille s'est glissée dans les analyses et dans la version publiée : le tributaire de la Mare a été incorrectement attribué à la rivière Malbaie. Cette erreur n'a toutefois aucune incidence sur les résultats et leur interprétation, puisque qu'il s'agit de très peu de spécimens et que les deux rivières ont de toute façon été traitées ensembles.

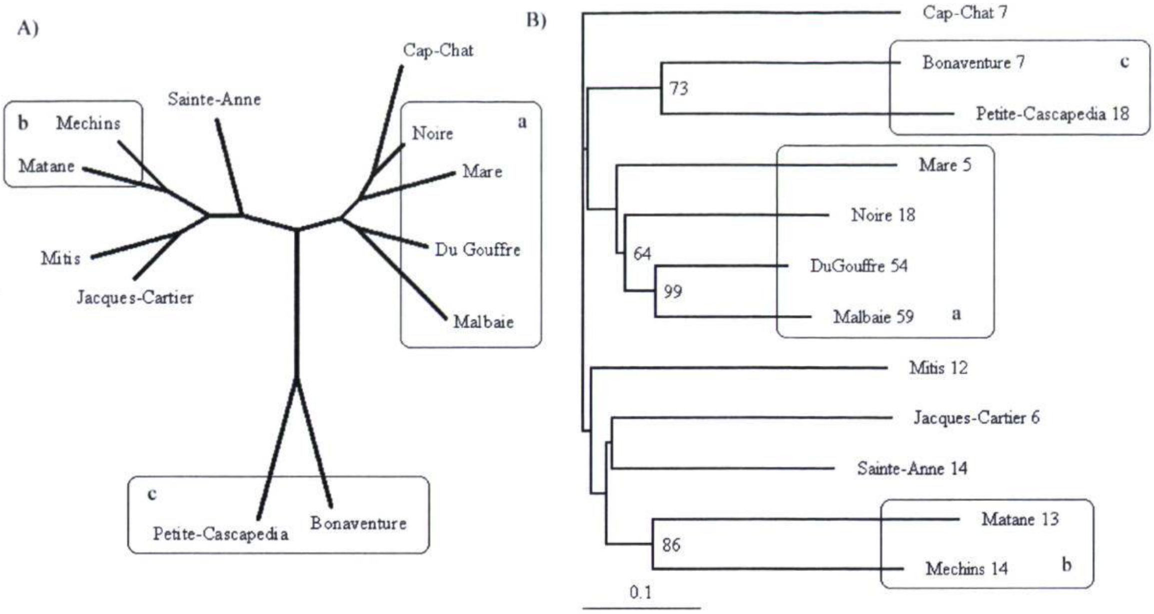

Figure 2.3 Unrooted neighbor-joining phylogenetic trees obtained with A) FLOCK and B) Cavalli-Sforza and Edwards distance methods. Rounded rectangles indicate clusters: (a) Charlevoix, (b) Matane-Mechins, (c) Baie-des-Chaleurs. Sample sizes are shown in graph B, and bootstrap values greater than 50% are presented at the nodes.

Table 2.6 Analysis of genetic similarity between clusters of rivers, based on re-assignment method: probability that each cluster belongs to one of the other clusters or source populations.

		Re-assigned cluster				
Origin	N	Charlevoix	Matane-Mechins	Baie-des-Chaleurs	Lake Memphremagog	Lake Ontario
Charlevoix	130	-	0.18	0.14	0.05	0.63
Matane-Mechins	27	0.11	-	0.07	0.07	0.74
Baie-des-Chaleurs	25	0.24	0.04	-	0.08	0.64

2.6. DISCUSSION

Despite huge introduction pressures around the world, the establishment of rainbow trout in new habitats appears difficult (Fausch 1988; MacCrimmon 1971), being restricted by a series of physical and climatic factors including the number of secondary tributaries, the stream slope, the flooding period, and water temperatures (Fausch et al. 2001; Chapter 3). This may explain why we find natural reproduction in only four rivers in Eastern Quebec. On the other hand, rainbow trout in Eastern Canada has been repeatedly and intensively stocked for many years in various watercourses. The spread of rainbow trout is facilitated by this variety of potential sources, as the number of foci is more important to invasion success than the size of individual foci (Hengeveld 1989). Moreover, despite the species apparent difficulty in colonizing new habitats, it nevertheless possess several characteristic of good invaders (Hänfling 2007; Moyle & Marchetti 2006), such as tolerance to fluctuations in salinity and pH (Kerr & Lasenby 2000) and excellent dispersal capacities, with an anadromous form (steelhead) that can migrate over many kilometers (Dumont 1991; Mongeau & Brisebois 1982).

2.6.1. Origins of rainbow trout in Eastern Quebec

The rainbow trout has been intensively stocked for many years in several streams and lakes in Southern Quebec, the Great Lakes and in the Maritime provinces. The origin of these fish has been very diverse, varying according to year and location. Therefore, it would not have been surprising to find that the invasion of rainbow trout in Eastern Quebec had many sources. Dumont et al. (1988) proposed that rainbow trout followed two routes to reach rivers in Eastern Quebec: (i) from established populations in the upstream part of the St. Lawrence River (such as Lakes Ontario, Memphremagog and Champlain) or (ii) from established populations and stocked fish from the Maritime provinces. To these possible colonization routes could be added the fish stocked yearly in Quebec province. Our population assignment analyses revealed that almost all rainbow trout captured in Quebec salmon rivers came from naturalized populations established in Lake Ontario (Ganaraska River population) and Lake Memphremagog. Only three fish appeared to belong to Maritime wild strains, Brudenell River (2) and Summerside Harbor (1), which represents only 1% of total captures. We are confident that they are not assignment errors as no fish from western source populations were re-assigned to Maritime populations in the analysis done to determine our level of resolution. Nevertheless, the quasi-absence of a Maritime signal clearly shows that the direction of the invasion process of rainbow trout is west-to-east, following the St. Lawrence River.

The spread of rainbow trout in Eastern Quebec strongly relies on established (naturalized) populations. We demonstrated that all fish captured outside the stocking zones (excluding fish that we were unable to assign) originated from a wild population of steelhead trout. Therefore, even if local and private stockings occur yearly in many watersheds, it seems that the contribution of cultured strains to the invasion process is weak, as no "hatchery signal" was found in Eastern Quebec. This may be explained by the use of sterile fish, that prevents reproduction and thereby establishment of domesticated rainbow trout in salmon rivers. In addition, even fertile hatchery females spawning in the wild tend to produce considerably fewer smolt and adult offspring *per capita* than wild females due to differences in egg production, timing of breeding and emergence, and genetic selection (McLean et al. 2003, 2004). Also, most of the local stocking have a put-and-take purpose (release of catchable fish before a fishing event to increase immediate success), such that the majority of stocked fish are believed to be quickly recaptured and have little chance to migrate elsewhere and reproduce. Finally, stocked rainbows are often freshwater resident strains and present a lower potential to migrate outside their watershed to colonize eastern rivers, unlike individuals from wild populations, mainly composed of anadromous fish (L. Gerardi & K. Kelsey, Vermont Fish and Wildlife Department, pers. comm.; F. Whoriskey, Atlantic Salmon Federation, pers. comm.).

2.6.2. Rainbow trout dispersion mode

Our results suggest that the invasion process of the rainbow trout in Eastern Quebec follows a complex stepping-stone dispersion mode along the St. Lawrence River system, leading to the establishment of a few new self-sustaining populations in salmon rivers, which in turn produce vagrants that will eventually colonize other rivers. However, the process also involves invaders still dispersing from western source populations, although a recently naturalized population is a more important source of new colonizers to Eastern

Quebec rivers. Thus, we demonstrated that rainbow trout first migrated downstream from established populations in Lake Ontario and, to a lesser extent, in Lake Memphremagog. Fish reached salmon rivers in Eastern Quebec and some established self-sustaining colonies in at least four rivers in the Charlevoix and Matane regions. According to individual-based analyses, the ultimate origin of these new populations is not the same, Les Mechins and Matane populations being more related to Lake Memphremagog fish, and Charlevoix rainbows being more similar to the Ontario strain. Furthermore, it appears that many rainbow trout originating from Charlevoix migrated to the East and are now found as far downstream as the Baie-des-Chaleurs region. For now, there is no evidence that Matane and Les Mechins populations contribute significantly to the continuing invasion by producing vagrants as no signal was observed when they were considered as source populations. Their establishment thus appears to be quite recent. However, we cannot discount the possibility that the small samples from these rivers may decrease population assignment success. Sample sizes were clearly too small to be representative of the genetic population diversity and in population assignment analyses, source populations should preferably include at least 30 individuals.

In a classical stepping-stone model, fish would have moved only between adjacent established populations (Kimura & Weiss 1964). In the St. Lawrence system, fish from at least three different populations (ON, M and Charlevoix) still continue to move far downstream and co-occur in many salmon rivers, thus forming multi-focal waves of invasion. This illustrates a complex dispersion process that is still in progress.

2.6.3. Consequence of the small temporal scale

The first observation of natural reproduction (captures of juveniles 0+) was in Du Gouffre River, in 1984 (Pelletier 1985). Thus, the oldest self-sustaining population outside the stocking area is about 25 years old. Considering that rainbow trout first reproduces at approximately 4 years of age (Scott & Crossman 1974), less than 10 generations have occurred since the founding of this population. Even if rapid genetic differentiation in salmonid populations is possible (Ayllon et al. 2006), this population is still similar to its founding population ($F_{ST} < 0.04$ between Du Gouffre R. and Ganaraska R. populations). This small temporal scale implies that differentiation between *mother* and *daughter* populations is still low, possibly because of both the short time frame since the founding of Du Gouffre River as well as ongoing gene flow from Ganaraska River which may have introduced some bias in our analyses. This probably explains the 21 fish from Du Gouffre and Malbaie rivers that were assigned to either Ontario (15.0%) or Memphremagog (3.5%) populations, instead of to the Charlevoix population.

2.6.4. Fish of unknown origin

It was not possible to identify the genetic origin of some rainbow trout (11% when CX added) captured in eleven rivers. During the analysis performed to determine the level of resolution, we obtained a much lower rate of un-assigned fish (4%), indicating that the unidentified fish do not simply reflect the error margin of the test. We thus conclude that some source populations are probably missing from our analysis. It was not possible to sample all the potential source populations as some strains were unavailable and some populations are either extinct or unidentified. According to our results, it seems unlikely that the sources of these un-assigned fish are domestic strains. Rather, we suggest that these fish came from unknown wild population(s), established either upstream of Quebec City or recently established in the St. Lawrence Estuary basin. The greatest number of un-assigned fish came from the Malbaie River. Genetic analysis revealed that Malbaie rainbows mainly originated from Lakes Ontario and Memphremagog. However, the high number of fish of unknown origin in that river also suggests that there might be an additional colonization source yet to be identified.

2.6.5. Concluding remarks

The introduction of rainbow trout in the western part of Quebec occurred many decades ago, but the species invasion in Eastern Quebec is a recent phenomenon, only observed in the last 35 years, and is still ongoing. We demonstrated that the invasion is driven by dispersal (most probably involving the anadromous steelhead ecotype) that originated from established populations in Lakes Ontario and Memphremagog. The invasion involves a complex stepping-stone dispersion mode along the St. Lawrence River system, leading to the establishment of a few new self-sustaining populations in salmon rivers, which in turn produce vagrants that will eventually colonize other rivers. We also observed that invaders still continue to migrate from Lakes Ontario and Memphremagog, but the recently established population in Charlevoix is a more important source of new colonizers to Eastern Quebec rivers.

The protection of native salmonids in eastern Quebec requires some management initiatives aimed at reducing the eastward spread of rainbow trout. Such initiatives could include (1) reducing the effective size of the Charlevoix population through a targeted sport fishery, (2) impeding reproduction in the Matane and Mechins Rivers as the number of reproduction events are believed to be few and localized, (3) halting the upstream migration of anadromous spawners in the Matane River by better monitoring of the fish passage located near the river's mouth, and (4) curtailing the establishment of new source populations by restricting repeated and massive stocking events inside the stocking area.

2.7. ACKNOWLEDGEMENTS

This work was funded by grants from the Natural Sciences and Engineering Research Council of Canada, CIRSA (Centre Interuniversitaire de Recherche sur le Saumon Atlantique), the Fédération Québécoise de la Faune and the Réseau Aquaculture de Québec. We thank our collaborators that helped to collect rainbow trout samples: Ministère des Ressources naturelles et de la faune, Québec Pêche, Fédération québécoise pour le saumon Atlantique, Fédération des gestionnaires de rivières à saumon du Québec, Simon Blanchet, the "field work team 2007", and all ZECs, organisations, sport and commercial fishermen that participated in the sampling campaigns. We are greatfull to Chris Wilson, Chris Mills, Darryl Murrant, Shawn Good, Fred Whoriskey, Jen van der Lee, Daryl Guignon, Rosie MacFarlane, Christine Pater, Todd Dupuis, the Province of PEI, the Pisciculture Jacques-Cartier and the Pisciculture Lac-des-Écorces who gracefully provided the source population specimens. A special thank to Pierre Duchesne, who helped us with FLOCK analyses, and to Olivier Langella and Julie Faure-Lacroix for their help with POPULATIONS software and tree draw. We also thank Françoise Colombani, Lucie Papillon and Vicky Albert for their help with DNA manipulations. Finally, we thank Pierre Duchesne, Pierre Dumont and two anonymous reviewers for their comments on earlier versions of the manuscript.

CHAPITRE 3. ABIOTIC VARIABLES ACCOUNTING FOR PRESENCE OF THE EXOTIC RAINBOW TROUT (*ONCORHYNCHUS MYKISS*) IN EASTERN QUEBEC RIVERS

Thibault, I., Hedger, R.D., Crépeau, H., Audet, C. & Dodson, J.J. 2010. Knowledge and Management of Aquatic Ecosystems, 398 : publié en ligne le 14 octobre.

3.1. ABSTRACT

Rainbow trout is an exotic fish species that has been introduced in Quebec (Canada) since 1893-94. Despite spatially-restricted stocking for recreational fishing, the species has spread throughout the Saint Lawrence River. In this study, the relationship between rainbow trout occurrence (presence or absence) and abiotic variables (river geomorphology and climate) was examined for 91 coastal rivers throughout Eastern Quebec in order to determine which variables promote or impede the ongoing invasion process. Results revealed that rainbow trout presence in Eastern Quebec was primarily determined by geomorphological parameters. The invader's presence was strongly related to the presence of tributaries (especially larger ones). To a lesser extent, the presence of rainbow trout was positively related to warm spring and summer temperatures and negatively related to the peak flood date occurring during the egg deposition period (May). This study proposes a parsimonious modeling approach to identify which environmental parameters favour the spreading of an invader, even when a limited dataset is available due to the incomplete invasion process.

3.2. RÉSUMÉ

Variables abiotiques expliquant la présence d'une espèce exotique, la truite arc-en-ciel (*Oncorhynchus mykiss*), dans les rivières de l'Est du Québec.

La truite arc-en-ciel est un poisson exotique qui a été introduit au Québec (Canada) en 1893-1894. Malgré un zonage piscicole restreignant spatialement son ensemencement à des fins de pêche sportive, l'espèce s'est dispersée le long du Fleuve Saint-Laurent. Dans cette étude, la relation entre l'occurrence de la truite arc-en-ciel (présence ou absence) et des variables abiotiques (géomorphologie fluviale et climat) a été examinée pour 91 rivières côtières situées dans l'Est du Québec, afin de déterminer quelles variables promouvoient ou limitent le processus d'invasion actuellement en cours. Les résultats indiquent que l'occurrence de la truite arc-en-ciel dans l'Est du Québec était principalement déterminée par des paramètres géomorphologiques. La présence de l'envahisseur était fortement associée à la présence de tributaires (principalement les plus gros). Dans une moindre mesure, la présence de la truite arc-en-ciel était positivement reliée à des températures printanières et estivales élevées, et négativement associée à la date de crue qui survient durant la période de dépôt des œufs (Mai). Cette étude propose une approche de modélisation parcimonieuse qui permet d'identifier quels paramètres environnementaux favorisent la dispersion d'un envahisseur, même si on ne dispose que de données fragmentaires en raison d'un processus d'invasion non complété.

3.3. INTRODUCTION

Rainbow trout[3] (*Oncorhynchus mykiss*, Walbaum 1792), originating from the North Pacific coastline, is currently found in watercourses on all continents, except Antarctica (Cambray 2003a). In Canada, it was first introduced in 1881 in the Great Lakes Basin. Eggs were first imported to the province of Quebec in 1893-94 (MacCrimmon 1971). Following repeated and massive stockings, the species now reproduces in the Great Lakes, Lake Memphrémagog and probably some tributaries located in the vicinity of Montreal (Dumont 1991; Kerr & Lasenby 2000; Mongeau et al. 1980a). In Quebec, stocking and farming of rainbow trout is limited to the upper region of the Saint Lawrence River (MAPAQ, 2005; Figure 3.1). However, the species has been captured in many tributaries in the downstream part of the Saint Lawrence River and its estuary since 1973 (Dumont et al. 1988; Whoriskey Jr. et al. 1981). Captures of rainbow trout, especially adults, are now frequently recorded along the Gaspesian coast and the lower Saint Lawrence shore (Bas-St-Laurent) as well as in the Charlevoix region. Self-supporting populations have been identified in four rivers in these regions (Chapters 2 & 5). Although globally there have been a large number of failed attempts to introduce rainbow trout (Fausch 1988, 2007; MacCrimmon 1971), it appears that the species is slowly colonizing rivers throughout Eastern Quebec.

The success of biological invasions depends on the invader's capacity to pass through a series of hierarchical filters associated with the different stages of the invasion process (introduction, establishment, spreading). The success of introduction depends on survival during transit between the native habitat and the new environment (Kolar & Lodge 2001) and the number of introduction events and introduced individuals (Colautti & MacIsaac 2004; Moyle & Marchetti 2006). As such, distance from the source populations may be a significant predictor of establishment success, with habitats located closer to source populations being the most likely to be colonized.

The success of establishment also depends on the species ability to survive in the face of abiotic resistance through either acclimatisation or adaptation to novel physical conditions (Moyle & Marchetti 2006; Quist et al. 2005; Williamson 1996), and the species

---

[3] The term "rainbow trout" is used for both resident and anadromous (steelhead) forms.

ability to survive in the face of biotic resistance exerted by the native fauna (Laurenson & Hocutt 1985; Quist et al. 2005). Finally, the success of spreading to new environments depends on the reproductive and dispersive capacities of the species (Colautti et al. 2006; Kolar & Lodge 2001; Laurenson & Hocutt 1985; Richards et al. 2006).

Abiotic conditions in the receiving environment generally constitute the most important filter (Moyle & Light 1996). In Eastern Quebec, it seems likely that the rainbow trout colonization process is driven in part by the river's morphology, as a river's attractiveness for rainbow trout may depend on characteristics such as slope, elevation, channel dimensions, accessibility and the presence of tributaries. Slope and elevation strongly influence the spatial distribution of rainbow trout, with densities being higher in downstream areas where elevation and slope gradients are less (Gard & Flittner 1974). The distribution of this species along an altitudinal gradient can be attributed to changes in current velocity, pool to riffle ratio, substrate size, and temperature variations. Slope, sinuosity and channel length also influence the flow regime and can modulate flood amplitude. The presence of dams will impede upstream movement of rainbow trout, whereas tributaries could provide safe habitats for eggs and juveniles.

The establishment of new populations will also depend on the local climatic conditions (temperature, precipitation and flood regime). Rainbow trout is adapted for cold-temperate environments but can tolerate warm temperatures, with critical thermal maxima in the vicinity of 28-30°C (Currie et al. 1998). The optimal temperature varies from 10 to 21°C according to life-stage (Boughton et al. 2007; Burgner et al. 1992; Garside & Tait 1958; Lefler et al. 2006; Nelitz et al. 2007). Discharge and the timing of peak flows, dependent on precipitation, also play an important role in defining suitable habitat for rainbow trout. The abundance of 0-group rainbow trout may be positively related to winter discharge (Mitro et al. 2003). Given that rainbow trout reproduce in spring, floods induced by snow melting may destroy nests and wash away eggs. Fausch et al. (2001) found that the worldwide establishment success of rainbow trout is closely related to the concordance of fry emergence and months of low flood probability.

The main objective of this study was thus to determine which abiotic factors explain the presence of rainbow trout in the rivers of Eastern Quebec. To do so, we identified the variables characterising geomorphology, temperature, hydrology and precipitation regime of those rivers in which rainbow trout occur relative to those where no trout have been detected. Insufficient data concerning water quality (e.g. pH, conductivity, and dissolved nutrient concentrations) precluded their inclusion in this analysis.Our initial hypothesis was that distance from the stocking area, river slope, temperature during the growing season, and the flood regime associated with spring precipitations would be the most important parameters influencing rainbow trout presence. Biotic resistance was not considered in this analysis as the distribution of the two species most likely to impede rainbow trout establishment, Atlantic salmon (*Salmo salar*) and brook charr (*Salvelinus fontinalis*), is ubiquitous at the spatial scale of this study. Multispecific interactions at smaller spatial scales are the subject of a parallel study (Chapter 4).

3.4. MATERIALS AND METHODS

3.4.1. Study area

Eastern Quebec (~46.5-52°N, ~70-60°W) bounds the Saint Lawrence Estuary (Figure 3.1) in eastern Canada. It is characterized by a cold-temperate climate, with mean coastal temperatures typically ranging between less than -12°C in January and greater than 16°C in July. Effective growing degree days (EGDD) above 5°C range from approximately 1700 in the south to 900 in the north. Water coastal temperatures are influenced by currents within the estuary - a warm current extends along the North Shore between Quebec City and the Saguenay Fjord crossing to the South Shore at the confluence with the Saguenay Fjord. To the east of the Saguenay, temperatures along the North Shore tend to be less than those on the South Shore. Mean precipitation along the coast varies between approximately 800 and 1200 $mm \cdot y^{-1}$.

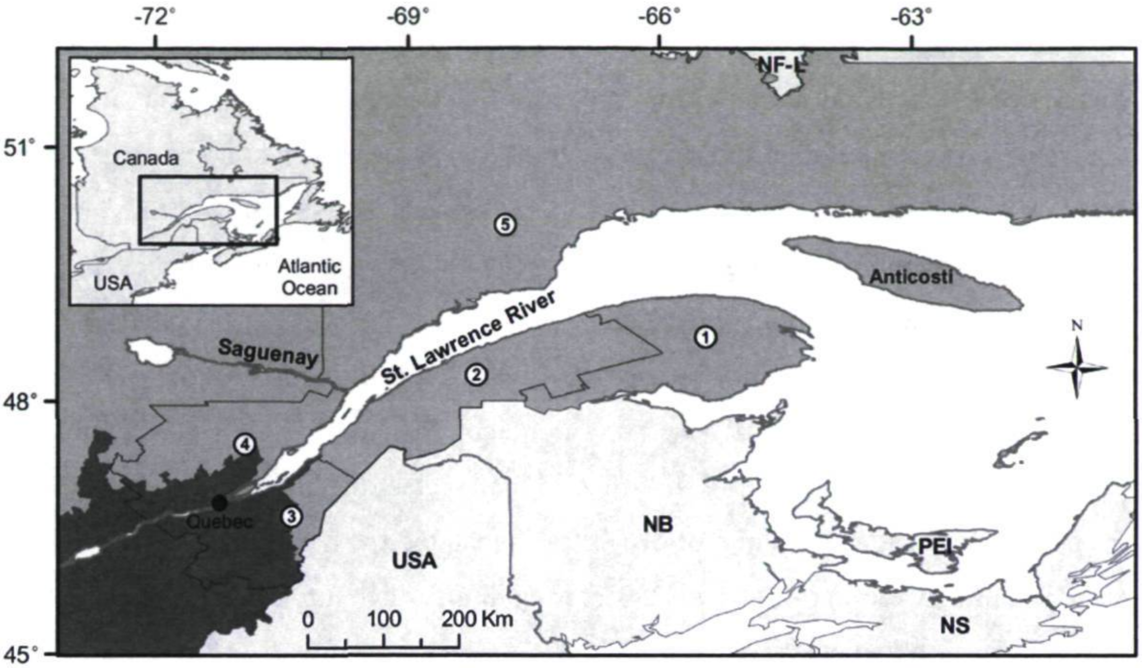

Figure 3.1 Study area in Eastern Quebec (Canada). Quebec province is in medium grey. Rainbow trout stocking area is in dark grey. 1: Gaspesia, 2: Bas-St-Laurent, 3: Chaudière-Appalaches, 4: Capitale-Nationale (including Charlevoix region), 5: Côte-Nord. NB: New Brunswick, NS: Nova Scotia, PEI: Prince Edward Island, NF-L: Newfoundland-Labrador.

3.4.2. Rainbow trout data

Rainbow trout occurrence was only considered for rivers located to the east of the zone where stocking has been permitted (i.e. rivers where rainbow trout have not been artificially introduced). Rainbow trout data were obtained from three sources: (i) the *Ministère des Ressources naturelles et de la Faune* (MNRF), (ii) commercial and sport fishing organizations and (iii) electrofishing surveys performed in 2007. Data recorded by MRNF, which constituted the major part of our rainbow trout database, were found in internal reports, scientific papers, fish record databases and more recently, in fishing survey datasets. The latter mainly consisted of electrofishing surveys performed periodically in rivers to monitor juvenile Atlantic salmon densities, and occasionally in non-salmon rivers (such as in Chaudière-Appalaches) for fish species inventories. Prevalence of rainbow trout was also registered during annual visual counts of salmon spawners. Moreover, a variety of capture devices (rotary trap, counting fence, migratory pass, etc.) are installed on several rivers to study the downstream migration Atlantic salmon smolt and the adult spawning migration. All captured rainbow trout are recorded. Commercial fishers have also been a source of information for MRNF for many years. Sport fishermen are not obliged to report rainbow trout and their input to the database has been sparse until recently. Increasing awareness concerning the invasion of rainbow trout has reversed this tendency, particularly within salmon sport fishing organizations (e.g. under the ZEC "controlled exploitation zone" management framework). To further increase the contributions of the sport fishery to the database, we invited sport fishers in 2006 and 2007 to record all their rainbow trout captures in targeted ZEC and MRNF offices. Finally, electrofishing surveys (about 10 to 20 open stations per river, parcel size of 100 m^2, separated by 1 km, two passes) of rainbow trout juveniles were performed in 2007, providing further information on rainbow trout incidence in eight targeted rivers (Chapter 4).

In total, more than 3300 records of rainbow trout have been registered in Eastern Quebec (Capitale-Nationale, Côte-Nord, Chaudière-Appalaches, Bas-St-Laurent and Gaspesia regions, Figure 3.1). More than 50% of records have been reported since 1999. Variation observed in the number of rainbow trout registered per river (one record up to several hundred) is not only explained by the spatial distribution of the species. It also relies on fishing effort, which varies between rivers according to the rivers' accessibility and attractiveness for fishers, and to the monitoring efforts of managers. Given that data quality varied according to data source (ranging from rivers with a single reference indicating the presence of rainbow trout to rivers having detailed surveys of the spatial variation in rainbow trout abundance), and that we could not control for fishing effort, data standardization was necessary. The binary variable *rainbow trout occurrence* was therefore established (with two options: "present" or "absent"). Rainbow trout was scored as being present within a river if there was any observation or capture in that river within the dataset. Otherwise, rainbow trout was scored as being absent. This was based on the assumption that the situation where other captures occurred, but were not registered by sport fishers, was a far more likely scenario than the situation where the only rainbow trout ever to enter the river had been captured and registered. To limit the situation where rainbow trout were present but not scored as such because of limited fishing effort or no registration, all rivers from remote regions were removed from the study: (i) rivers north of 50.25°N and east of 66.5°W along the Côte-Nord, (ii) rivers east of 63.4°W on Anticosti Island, and (iii) rivers distant from the coast. Finally, we analysed a subset of rivers to assess the potential bias of variable fishing effort in modelling relationships between rainbow trout prevalence and environmental factors (see below).

3.4.3. Abiotic data

Abiotic data were acquired on river geomorphology and climate (a list of abbreviations for the abiotic variables is presented in Table 3.1).

Geomorphological variables. Mean channel slope (MS) was determined for the most downstream 20 km of the principal channel (or the total length of the principal channel if this length was less than 20 km). Minimum and maximum channel elevations (MinE and MaxE) were estimated on the total length of the main watercourses by integrating a DEM (Canadian Digital Elevation Data, obtained from GeoBase; www.geobase.ca) with the coordinates of each channel (MRNF (Québec 2000)). Sinuosity (Sin) was estimated as the ratio of the along-channel distance to the Euclidean distance from the river mouth to a position along the principal channel 20 km upstream (or the most upstream part of the watercourse if the total channel length (Len) was less than 20 km). The number of tributaries that flowed into the principal channel was enumerated at two spatial scales: larger tributaries (LTrib) at a scale of 1:1,000,000 ("hydro_l_arc" MRNF shapefile (Québec 2000)) and smaller tributaries such as creeks or intermittent streams (STrib) at a scale of 1:50,000 ("QCmnwtl" Canadian hydrographic network shapefile (DMTI Spatial, 2005)). We estimated an error of ± 5 in the count of small tributaries. The number of dams (Dam) greater than 2 m in height within the downstream 10 km of each river was estimated using data obtained from the *Centre d'expertise hydrique du Québec*. For rivers along the North and South Shore of the Saint Lawrence, the distance from the stocking zone (SZD) in southern Quebec (Figure 3.1) was estimated along the coastline. For rivers on Anticosti Island, distance was estimated from the stocking zones along the coast to the apex of the Gaspesian peninsula, plus a Euclidean distance between this apex and the island, plus a distance around the island to the rivers in question. A rainbow trout aquaculture industry and naturalized populations also exist in the Maritime Provinces, but these populations are not a significant source of trout in the St. Lawrence study area (Chapter 2).

Table 3.1 Thirty-five geomorphological and climatic variables used in the analysis, grouped into compartments used for modelling.

Variables	Abbreviation
Geomorphological variables	
Initial mean slope	MS
Sinuosity	Sin
Minimum elevation	MinE
Maximum elevation	MaxE
River length	Len
Number of large tributaries	LTrib
Number of small tributaries	STrib
Presence of a dam	Dam
Distance from the stocking zone	SZD
Climatic variables	
Temperature	
Mean monthly water temperature ($n = 12$)	T_Jan to T_Dec
Effective growing degree days (> 5°C)	EGDD
Precipitation	
Total monthly precipitation ($n = 12$)	P_Jan to P_Dec
Peak flood date	PFD

Climatic variables. Climatic data were obtained from the *Canadian Weatheroffice* (1971-2000 Canadian Climate Normals, www.climate.weatheroffice.ec.gc.ca). These data included 30-year means of monthly temperatures and total monthly precipitation (P) for 430 weather stations throughout Quebec. Climatic variables only showed climate properties at the weather stations, and not at the rivers where rainbow trout prevalence had been estimated. Variograms were used to establish the spatial dependence in climatic variables, and kriging was used to estimate climate variables at the river mouths, using the sgeostats package developed by J.J. Majure and A. Gebhardt in R (Hornik 2007). River water temperature was estimated from air temperature using a non-parametric regression relationship established between water and air temperature for selected rivers where concurrent data were available. Water temperatures were obtained from thermograph data collected in 26 rivers throughout Quebec by the MRNF. The temporal ranges of these thermograph data varied according to river, but most data were obtained from 2001-2005, so data from outside of this time range were removed. The relationship between daily median water temperature (the response variable) and (i) daily median air temperature, (ii) longitude and (iii) latitude was determined using generalized additive modelling. Longitude and latitude were included as predictors because the response of water temperature to air temperature was geographically dependent. Using the three predictors, the generalized additive model explained 86.2% of the variance in daily median water temperature. The generalized additive model was then used to predict mean water temperature as a function of day of the year in all rivers, using the kriged estimate of air temperature at the river, river latitude and river longitude. Latitude and longitude were included as predictors because the relationship between air temperature and water temperature varied spatially. Means of monthly water temperature (T) and effective growing degree days (EGDD, that is the sum of the difference between mean daily temperature and 5°C) were calculated from these estimated daily values. Finally, peak flood date (PFD) in each river was estimated from a hydrographic database amassed by the *Centre d'expertise hydrique du Quebec* which contained data from hydrographic stations in 38 rivers. The spatial dependence in PFD of the hydrograph data was modelled using variograms, and kriging was used to interpolate PFD for each river in the current study. Kriging meant that the estimated PFD for each river was a weighted function of neighbouring hydrograph PFDs (the weight being an inverse function of distance of separation). The rationale for use of kriging was that PFD was dependent on the local climate, so neighbouring rivers would have had similar PFDs.

3.4.4. Modelling the relationships

In this section, we briefly present the approach used for modelling the relationship between rainbow trout prevalence and the geomorphological and the climatic variables separately (Table 3.1), using logistic regression models (SAS v9 2001). Models were fitted based on original variables (geomorphological data only) or on the principal components (PCs) of a principal component analyse (PCA). The use of regressions based on PCA products was justified by the presence of a large number of correlated variables, especially among climatic variables.

For original variables, tests for potential inclusion in the multivariate model were F-tests, student tests and the Hosmer & Lemeshow (1989) criteria (p-value less than 0.25, see Appendix A). The criteria for inclusion of a PC was that it had an eigenvalue greater than 1. Variable transformations (either by x^2 for a quadratic relationship, or categorization) were applied when the relationship with the logit was not linear (Appendix A).

The large number of variables in the dataset necessitated the use of an automatic selection procedure (*stepwise*, with entry and stay level fixed at 0.10) to identify the most parsimonious models. Associated statistics, such as AICc, max-rescaled-R^2, and percentage of correct classifications were calculated for each model.

As we had a single set of data, it was not possible to do cross-validation with a second dataset to test our models. We therefore included a *leave-one-out* cross-validation method (*ctable* option available in the SAS logistic procedure) in the logistic models.

3.4.5. Influence of the detectability in the models

The probability of rainbow trout detection is expected to be higher in rivers where there is more monitoring and/or more sports fishing. Thus, the apparent absence of rainbow trout in some rivers may be explained by the absence of fishing in these rivers. However, as the variation in fishing and monitoring efforts among rivers was unknown, it was not possible to estimate the detection probabilities among all capture sites. A conventional way to deal with this potential bias would have been to perform occupancy models (MacKenzie et al. 2006), but the way data were collected over years did not allow us to use this approach. Instead, we conducted analyses on a subset ($N = 44$) of rivers. For these salmon rivers, we knew the number of salmon fishing-days per year and/or where there was an annual salmon count (by fence or by snorkelling). These detection-effort variables (fishing and monitoring efforts) were included in the selected multivariate models based on abiotic variables (Appendix B) in order to determine their contribution to the rainbow trout presence. Although detection effort was not targetted on rainbow trout, we considered that the probability of detecting rainbow trout would increase as a function of the number of days of sport fishing and hence potentially bias the relationship between rainbow trout presence and environmental characteristics.

3.5. RESULTS

3.5.1. Spatial distribution of rainbow trout prevalence

In total, 91 rivers were retained for analysis, including 36 rivers in which rainbow trout were reported. The spatial distribution of rainbow trout prevalence is shown in Figure 3.2. The species was found throughout Eastern Quebec, on both the North and South Shores of the Saint Lawrence Estuary. Rainbow trout was only observed in one river on Anticosti Island (Jupiter). Almost all captures were adults, usually caught in the river mouths or in the downstream part of the rivers. Young-of-the-year (YOY) rainbow trout were found in four rivers (Du Gouffre, Malbaie, Grands Méchins and Matane). This constitutes the only documented evidence for natural reproduction outside the stocking zones in Quebec. Of these four rivers, a higher presence of rainbow trout was found in tributaries (present in 56% of the 18 sampled stations) than in the principal channel (present in 16% of the 56 sampled stations) (Chapter 4).

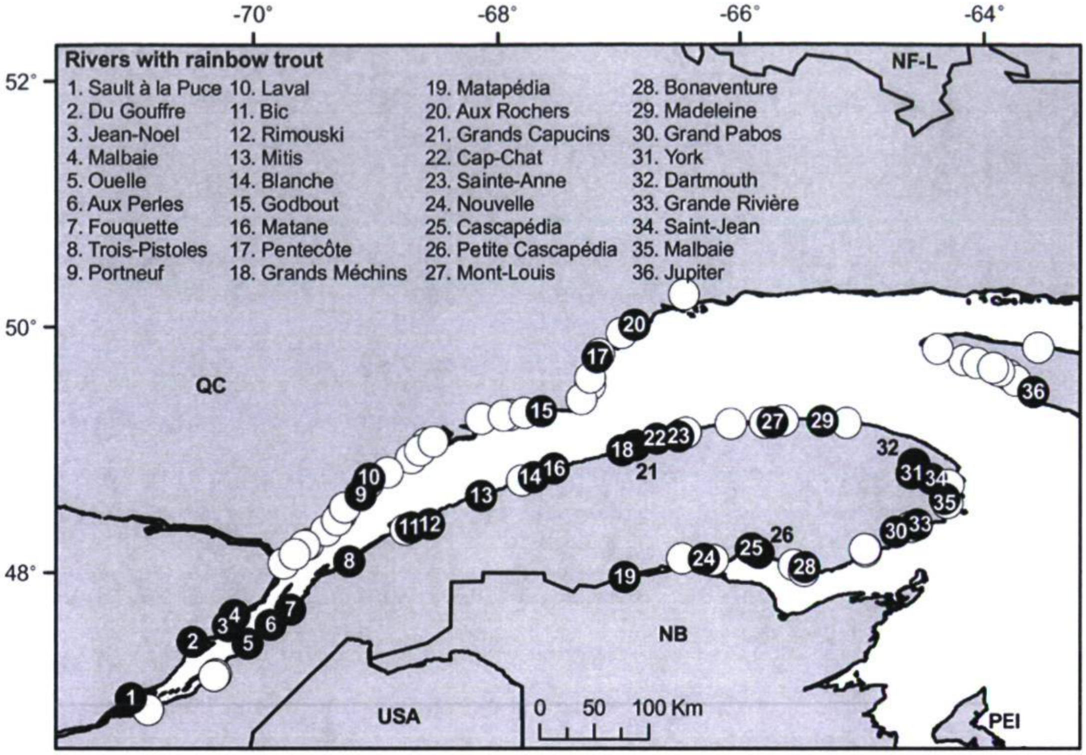

Figure 3.2 Spatial distribution of rivers used in the modelling of rainbow trout presence in Eastern Quebec. White circles represent rivers (N = 55) where rainbow trout has not been found. Black circles represent rivers where rainbow trout has been found (N = 36). QC: Quebec, NB: New Brunswick, NF-L: Newfoundland-Labrador, PEI: Prince Edward Island.

3.5.2. Relationship between rainbow trout prevalence and abiotic variables

Geomorphological models explained nearly half the variation in the prevalence of rainbow trout in Eastern Quebec. The explanatory power of the climatic models was clearly lower, explaining less than 10% of the observed variation (Table 3.2). Moreover, when both categories of variables were fitted into a final model, only geomorphological variables accounted for the observed variation (data not shown).

Table 3.2 Variables used and selected by the models, coefficients and associated statistics. Variable abbreviations are described in Table 3.1. 'Type' indicates whether the logistic regression was based on original variables or on principal components of a principal component analysis. The most significant geomorphological models are shaded. Categories of the LTrib variable are: no tributary [0], 1 or 2 tributaries [1-2], and 3 or more tributaries [3+].

Model ID	Type	Initial model	Model statistics		% correct classifications	Selected variables		
			AICc	Max-r-R^2		Name	Khi2 p-value	β estimate (SE)
Geomorphological variables								
G1	Original[a]	MS MS^2 MaxE Len STrib and LTrib	85.64	0.49	85.7	LTrib	< 0.01	0.95 (0.20)
G2	Original[a]	MS MS^2 MaxE Len STrib and LTrib[0/1-2/3+]	87.41	0.49	80.2	LTrib[1-2 vs 0]	0.02	1.57 (0.68)
						LTrib[3+ vs 0]	< 0.01	3.72 (0.73)
G3	Original[a]	MS MS^2 MaxE Len STrib and LTrib[0/1+]	90.21	0.46	79.1	STrib	0.04	0.02 (0.01)
						LTrib[1+ vs 0]	< 0.01	2.07 (0.60)
G4	PCA	PC1 PC2 PC3 and PC4	95.07	0.39	83.5	PC1	< 0.01	0.87 (0.20)
Climatic variables								
C1	PCA	PC1 PC2 PC3 and PC4	122.38	0.06	64.8	PC1	0.05	0.12 (0.06)

[a] Sin, MinE and Dam were excluded according to Hosmer & Lemeshow criterion

Tributaries and the first principal component (PC1) were the only variables selected by the stepwise procedure among the geomorphological models (Table 3.2). Coefficients of the regressions based on original variables revealed that the presence of rainbow trout in a river is strongly related to the presence of large tributaries, whereas p-values indicated that the importance of small tributaries is lower than that of larger ones. The first principal component, explaining 33% of the variation, was strongly associated with the presence of tributaries and the river length (Figure 3.3A).

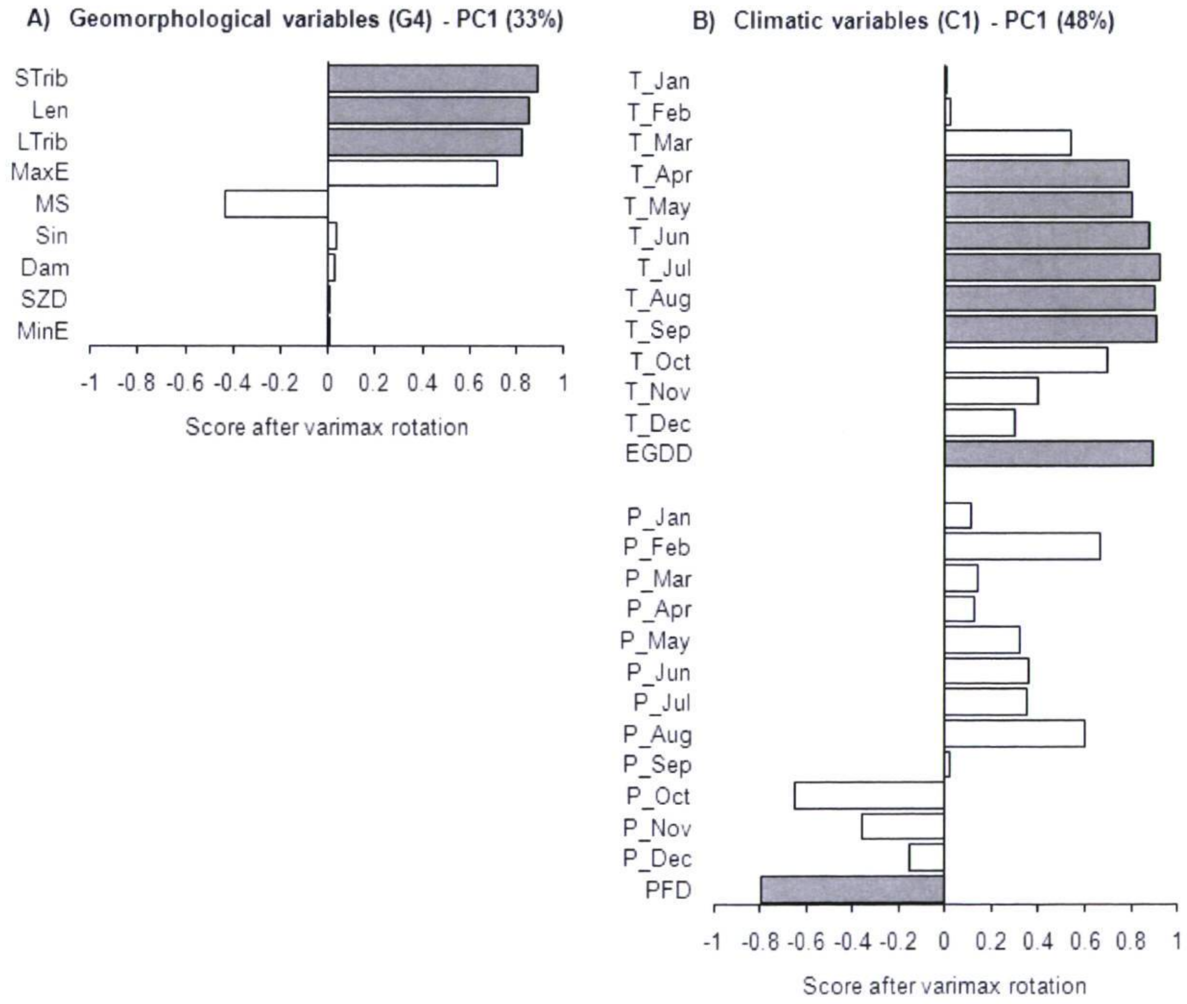

Figure 3.3 Scorings (after varimax rotation) on the selected principal components of the models based on A) geomorphological variables, and B) climatic variables. Significant scorings are shown by filled bars.

For the climatic model, only the first principal component was retained by the stepwise procedure (Table 3.2). The relation between the principal component and the presence of rainbow trout was marginally significant ($p = 0.05$). The selected PCA axis (PC1, explaining 48% of the variation) was strongly associated with temperature from April to September and to degree days, and negatively related to peak flood date (Figure 3.3B).

Although there was a positive significant relationship between the presence of rainbow trout and the detection (monitoring and fishing) effort prevaling in the subset of 44 rivers, when included in the two most significant geomorphological models, this variable was not significant (results presented in Appendix B). We thus considered that fishing and monitoring efforts did not significantly influence the relationships between trout presence and the abiotic characteristics included in this analysis.

3.6. DISCUSSION

3.6.1. Geomorphological and climatic controls on the presence of rainbow trout

Geomorphological variables influenced the distribution of rainbow trout within Eastern Quebec to such an extent that no climatic variable was selected for in the final models. The number of tributaries (especially large ones) is the most important variable affecting rainbow trout presence. Tributaries may offer slower current speeds, less severe flooding, and more cover than the principal channel, providing a more suitable environment for juveniles (Molony 2001). Tributaries may also provide important coolwater refuges for rainbow trout during their spawning migration (High et al. 2006). Tributaries may also increase the complexity of the principal channel, in terms of changes in current speed, depth and substrate size, offering a range of habitat types which can satisfy the changes in requirements of rainbow trout at different life-stages.

The number of tributaries had a far stronger influence on the presence of rainbow trout than the initial slope of the river. We found a slight but significant correlation between the number of large tributaries and mean initial slope ($r_{\text{Pearson}} = -0.48$, $p < 0.01$, data not shown), indicating that rivers with gentle gradients tended to have several tributaries. However, the inclusion in the models of an interaction term between initial slope and the number of tributaries (large or small) did not account for any additional variation (results not shown). As such, the importance of slope documented by Gard & Flittner (1974) might have been an artefact of the influence of the presence of tributaries. River length was also identified as an important explanatory variable. There was a significant correlation ($p < 0.01$) between this variable and the number of tributaries ($r_{\text{Pearson}} = 0.67$ (LTrib) and $r_{\text{Pearson}} = 0.64$ (STrib), data not shown), indicating that the number of tributaries increases with river length. However, the higher incidence of juvenile rainbow trout in tributaries relative to the main stem of four rivers with a self-sustaining population indicates that the importance of tributaries is not simply an artefact of the total length of available stream channel in the stream network.

Surprisingly, the distance to the stocking zone had no significant effect on the presence of rainbow trout, probably because a more recent source of colonists has been established in Charlevoix (Chapter 2), outside the stocking zone. Multiple sources of colonists, including recently founded populations, may thus mask the expected relationship. Dams in the downstream 10 km did not prevent rainbow trout colonization, with rainbow trout being present in 9 out of the 19 rivers which had one or more dams. It is possible that rainbow trout presence had been detected downstream of these dams. Moreover, it is known that some adult rainbow trout have passed through a few dams using fish passages due to inadequate monitoring (SOGERM – Société de gestion de la rivière Matane, pers. comm.).

Even if the climate model only explains a marginal portion of the variation in the presence of rainbow trout, climatic variables may nevertheless influence rainbow trout presence in rivers that are geomorphologically suitable. In the climate model, rainbow trout presence was positively related to spring and summer temperature (from April to September) and effective growing degree days (EGDD). Fausch (2007) predicted that rainbow trout required about 900-1000 EGDD for successful recruitment. Almost all studied rivers reached this range, but higher degree days on average were found in rivers where rainbow trout was reported (1138.3 EGDD) than in rivers where it was not (1072.8 EGDD). The optimal temperature for reproduction ranges from 10-15°C (Burgner et al. 1982), whereas the temperatures in the rivers in this study at the time of reproduction (mid-May to early-June in Quebec) tended to be less than this, with mean monthly temperatures varying according to river from 3.2-10.1°C in May and from 8.2-13.9°C in June. The optimal temperature for adult growth and survival is approximately 21°C (Scott & Crossman 1974), whereas all rivers had mean monthly temperatures less than this throughout the year. However, moderate maximum summer water temperatures (13-19°C) can also support high trout densities (Molony 2001). It is thus probable that rainbow trout prevalence was positively related to spring and summer temperatures because river temperatures were generally below the optimal levels for adult rainbow trout. Therefore, rivers with greater temperatures could support higher growth and survival rates. This also suggests that climatic warming could facilitate the establishment of rainbow trout in the rivers of Eastern Quebec over the next few decades (for rivers which have suitable geomorphological characteristics).

The climate model also identified the impact of spring precipitations on species colonization, as peak flood date scored highly on the first principal component (Figure 3.3B): the later the peak flood date, the lower the rainbow trout occurrence. Fausch et al. (2001) found that the invasive success of rainbow trout is related to the match between the timing of fry emergence and low probability of flood disturbance. Blanchet (2007) observed an emergence period between June 26 and July 9 in the Malbaie River (for 2004 and 2005), one of the four rivers with an established self-supporting population. In Eastern Quebec, the peak flood date occurs between 1 May and 17 May according to river, which is long before the fry emergence period. Our results therefore suggest that high flow levels later in May could, instead of influencing fry survival, have an impact on spawning and egg deposition, which occurs 5 to 8 weeks before emergence.

3.6.2. Scale effect

Even if some climatic variables showed a slight relationship with rainbow trout prevalence, we expected a greater contribution of water temperature, flood regime and precipitation for explaining the presence of this invasive fish in Eastern Quebec rivers. One explanation for the marginal role of climatic factors might be the spatial scale used in this study. The area covered by our modelling was relatively small: there was less than 650 km between the most distant rivers. On the contrary, studies that have found a significant influence of the flood regime or temperature on the rainbow trout invasion success, (e.g. Fausch 2001, 2007), have compared rivers located in much more distant regions (country scale). Thus, the climatic variation observed between Eastern Quebec Rivers may not be great enough to drive the rainbow trout invasion, as compared to geomorphological characteristics.

3.6.3. Conclusion

A regional spatial and temporal scale survey allowed us to determine the distribution of the nonnative salmonid rainbow trout in Eastern Quebec. Adults have been found in several rivers of Eastern Quebec for many years, although self-established populations are at present found in only four rivers. Other lines of evidence suggest the existence of unknown established populations, especially in Gaspesia (Chapters 2 & 5). It therefore seems that the invasion is still in progress and our modelling showed that abiotic factors strongly influence this process. The presence of tributaries (especially larger ones) is the most important variable, followed by climatic variables such as warm temperatures (monthly means and degree days) and timing of the spring flooding period. As the founding of new populations continues, rivers characterised by these abiotic attributes can be expected to be colonized in the short term.

In Eastern Quebec, the invasion of rainbow trout is a slow but persistent process. Dealing with this kind of ongoing invasion, whatever the species, poses several modelling challenges, such as small sample sizes (number of colonized rivers) and the use of presence/absence data instead of densities. We do not have the luxury to wait until the establishment of many new populations and new monitoring plans to improve our data base before deciding on management actions. Waiting for colonisation to procede inevitably weakens attempts to mitigate the invasion. It would be probably difficult to reverse the situation in the two Eastern Quebec rivers (Malbaie and Du Gouffre Rivers) that have supported established populations of rainbow trout for several decades. However, the identification of rivers with higher probabilities of future colonisation at least provides an opportunity for managers to undertake some proactive mesures, such as the installation of fish passage structures, to control the invasion process.

3.7. ACKNOWLEDGEMENTS

This work was funded by grants from the Natural Sciences and Engineering Research Council of Canada to JJD, the Réseau Aquaculture Québec to JJD and CA, the Centre Interuniversitaire de Recherche sur le Saumon Atlantique, and the Fédération Québécoise de la Faune. IT was supported by an Alexander Graham Bell Canada Graduate Scholarship (NSERC). We thank our collaborators that helped to collect rainbow trout data: Ministère des Ressources naturelles et de la faune, Québec Pêche, Fédération québécoise pour le saumon Atlantique, Fédération des gestionnaires de rivières à saumon du Québec, the *fieldwork team 2007* and all ZECs, organisations, sport and commercial fishers that participated in the sampling campaigns. We are greatfull to Dr Kurt D. Fausch for his usefull comments on an earlier version of the manuscript.

CHAPITRE 4. BIOTIC RESISTANCE AS FACT OR FICTION; INTERSPECIFIC COMPETITION BETWEEN INTRODUCED AND NATIVE JUVENILE SALMONID SPECIES AT AN EARLY INVASIVE STAGE

4.1. ABSTRACT

The detrimental impact of introduced rainbow trout on native communities has been well documented around the world. However, previous studies have focussed on streams where the invasion has been successful and the species, fully established. In Eastern Quebec (Canada), invasion of rainbow trout is a slow, ongoing process, and for now, established populations are still few and small. The presence of two native salmonids, Atlantic salmon and brook charr, may constitute a biotic filter that slows the establishment of the exotic species via interspecific competition, since all three species are known to use similar resources. We sampled nine streams (five with rainbow trout and four free of rainbow trout), and characterized the habitat used by the three salmonids at the juvenile stage. We aimed to evaluate the strength of the biotic resistance exerted by native species. At a large spatial scale, we found that densities were maintained at a low level, and that the distribution of the invader was mainly restricted to tributaries, but this may be the result of abiotic parameters rather than strong biotic resistance. However, at a smaller spatial scale, little evidence of biotic resistance was seen. Rainbow trout competed effectively with indigenous species, as demonstrated by its high growth rate and the modification of habitat used by salmon and charr in the presence of the invader.

4.2. RÉSUMÉ

Résistance biotique, réalité ou fiction? Compétition interspécifique à un stade précoce d'invasion entre salmonidés juvéniles introduits et natifs

L'impact négatif de l'introduction de la truite arc-en-ciel sur les communautés natives a été bien documenté partout dans le monde. Toutefois, ces études portaient sur des cours d'eau où l'invasion avait bien réussi et où l'espèce était pleinement établie. Dans l'Est du Québec (Canada), l'invasion de la truite arc-en-ciel est un processus lent, toujours en cours, et pour l'instant, les populations établies sont petites et peu nombreuses. La présence de deux salmonidés natifs, le saumon atlantique et l'omble de fontaine, pourrait constituer un filtre biotique qui ralentit l'établissement de l'espèce exotique via la compétition intraspécifique, puisque les trois espèces sont reconnues pour utiliser des ressources similaires. Nous avons échantillonné neuf cours d'eau (cinq avec truite arc-en-ciel et quatre sans truite arc-en-ciel) et nous avons caractérisé l'habitat utilisé par les trois salmonidés au stade juvénile. Notre objectif était d'évaluer la force de la résistance biotique exercée par les espèces natives. À grande échelle spatiale, nous avons trouvé que les densités de truite arc-en-ciel étaient maintenues à de faibles niveaux et que la distribution de l'envahisseur était principalement restreinte aux tributaires, mais il est possible que ce soit le résultat de paramètres abiotiques plutôt que la conséquence d'une forte résistance biotique. À petite échelle spatiale, nous avons trouvé peu d'évidence d'une résistance biotique. La truite arc-en-ciel s'est avérée en mesure de compétitionner efficacement avec les espèces indigènes. En effet, nous avons d'une part mesuré un fort taux de croissance chez la truite arc-en-ciel, et d'autre part nous avons observé des modifications dans l'utilisation de l'habitat faite par le saumon atlantique et l'omble de fontaine en présence de l'envahisseur.

4.3. INTRODUCTION

Biological invasions constitute one of the major contemporary threats to aquatic fauna. Ecological and evolutionary impacts of biological invasions on native fauna and ecosystems are numerous (Hutchinson 1959; Kohler & Courtenay 1986; MacArthur & Levins 1964; Mooney & Cleland 2001; Welcomme 1984; Williamson 1996), but the interspecific competition exerted by an invader is generally the most important consequence of an alien species' establishment (Williamson 1996), even sometimes leading to the competitive exclusion of the native species (e.g. Bøhn et al. 2008). Paradoxically, interspecific competition from native species may also represent a significant curb to biological invasions (Colautti & MacIsaac 2004; Moyle & Light 1996).

Rainbow trout[4] (*Oncorhynchus mykiss*) is one of the most introduced fish species worldwide (Cambray 2003a; Crowl et al. 1992; MacCrimmon 1971), and its impacts on native fauna – including fish, amphibians and invertebrates – are extensively documented (e.g. Baxter et al. 2007; Cambray 2003a and references therin; Crowl et al. 1992; Fausch 1988; Hasegawa & Maekawa 2006; Hitt et al. 2003; Krueger & May 1991; Larson & Moore 1985; Welcomme 1984). The most serious impacts of introduced rainbow trout on native fish involves other salmonid species (Crowl et al. 1992).

Despite strong competitive capacities (e.g. Blanchet et al. 2007; Hasegawa et al. 2004; Hearn & Kynard 1986; Volpe et al. 2001), great tolerance to a wide range of environmental conditions (Kerr & Lasenby 2000) and huge introduction pressures (Fausch 1988; MacCrimmon 1971), the establishment of rainbow trout has often failed. In Quebec (Canada), rainbow trout was introduced at the end of the XIXth century and in spite of intensive stocking efforts in the southwestern part of the province, only a few established populations have been documented in Eastern Quebec, outside the stocking area (Chapter 2). One reason that could explain this apparent difficulty to invade is the presence of native salmonids, Atlantic salmon (*Salmo salar*) and brook charr (*Salvelinus fontinalis*), that might compete successfully with rainbow trout at the juvenile stage, thus limiting the survival and spread of rainbow trout. Both native species are territorial, salmon being more

---

[4] Rainbow trout refers to both freshwater resident and anadromous (steelhead) forms.

aggressive and well adapted to exploiting riffles, whereas the earlier emergence of brook charr ensures a size advantage (Gibson 1981; Rodríguez 1995 and references therein). Several authors demonstrated that the habitat used by rainbow trout is similar to that of salmon (Fausch 1988; Gibson 1981; Hearn & Kynard 1986) and charr (Blanchet et al. 2007; Larson & Moore 1985; Magoulick & Wilzbach 1998; Rose 1986). Strong interspecific competition may thus limit the expansion of the invading species.

Whereas previous studies have demonstrated the negative impacts of introduced rainbow trout on indigenous salmonids once the invader is fully established, questions remain concerning how much rainbow trout can impact native conspecifics, and vice versa, at an early stage of the invasion process. In this study, we aimed to evaluate to what extent salmon and charr are capable of constraining the exotic invader. To achieve this objective, we conducted electrofishing and habitat quality surveys in rivers supporting recently established rainbow trout populations in sympatry with Atlantic salmon and/or brook charr populations, and in rivers free of rainbow trout. Given the early stage of the invasion process, no rivers exist supporting an allopatric rainbow trout population inside the study area. We hypothesize that native species, through competition at the juvenile stage, slow the population growth and the spreading of rainbow trout. We tested three predictions. First, if indigenous salmonids provide a strong resistance against rainbow trout invasion, we should see at the river scale low densities and a spatial segregation of the invader in less optimal habitats. At a smaller spatial scale, we would expect spatial segregation of the rainbow trout to result in small niche overlaps between the invader and native species for habitat and food. Second, young-of-the-year rainbow trout are known to have a high growth rate related to their aggressive behaviour in foraging and territorial defence (Gibson 1981; Rose 1986; Whitworth & Strange 1983). However, in Eastern Quebec, rainbow trout emergence occurs later than that of native species, such that trout start their first growing season with a size disadvantage relative to competitors. If indigenous salmonids exert strong resistance against the rainbow trout, we should then see low growth rates for rainbow trout as compared to what is observed in well established populations. Finally, we initially aimed to evaluate the biotic resistance by comparing the habitat use of rainbow trout in the absence and presence of its native competitors. As there is no river in Eastern Quebec where trout can be found in allopatry, we instead compared habitat use of native species in the absence and in the presence of the exotic species. We predicted that if indigenous fish efficiently resist the invasion, no difference in habitat use by native species should be observed in the presence or the absence of the exotic trout.

4.4. MATERIALS AND METHODS

4.4.1. Study area

A total of nine rivers, distributed in Eastern Quebec (Canada) on both shores of the St. Lawrence Estuary (Figure 4.1), were sampled during the summers 2007 and 2008. Five rivers supported a self-sustaining rainbow trout population (designated as *study rivers*: Malbaie, Du Gouffre, Matane, Mechins, Tortue rivers), and the four remaining streams were free of the invader (designated as *control rivers*: Calway, Petit-Saguenay, Trois-Pistoles, Sud-Ouest rivers). All rivers supported a brook charr population, but Atlantic salmon was present in only five, including three study rivers (Malbaie, Du Gouffre, Matane, Petit-Saguenay, Sud-Ouest rivers). Refer to Annexe C1 for more details. Since sampling took place exclusively during the summer season, we assumed minimal variations in water temperature, and in fish distribution and habitat preferences (e.g. Sotiropoulos et al. 2006; Vondracek & Longanecker 1993).

Thermographs were installed by the *Ministère des ressources naturelles et de la faune* (MRNF) in three study rivers, and water temperature was monitored twelve times a day during the sampling period (see next section). Mean temperatures were similar among rivers: 14°C [12-18°C] in Du Gouffre River, 16°C [11-20°C] in Malbaie River, and 16°C [14-20°C] in Tortue River. No water temperature data were available for the other streams. Instead, we used daily mean air temperature, registered at the closest meteorological stations (*Environnement Canada*), to extrapolate water temperatures during the sampling periods, which varied from approximately 14.6°C to 22.1°C in Sud-Ouest and Trois-Pistoles rivers, and between approx. 11.5°C to 15.2°C in the Matane and Mechin rivers. This temperature range maximises growth in juvenile rainbow trout (12-19°C, Boughton et al. 2007; Nelitz et al. 2007), Atlantic salmon (15-19°C, Elliott & Hurley 1997 and references therein) and brook charr (11-16°C, see references in Drake & Taylor 1996).

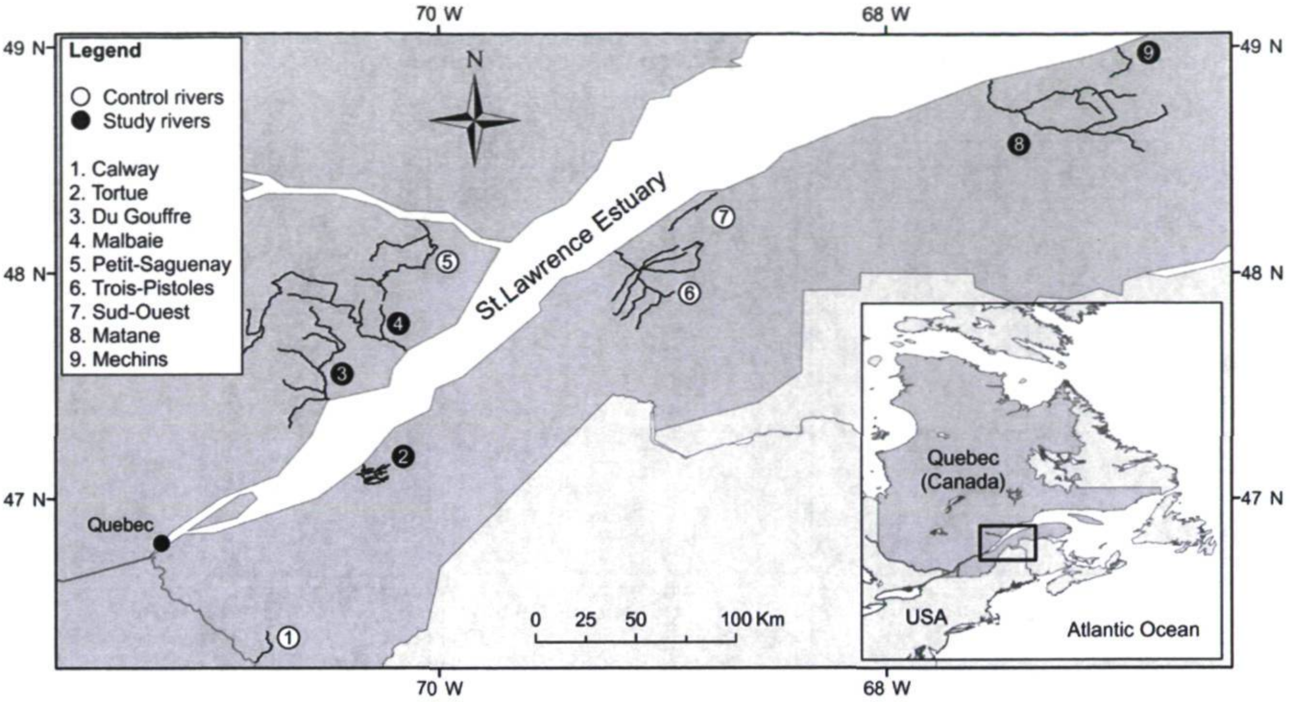

Figure 4.1 Location of the nine sampled rivers in Eastern Quebec (Canada) during summers 2007 and 2008. The four control rivers (without rainbow trout) are identified by empty circles, whereas full circles represent the five study rivers (with rainbow trout).

4.4.2. Sampling and habitat characterization

Sampling took place between mid-June and the end of August 2007, and during August 2008 (for Tortue River). Fishing was done during daytime using portable electrofishers. We first sampled between nine and 25 stations of 100 m², spaced by 1 km, in each river (except for Tortue River) and some of their tributaries (Figure 4.2, and see Annexe C1). Stations were sampled twice, with a pause of 10 to 15 min between passages. At each station, we noted salmonid density, vegetation cover (total, partial, null), velocity (qualitatively), mean depth (± 1 cm, from three measurements), slope (%), facies type (channel, riffle, run), station's position (stream's center or near the shores), and substrate composition (%) estimated using the following key: sand (< 5 mm), gravel (5 – 40 mm), pebble (40 – 80 mm), cobble (80 – 250 mm), block (> 250 mm), bed rock. Proportions of each category were thereafter multiplied by the median size of their own category, and summed to obtain one relative substrate size per station. Some stations selected for their abundance of rainbow trout were re-sampled in 2008 to capture additional specimens.

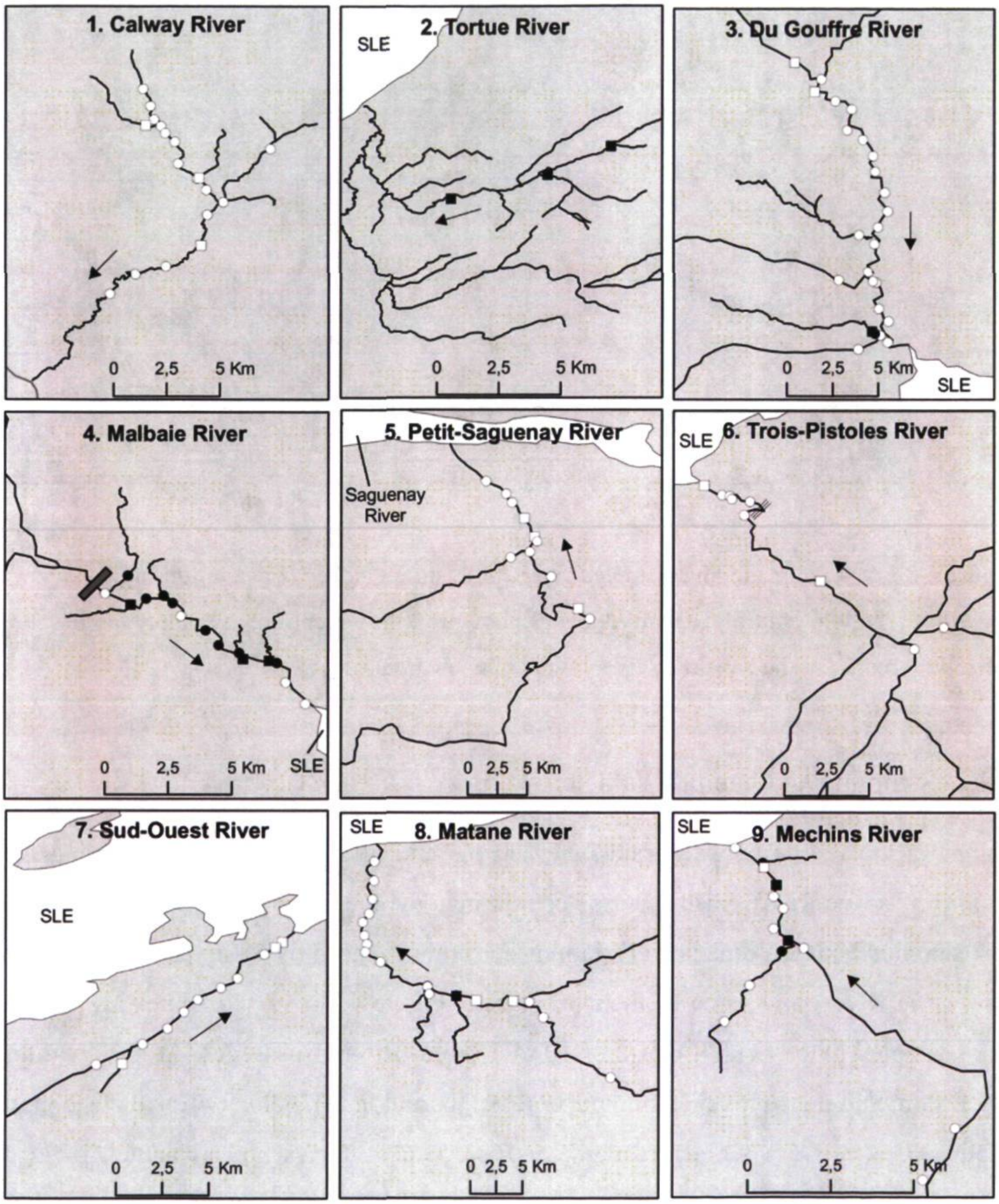

Figure 4.2 Location of the 100 m²-stations along the nine sampled rivers. Squares represent selected sites where additional sampling (transects) was done for small scale habitat characterization. Filled symbols indicate where rainbow trout was found. Grey rectangles are dams. Black arrows indicate the flow direction. SLE: St. Lawrence Estuary.

Among locations previously sampled, three sites per river (two in Trois-Pistoles River) were selected for more exhaustive sampling, according to the observed abundance and composition in salmonid species (Figure 4.2). For Tortue River, selection of the sites was based on an electrofishing survey performed by the MRNF in July 2008. Depending on the river width, two or three transects of 2 x 30 m were sampled parallel to the stream banks in habitats that seemed suitable for salmonids, near the shores and in the river center (see Annexe C1). Each transect was separated into 15 units of 2 x 2 m. Two electrofishing passes, spaced approximately 0.5 m apart, were performed in each unit, from side to side. Position of each salmonid (first sighting point) was identified with a weighted flag of different colour according to the species. At the flagged position, we determined vegetation cover (total, partial, null), depth (± 1 cm), distance to the nearest shore (± 0.01 m), and relative substrate size (as before) within an 8 cm-diameter circle centered on the flag (corresponding roughly to the mean territory size of juvenile rainbow trout, Keeley 2000). Moreover, for each 4 m^2-unit, we noted vegetation cover (total, partial, null), mean depth (± 1 cm, from three measurements), mean water velocity ($m \cdot s^{-1}$)[5], and substrate size using a d_{50} index (Guay et al. 2003). Briefly, we systematically measured the intermediate axis (β, ± 0.5 cm) of 30 sediments systematically distributed across the sampling unit. A value of "0" was attributed to sand, and a value of "99" to bedrock and large blocks. The d_{50} was equal to the median value of sediment size.

All captured fish were held until sampling was completed. Salmonids were measured (± 1 mm). Fish of less than 175 mm were considered as juveniles (age 0 to 2), larger fish were considered as adults and removed from the analysis. All captured fish were thereafter released at the site of capture, except for a maximum of 10 individuals by age class (visually estimated) and species at each sampling site. For these specimens, sex was determined by visual observation of the gonads, and stomachs were extracted and preserved in 4% formaldehyde.

---

[5] The means used to determine water current differed between the two sampling years, thus velocity data from Tortue River were treated separately.

4.4.3. Food availability and fish diet

The macroinvertebrate community was sampled at each transect. Organisms were collected using a Surber net (0.7-mm mesh, mouth 27 x 31 cm) placed facing upstream. The frame was set on the stream bottom and all the rocks and sediments within the frame were scoured for 1 minute. Organisms were then washed into the net by the current and thereafter gently collected and conserved in ethanol 95%. In the laboratory, macroinvertebrates were sorted and identified to order.

Gut fullness of salmonids sampled in study rivers was qualitatively assessed. Fish with empty stomachs (4 trout and 3 salmon) were thereafter excluded. A total of 107 specimens were retained for diet comparisons. Each stomach was weighed (± 0.0001 g) before and after prey were removed. Food items were identified to the order, and counted for relative abundances of different prey items. Digested prey were classified as unidentified organisms.

4.4.4. Data analysis

Habitat heterogeneity According to a principal component analysis (PCA, *princomp* procedure (SAS 2001)) performed on habitat variables measured in 100 m^2-stations, followed by a discriminant analyse (DA, *discrim* procedure) performed on the eigenvalues, habitat heterogeneity within rivers was so great that only 28% of the stations were correctly reassigned to their river of origin. We thus pooled sampling sites together in subsequent analyses, regardless of the river of origin. Based on rotated eigenvectors (varimax transformation), the variation explained by the first principal component (28%) was related to the presence of a shore, cover and depth. The facies, water velocity and substrate explained another 21% of the variation on the second axis (Annexe C2).

Prediction 1: Distribution, density and niche overlap Within rivers, distribution and density of fish species (the large spatial scale) were evaluated using data obtained at the 100 m^2-stations. Habitat niche overlap was estimated at a small spatial scale for three quantitative variables (depth, water velocity and substrate) using data obtained along the 60 m^2-transects. Estimates of niche overlap were calculated based on non-parametric indices developed by Mouillot et al. (2005). Two indices assessing the superposition strength of non-parametric kernel density functions were used: (i) NO_{Kt}, which estimates the niche overlap for one variable between two species, and (ii) NO_{Kw}, which estimates the niche overlap for several variables between two species. A detailed description of the formulas is presented in Mouillot et al. (2005).

Diet overlap was first estimated using the traditional Schoener's index (D) that uses the proportion (in number) of prey of each category. This index pools all samples together and does not consider intersite variability. However, preliminary analyses showed that composition of the macroinvertebrate community varied between sites within rivers (data not shown). We thus also used an amended Schoener's index (D^a), which involves comparisons of the diet overlap among individuals of a given species, and between species, within a site (Lecomte & Dodson 2005). Mann-Whitney U-Tests were performed with XLSTAT v.2009.6.03 to compare intra- *vs* interspecific diet overlap.

Prediction 2: Growth rate We restricted the analysis of growth to young-of-the-year fish. Slopes of the regressions of fish length on date of capture were compared two-by-two using a 2-factor ANCOVA (date, species, date•species) in SAS (SAS 2001).

Prediction 3: Changes in habitat use To evaluate habitat use of native species in the presence and absence of the invader, we considered three parameters: i) the most preferred habitat variables according to available habitat, ii) the individual habitat values, and iii) the degree of the native species niche overlap (see Prediction 1 for method).

Habitat preference, that is habitat use according to habitat availability, was calculated at small spatial scale using the method of Blanchet et al. (2007), which is based on the preference index developed by Beecher et al. (1993). The following formula was used:

$$M_i = \left(\frac{(n_i/n_t) \,/\, (p_i/p_t)}{[(n_i/n_t) \,/\, (p_i/p_t)]\max} - 0.5 \right) \text{x } 2 \qquad (1)$$

where M_i is the normalised habitat index for category i, n_i is the number of samples with fish in the considered category, n_t is the total number of specimens, p_i is the number of samples belonging to the category i, and p_t is the total number of samples. Positive values indicate preference for a habitat category, whereas negative values indicate avoidance of a given category. The three quantitative variables (depth, substrate and velocity) were subdivided in five categories.

Microhabitat used individually was compared for native species within sites where both co-existed with or without exotic trout. Average water depth, distance from the nearest shore, current speed and substrate size were calculated for each species and compared using Wilcoxon-Mann-Whitney tests in SAS (SAS 2001). Once sites with an insufficient number of specimens by species were removed, five sites remained: three with salmon and charr, and two containing all three species.

4.5. RESULTS

4.5.1. Distribution, density and niches overlap

Rainbow trout distribution within rivers was associated with the stream order (main channel or tributaries). In Malbaie, Du Gouffre, Matane and Mechins Rivers, rainbow trout was found in 58% of the stations sampled in tributaries as compared with 16% of the stations sampled in the main channel. Malbaie River was the only stream where rainbow trout was predominantly found in the main channel. Among the 20 stations where rainbow trout was sampled in 2007, 80% also contained one or both native salmonid species.

When present, the mean density of trout was low (< 0.05 fish/m²), whereas that of salmon and charr was the double (Table 4.1). However, considering only the study rivers (with rainbow trout) mean densities of brook charr were as low as that of the invader, whereas salmon remained dominant. Mechins River, which does not support a salmon population, was the only stream where mean density of rainbow trout was important (> 0.08 fish/m²). In parallel, the most important densities of brook charr were also observed in that river.

Niche overlap between native salmonids and rainbow trout was higher than 0.80, except for the substrate with salmon, and surpassed that of the two indigenous species (Table 4.2). On average, niche overlap between charr and trout was superior to that of salmon and trout.

Table 4.1 Mean density (fish/m²) ± SE of the three species when present. Number of stations are in parenthesis. Different letters indicate significant differences in density between species (two-sided Wilcoxon test, $p < 0.05$).

River	Trout	Salmon	Charr
Du Gouffre	0.019 ± 0.006 (3)	0.089 ± 0.025 (20)	0.033 ± 0.009 (11)
Malbaie	0.046 ± 0.023 (12)	0.061 ± 0.028 (9)	0.046 ± 0.017 (4)
Matane	0.026 ± 0.016 (2)	0.101 ± 0.024 (17)	0.012 ± 0.003 (3)
Mechins	0.083 ± 0.070 (3)	na	0.199 ± 0.057 (14)
All rivers with trout	0.045 ± 0.067 (20)^{a}	0.088 ± 0.015 (46)^{b}	0.105 ± 0.029 (32)^{ab}
Petit-Saguenay	na	0.183 ± 0.054 (7)	0.040 ± 0.021 (3)
Sud-Ouest	na	0.020 ± 0.010 (3)	0.390 (1)
Calway	na	na	0.060 ± 0.018 (16)
Trois-Pistoles	na	na	0.047 ± 0.022 (3)
All rivers	0.045 ± 0.067 (20)^{a}	0.096 ± 0.015 (57)^{b}	0.090 ± 0.019 (55)^{b}

Table 4.2 Non-parametric niche overlap indices (NO_{Kt} and NO_{Kw}) for quantitative habitat variables (substrate, depth and velocity[1]) at small spatial scale. Mb: Malbaie River, G: Du Gouffre River, Mt: Matane River, Me: Mechins River, To: Tortue River, SO: Sud-Ouest River, and PS: Petit-Saguenay River.

Rainbow trout occurrence	River type	Rivers selected	Habitat variable	Trout & Salmon^2	Trout & Charr	Salmon^2 & Charr
present	study	Mb, G, Mt, Me & To	Substrate	0.64	0.84	0.76
			Depth	0.94	0.92	0.89
			Velocity	0.81	0.88	0.68
			Substrate, Depth & Velocity	0.80	0.87	0.78
absent	study	Mb, G & Mt	Substrate	-	-	0.76
			Depth	-	-	0.79
			Velocity	-	-	0.65
			Substrate, Depth & Velocity	-	-	0.73
	Control	PS & SO	Substrate	-	-	0.62
			Depth	-	-	0.78
			Velocity	-	-	0.69
			Substrate, Depth & Velocity	-	-	0.70

[1] Tortue River was excluded.

[2] Mechins and Tortue Rivers were not used for interactions with salmon.

Size of fish used to evaluate diet overlap varied greatly, from 26 to 99 mm, with brook charr being larger (60 ± 15 mm, N = 40) than the two other species (trout: 47 ± 17 mm, N = 38; salmon: 53 ± 13 mm, N = 29). However, specimens from the same stream generally had a similar mass of gut content (Annexe C3). For all salmonid species, diet composition was similar, with the more consumed prey being diptera larvae, trichoptera and ephemeroptera (Figure 4.3). These three macroinvertebrate orders were also the most available in the habitat. According to the traditional and modified Schoener's index, interspecific diet overlap was stronger between trout and salmon or charr, than between the two native fish (*D*), but the interspecific diet overlap did not differ from intraspecific diet overlap (D^a) (Table 4.3).

4.5.2. Growth rates

During their first year of life (0+), growth rate was similar for salmon and charr (0.29 and 0.26 mm d^{-1} respectively, $p = 0.27$), but was significantly greater for rainbow trout (0.46 mm•d^{-1}, $p < 0.01$, Figure 4.4). Despite a later emergence date, and assuming constant growth rates until the end of the growing season, rainbow trout would have almost achieved salmon's size before winter, and would only present a small difference of size with charr.

4.5.3. Changes in habitat use

Habitat preferences Regarding habitat preferences at a small spatial scale, cover was the only variable for which we saw an evident modification in the habitat selection of native species in response to the presence of rainbow trout. In the absence of rainbow trout, Atlantic salmon and brook charr showed a clear preference for highly covered habitats, but in sympatry with rainbow trout, which also preferred a full cover, they shifted towards more opened habitats (Figure 4.5).

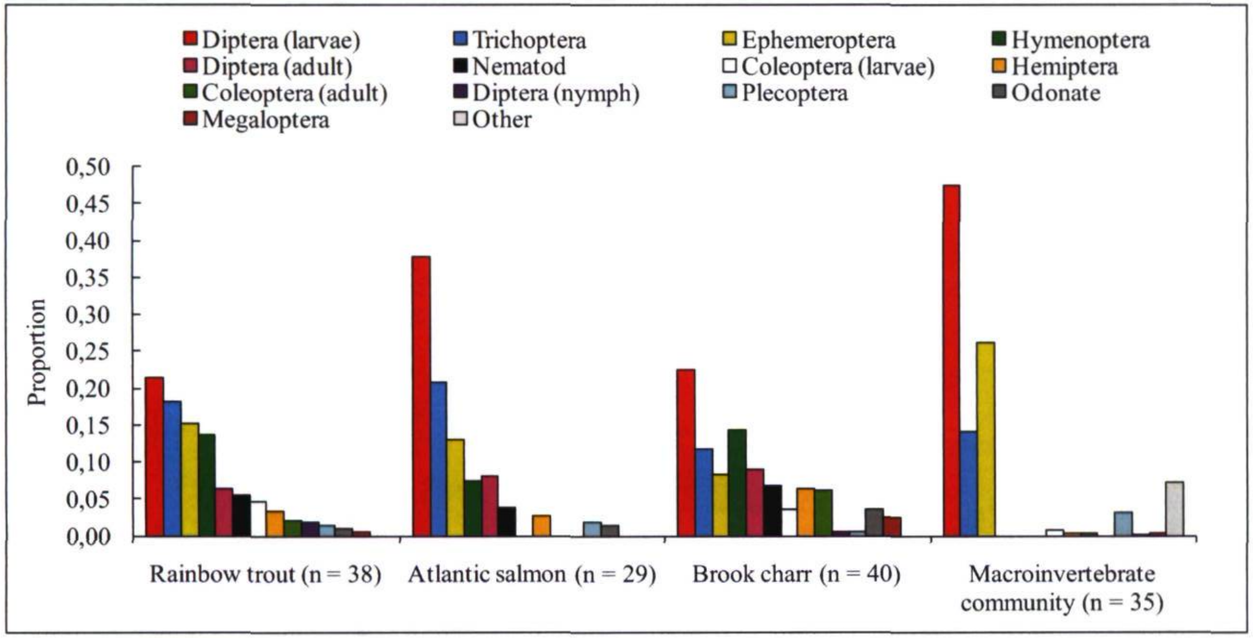

Figure 4.3 Proportion of the different macroinvertebrate preys (order) found in gut of salmonids, and composition of the macroinvertebrate community in Malbaie, Du Gouffre, Matane and Mechins Rivers in 2007.

Table 4.3 Diet overlap Schoener's index (*D* and D^a) based on the number of prey consumed by juvenile salmonids in Malbaie, Du Gouffre, Matane and Mechins Rivers in 2007.

Comparisons	Schoener's *D*	Sample size		D^a contrast	Schoener's D^a - Number		
	(all rivers pooled)	N river	N fish	intra : inter	intra	inter	*p-value*
Trout *vs* Salmon	0.82	4 : 3	38 : 29	9 : 12	0.49	0.57	0.31
Trout *vs* Charr	0.74	4 : 4	38 : 40	12 : 16	0.48	0.50	0.98
Salmon *vs* Charr	0.64	3 : 4	29 : 40	9 : 12	0.54	0.52	0.75

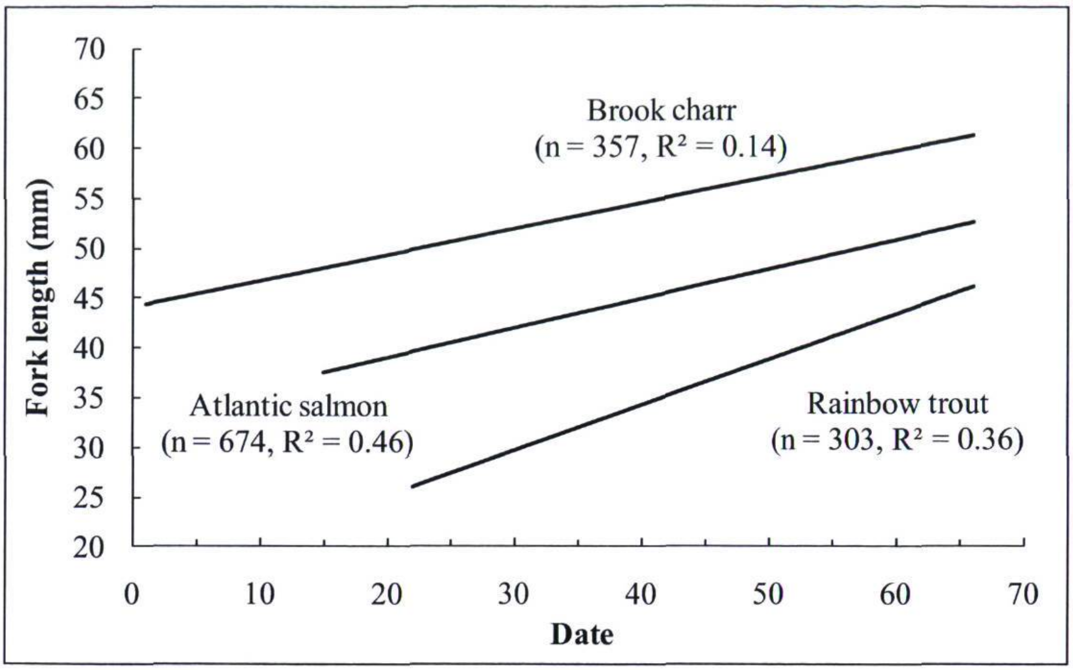

Figure 4.4 Growth rate (size at date of capture) of the three salmonid species during their first year of life (age 0). Day 0 corresponds to June 17th, which was the first sampling date. Specimens were sampled in nine rivers. Each regression is significant ($p < 0.0001$).

Individual habitat use At a finer scale, native species used in general the same microhabitat when found in sympatry within a site. They used the same depth and substrate in all three sites tested (Figures 4.6A&D), whereas they were found at the same distance from the shore and in similar water velocity in two of the sites (Figures 4.6B&C). However, in the two sites where native species co-occurred with the exotic trout, they diverged in their utilisation of the four habitat variables half of the time (Figure 4.6).

Native niche overlap In sites where rainbow trout were present, niche overlap between the native species was near of 0.80 for the three habitat variables (depth, substrate and velocity). However, in sites and rivers free of rainbow trout, the niche overlap between the two indigenous species decreased significantly (Table 4.2).

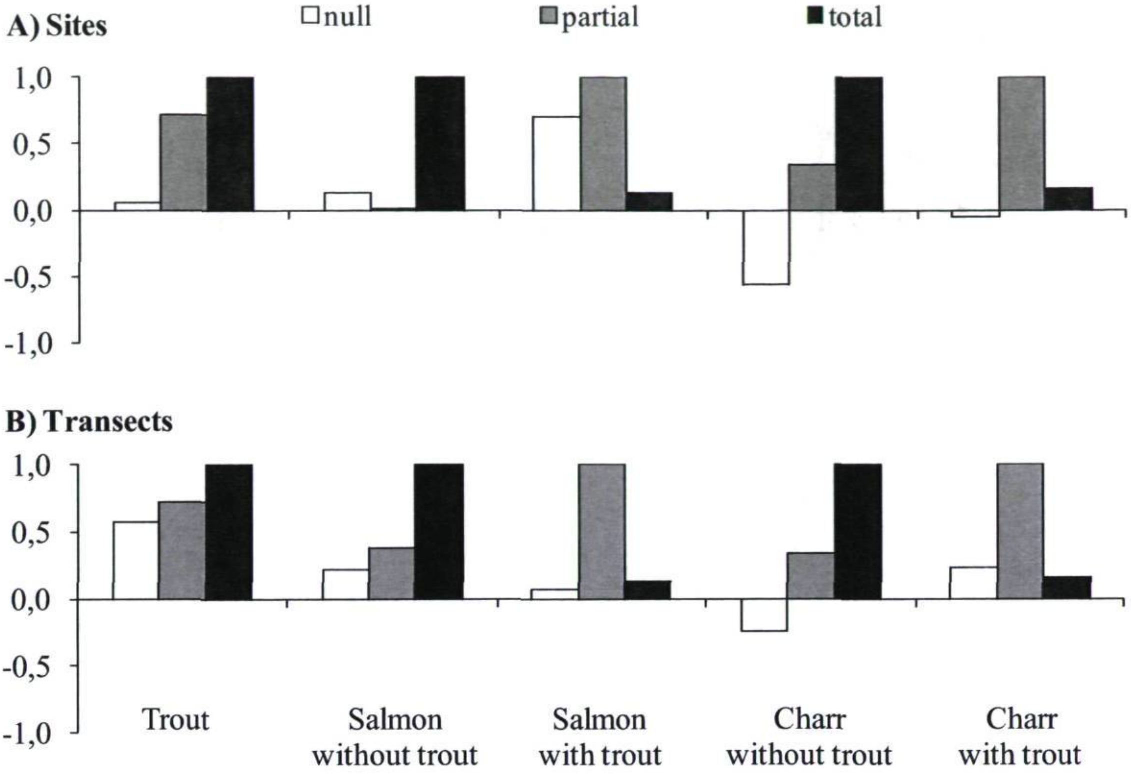

Figure 4.5 Preference of rainbow trout, Atlantic salmon and brook charr for cover, at small spatial scale, in A) sites (3 transects), and B) transects (60 m²) where rainbow trout has been found or not. A value near 1 indicates an active selection for a cover category, a value near -1 indicates an active avoidance of a cover category, and a value near 0 indicates that habitat use is proportional to habitat availability.

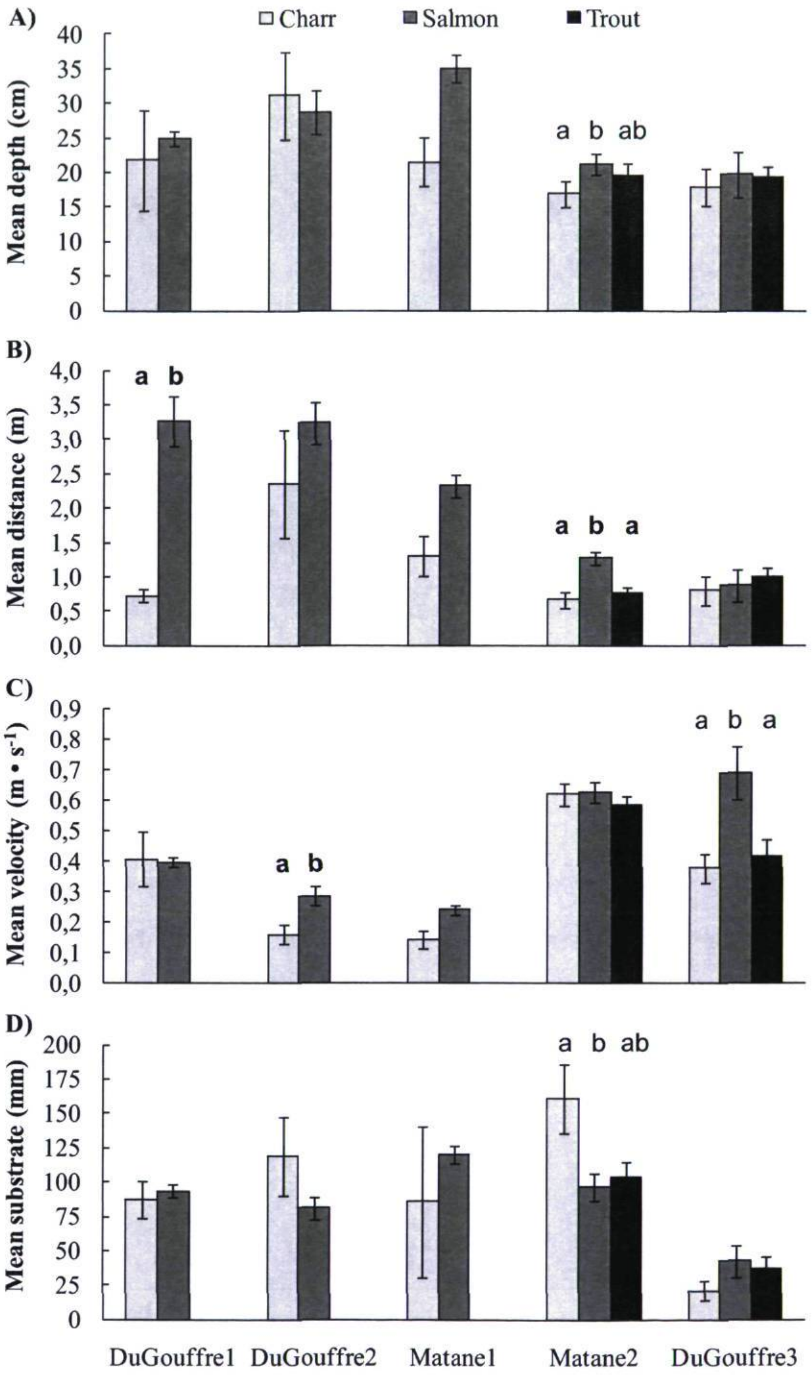

Figure 4.6 Microhabitat utilisation by juvenile brook charr, Atlantic salmon, and rainbow trout when they co-occurred within a sample site. Bars illustrate mean (± SE) values of A) water depth, B) distance from the nearest shore, C) current speed, and D) relative substrate size. Significant differences between species are represented by letters (in bold: $p < 0.05$, unbold: $p < 0.10$).

4.6. DISCUSSION

Introduced rainbow trout has been shown to outcompete native salmonids where populations are well established, or in experimental designs. But at an early stage of establishment and dispersal, interaction with indigenous species might not systematically favour rainbow trout. In Eastern Quebec, biotic resistance could be enhanced by the presence of two related native competitors. This, added to a natural *lag effect* associated with adaptation to the new environment and/or to an Allee effect (Mooney & Cleland 2001), could lead to invasion delay or failure.

4.6.1. Are native salmonids able to exert a biotic resistance to rainbow trout invasion?

At a large spatial scale (100 m^2-stations), the evidence for biotic resistance was ambigous. In four rivers colonized by rainbow trout, the invader was found in less than 30% of the sampled stations, and densities remained generally low. We observed a certain spatial segregation since rainbow trout, when present, was mainly constrained to the tributaries. However, instead of being the consequence of the biotic resistance at large spatial scales, this distribution is probably more related to environmental parameters. In Chapter 3, we showed that the presence of tributaries was the most important abiotic parameter explaining the presence of rainbow trout in Eastern Quebec rivers. It has been suggested that tributaries provide a refuge against seasonal flow variations, especially during the spring flooding period, and against warm temperatures during summer (Godby et al. 2007). Thus, the apparent segregation of rainbow trout in tributaries might rather be the consequence of environmental limitations impeding reproduction and/or juvenile survival in main channels. Elsewhere, in Malbaie River, which was the only stream where rainbow trout was able to colonize the main channel, the section of the main channel where rainbow trout is found is located downstream from a dam. In regulating the flow regime, this dam may have allowed rainbow trout to colonize the main stem. This alternative hypothesis, however, needs further investigation.

Biotic resistance exerted by Atlantic salmon and brook charr appeared to be weak when a smaller spatial scale was considered. Contrary to what was expected, niche overlap was important between the invader and the native fish. It reached 80%, which is considered as a strong overlap (Blanchet et al. 2007; Mouillot et al. 2005), and is higher than what was observed for the two co-evolved competitors. Niche overlap for food was also elevated, diet being as similar between species than between individuals of the same species.

When considering the species' preference for three categories of cover (null, partial and total), we found that it changed for both native fish according to trout occurrence. In the absence of trout, the two indigenous species preferred full cover, but in the presence of trout, which also preferred full cover, they switched to use only partially covered habitats. Our analyses demonstrated that cover was the most important variable explaining spatial distribution of the three species in this study (data not presented). Cover has been identified as an important habitat variable for salmonids, especially for rainbow trout (Gatz et al. 1987 and references therein; Gibson 1978; Platts 1976), and exclusion of native fish from the more shaded areas indicates that native salmonids are unable to resist displacement of invading rainbow trout.

The increase in habitat niche overlap between the two indigenous salmonids in the presence of rainbow trout, in comparison to sites or rivers where the exotic was not found, also suggests weak biotic resistance to the spread of rainbow trout. Usually, in the absence of rainbow trout, sympatric salmon and charr segregate spatially, with salmon displacing charr to less optimal habitats (Rodríguez 1995). It appears that the presence of the invader changed the habitat uses of both species, forcing them to share more similar resources. At a finer scale, this spatial convergence seems to have resulted in a divergence of the microhabitat used at the individual level. We effectively found significant differences in the microhabitat use between salmon and charr when the three species were in sympatry, as compared to sites when only the two native fish were present. This microhabitat segregation might be a means to reduce competition between the two native species in partitioning the resource.

4.6.2. Competitive abilities of rainbow trout

Growth rate measured in Eastern Quebec for subyearling rainbow trout was similar to that observed in the Great Lakes (0.32 to 0.42 mm d^{-1}, Johnson 1980; Rose 1986), where the invader has been naturalized for so long that the species is now considered as indigenous. Moreover, as demonstrated by the length-at-age relationships, the growth of rainbow trout during its first year of life was superior to that of the two native species, regardless of the delay caused by a later emergence date, which is consistent with other studies (Whitworth & Strange 1983). It has been shown that fast growth increases survival of juvenile rainbow trout (Boughton et al. 2007). It thus appears that the competitive abilities of age-0 rainbow trout are strong enough to allow an optimal food intake and habitat selection, despite the presence of two competitors. This is consistent with Hasegawa et al. (2004), who found superior competitive capacities for introduced rainbow trout in comparison to larger native white-spotted charr (*Salvelinus leucomaenis*), and with Rose (1986), who observed in Lake Superior that the emergence of the exotic trout had reduced growth rate of native charr from 0.51 to 0.12 mm d^{-1}.

4.6.3. A potentially greater impact on brook charr

Consequences of the successful establishment and spreading of rainbow trout in Eastern Quebec could initially represent a greater impact on brook charr than Atlantic salmon. Habitat use was similar between rainbow trout and the two native salmonids, as shown by the high niche overlap indices for depth, substrate, current velocity and diet. However, the competition could be greater between rainbow trout and brook charr since their niches appear more similar. Moreover, the higher density of rainbow trout was observed in Mechins River, where salmon is absent, but densities of charr were also high.

Evidences of brook charr displacement by rainbow trout are more numerous than for Atlantic salmon in the literature (e.g. Fausch 1988, 1998, 2008; Larson & Moore 1985; Moore et al. 1986). However, some authors have suggested that the decline of charr populations after the introduction of rainbow trout was probably more the consequence of the weak reproductive success of the native species (Clark & Rose 1997) **in combination** with the impact of the invader, rather than to the rainbow trout invasion itself, a tendency that has also been observed with the introduction of brown trout (*Salmo trutta*) (Waters 1983). Thus, intrinsic problems in native species populations may permit rainbow trout invasion to have a greater impact on indigenous communities. Since both charr and salmon populations are declining in Eastern Quebec, because of habitat degradation and overfishing of the former (M. Arvisais, MRNF, pers. comm.), a high mortality rate in the sea and various impediments to upstream movements for the latter (Friedland et al. 1993; Hansen & Quinn 1998; Hansen & Windsor 2006; ICES/CIEM 2008), both species may be unable to resist competition with the rainbow trout.

4.6.4. Conclusion

Impacts of introduced rainbow trout on native salmonids have been documented in ecosystems where it is well established. The invasion of rainbow trout in Eastern Quebec is slow and still ongoing: known established populations are rare and often of a small size. Therefore, we expected strong biotic resistance on the part of native salmonids, which could have explained the apparent difficulty of rainbow trout to establish, despite considerable introduction pressure. We found that rainbow trout densities were low and that its distribution was mainly limited to the tributaries. However, this spatial segregation is probably also the result of abiotic resistance instead of a real biotic resistance. Moreover, within the few sites where it has been observed, juvenile rainbow trout showed a higher growth rate than its competitors, revealing its ability to effectively exploit the resources despite the interspecific competition. Finally, at small spatial scale, we observed that salmon and charr modified their habitat use in presence of the invader.

Our study thus demonstrated that introduced rainbow trout in Eastern Quebec, despite the precocious stage of the invasion, is likely to compete with indigenous salmonid species for food and habitat and even modify the habitat use of Atlantic salmon and brook charr. The increase in native fish niche overlap at small spatial scale is an indirect effect of the introduced salmonid, whereas the shift in preferred habitat categories of native species demonstrates a direct impact of the invader (Hasegawa & Maekawa 2006) and the inability of the native species to resist the invasion. These results increase our concerns about the future impacts of the invader on native fish and are consistent with the findings of Baxter et al (2007) who demonstrated in a field experiment that even at low density (0.2 fish/m^2), introduced rainbow trout can decrease by 75% the biomass of native Dolly Varden charr (*Salvelinus malma*).

Finally, results of this study imply that not only the biotic filter may not impede the invasion process in Eastern Quebec, but also that the impacts of rainbow trout on salmon and charr should increase as long as populations increase and proliferate, especially for brook charr, which is known to be less aggressive than salmon (Gibson 1978), and seems to use a more similar habitat to that of rainbow trout than salmon. Thus, since the invasion is not expected to be slowed by this natural barrier, management measures should be adopted in the short term to actively impede the rainbow trout invasion in Eastern Quebec rivers, and to reduce its impacts on native salmonids that are outcompeted by the invader.

4.7. ACKNOWLEDGEMENTS

This work was funded by grants from the Natural Sciences and Engineering Research Council of Canada to JJD, the Réseau Aquaculture Québec to JJD, the Centre Interuniversitaire de Recherche sur le Saumon Atlantique, and the Fédération Québécoise de la Faune. IT was supported by an Alexander Graham Bell Canada Graduate Scholarship (NSERC). We thank all the field assistants for their help with fish sampling, habitat characterisation, and laboratory: François Colas, Marc-Antoine Couillard, Marie Chantal Émond, Julie Faure-Lacroix, Julien Forestier, Jessie Motard-Côté, Geneviève Ouellet-Cauchon, Rémy Pouliot, Marion Trudel and Mélanie Trudel. We are also grateful to Jean-Guy Frenette and Pierre-Yves Collin, technicians for the Ministère des Ressources naturelles et de la Faune, for their assistance on the field and equipment loan.

CHAPITRE 5. ANADROMY AND THE DISPERSAL OF AN INVASIVE FISH SPECIES (*ONCORHYNCHUS MYKISS*) IN EASTERN QUEBEC, AS REVEALED BY OTOLITH MICROCHEMISTRY

Thibault, I., Hedger, R.D., Dodson, J.J., Shiao, J.C., Iizuka, Y. & Tzeng. 2010. Ecology of Freshwater Fish, 19 : 348-360.

5.1. ABSTRACT

Rainbow trout (*Oncorhynchus mykiss*) is invading rivers bordering the St. Lawrence Estuary (Quebec, Canada). Some rivers in Eastern Québec support self-sustaining populations while adult vagrants are frequently captured in rivers where no reproduction has been confirmed. We hypothesized that the development of anadromy has promoted the species dispersal. Otolith Sr:Ca analyses revealed that although all fish captured in the upstream stocking region were freshwater residents, both anadromous and freshwater resident phenotypes were found downstream in Eastern Quebec. The proportion of fish exhibiting the anadromous life cycle increased with the distance from the stocking zone. Eastern Quebec steelhead migrated to sea at the same age but at a larger size than steelhead within their native range. Age at first reproduction was similar to that observed in native populations. The development of the anadromous life cycle enables this species to colonize new rivers following long-distance migrations along the St. Lawrence Estuary corridor.

5.2. RÉSUMÉ

L'anadromie et la dispersion d'une espèce envahissante de poisson (*Oncorhynchus mykiss*) dans l'Est du Québec, révélées par la microchimie des otolithes

La truite arc-en-ciel (*Oncorhynchus mykiss*) envahit actuellement les rivières qui bordent l'estuaire du St-Laurent (Québec, Canada). Certaines rivières de l'Est du Québec supportent des populations autoperpétuatrices, alors que des vagabonds adultes sont fréquemment capturés dans des rivières où aucune reproduction n'a été confirmée. Notre hypothèse était que le développement d'un mode de vie anadrome avait favorisé la dispersion de l'espèce. L'analyse des ratios de Sr:Ca dans les otolithes a révélé que si tous les poissons capturés dans la région où l'espèce est ensemencée (amont) étaient des résidents d'eau douce, les phénotypes anadromes et résidents ont tous deux été observés chez les spécimens capturés dans l'Est du Québec (aval). La proportion de poissons démontrant un cycle de vie anadrome a augmenté avec la distance à la zone d'ensemencement. Les truites anadromes dans l'Est du Québec migreraient vers la mer au même âge, mais à une taille plus élevée que celles que l'on retrouve dans l'aire de distribution d'origine de l'espèce. L'âge à la première reproduction serait semblable à celle observée dans les populations natives. Le développement d'un mode de vie anadrome permet à l'espèce de coloniser de nouvelles rivières en effectuant des migrations sur de longues distances le long du corridor de l'estuaire du St-Laurent.

5.3. INTRODUCTION

Once established in a new habitat, the success of an exotic invader will depend on the species' capacity to disperse in that habitat and to increase its population size (Theoharides & Dukes 2007). This is the last of the hierarchical filters which determine the success of biological invasions (Colautti et al. 2006; Kolar & Lodge 2001; Moyle & Marchetti 2006; Theoharides & Dukes 2007). Characteristics associated with invaders capable of surpassing this last filter are numerous, including long distance dispersal capacities, small body size, high fecundity, asexual reproduction, rapid growth and early maturity (Kolar & Lodge 2001; Moyle & Marchetti 2006; Theoharides & Dukes 2007).

Rainbow trout (*Oncorhynchus mykiss*, Walbaum 1792) is one of the most widely introduced fish species in the world (GISD 2005). Stocking of this salmonid, originating from the Northern Pacific Ocean, has occurred throughout the world since 1874 with varying levels of success (Burgner et al. 1992; MacCrimmon 1971). Like several of its relatives of the Salmonidae family, rainbow trout may adopt two life-cycle forms: the anadromous phenotype, with a growth phase in saltwater, or the freshwater resident phenotype. Despite a prevailing tendancy toward philopatry (Burgner et al. 1992), the anadromous phenotype may nevertheless migrate into new streams, hence increasing the species' capacity to disperse. Anadromy also implies larger size at reproduction for males and females. Larger body size is generally related to higher fitness, particularly among females who produce more and larger eggs with increasing body size (DuBois et al. 1989; Seamons et al. 2007 and references therein). However, the few naturally spawning populations of rainbow trout that have been established after an introduction event are usually composed of freshwater residents. The introduced self-sustaining population in the Santa Cruz River (Southern Patagonia) is the only one known to have developed an anadromous run (Pascual et al. 2001; Riva-Rossi et al. 2004). The reason for the dominance of residency among introduced populations is not clear. It may be related to the phenotype of the introduced populations, which is usually resident. It may also be that the costs associated with anadromy in recently founded populations are higher than for residency, resulting in selection against migrants.

In Eastern Canada, stocking of rainbow trout has been conducted for several years in the upper St. Lawrence River system, from the Great Lakes to the vicinity of Quebec City, leading to the establishment of some self-sustaining populations in Eastern Quebec outside the area where stocking and farming of rainbow trout are permitted (Chapter 2). The first such population was discovered in the 1980s and reproduces in two rivers, Du Gouffre and Malbaie, located in the Charlevoix region, on the north shore of the St. Lawrence Estuary. In 2007-08, young of the year (0+) and other juveniles were also observed in two rivers (Matane and Les Mechins) located downstream, on the south shore of the St. Lawrence Estuary. Other than these established populations, adults have been frequently captured during many years in streams all along the estuary. Given that no reproduction has been detected in these rivers, captures are believed to be composed of vagrant fish. Genetic analyses revealed that such vagrants mainly originate from a population founded in Lake Ontario, and also from the recently established population in Charlevoix (Chapter 2). These findings suggest the presence of anadromous individuals in the population of the Malbaie and Du Gouffre rivers, which contradicts the belief that introduced self-sustaining populations of rainbow trout only support the freshwater resident form (Pascual et al. 2001; Riva-Rossi et al. 2004).

The main objective of this study was to demonstrate that anadromy is involved in the colonization process of Eastern Quebec by rainbow trout. We aimed to determine if the anadromous phenotype is present in recently naturalized populations in Eastern Quebec, which are believed to consist of mainly freshwater residents. We also tested the hypothesis that all vagrants should be anadromous. To determine the occurrence of anadromy, both direct (i.e. individual migratory behaviour) and indirect (maternal phenotype) observations were used. Our second objective was to characterize the anadromous phenotype in Eastern Quebec rivers. We thus determined the age and size at migration and at reproduction for steelhead (anadromous rainbow trout), and compared growth rates between the anadromous and resident phenotypes. Finally, we compared these characteristics to what is observed in populations found within their native range.

5.4. MATERIALS AND METHODS

5.4.1. Sampling and measurements

In 2005 and 2006, we obtained more than two hundred rainbow trout from different sites in Quebec waters, including rivers, lakes, creeks, and the St. Lawrence River and Estuary. Most rainbow trout (77%) were provided by recreational fishers, whereas the remaining specimens came from commercial fisheries, the monitoring of dams and surveys performed by biologists and river managers. The majority of fish were captured from June to August. As fishing effort varied between sample locations, our sample did not reflect the real distribution and abundance of the species.

Fish were weighed, measured (fork length), and sexed. Since biological information was mainly provided by fishers, some data were missing (especially mass) and their precision is somewhat uncertain. When possible, size and mass were measured again and sex was confirmed in the laboratory. A tissue sample was collected to determine if fish captured outside the stocking area originated from a domestic sterile strain used for stockings (triploid fish – 3N) or a wild population (refer to Chapter 2 for more details on the method). Sagittal otoliths were extracted, cleaned with distilled water, dried in air and conserved in plastic eppendorf tubes until otolith microchemistry analyses were performed (see next section). For the purpose of this study, only 140 specimens were kept for the otolith microchemistry analyses. Our selection criteria were: i) the capture location, in order to represent different habitats, favouring fish captured to the east of Quebec City, ii) the fish size, as larger individuals were believed to be older and therefore more likely to present a more complete life-cycle, and iii) the fish sex, to ensure a sample with an almost equal sex ratio. Ten farmed rainbow trout (3+ years of age) provided by a governmental hatchery (*Lac-des-Écorces*, LDE) were also analysed.

5.4.2. Otolith Sr:Ca analysis and interpretation

Samples preparation for electron probe micro-analysis of otoliths was done in National Taiwan University. Quantitative chemical analyses of strontium (Sr) and calcium (Ca) in otoliths were carried out by an electron probe micro analyzer (EPMA: JEOL JXA-8900R) and a wave-length dispersive spectrometer (WDS) at the Institute of Earth Sciences, Academia Sinica in Taipei. Secondary- and backscattered electron images were used to guide the analysis on target positions located along an axis from the core of the otolith to the edge at 10 μm intervals. Beam conditions were 15 kV for the acceleration voltage and 3 nA for the current, and a 5 × 4 μm rectangular scanning beam was used. The Sr *Lα* peak position was measured for 80 seconds and each of the upper and lower baselines for 20 seconds. The peak concentration of Ca *Kα* was measured for 20 seconds and each of the upper and lower baselines for 10 seconds.. The beam power density of 2.25 Wm^{-2} was within the range of 0.5 to 3 Wm^{-2} as suggested by Gunn et al. (1992), and the counting time was sufficient to ensure effective measurement.

The measured X-ray intensities were corrected by the PRZ (phi-rho-z, Reed (1993)) method using the standard calibration of natural and synthetic chemical-known standard minerals; a strontianite ($[Sr0.95Ca0.15]CO_3$: NMNH-R10065 from National Museum of Natural History, Smithsonian Institution, Washington DC) for Sr and a synthesized aragonite ($CaCO_3$) for Ca. Detection limits based on 3σ of standard calibration were less than 400 ppm for Sr.

As the otolith Sr:Ca ratio increases with salinity (Zimmerman 2005), it is possible to distinguish periods when the fish grew in freshwater or the sea. Among the 150 otoliths selected for the analysis (140 captures + 10 farmed specimens), some broke during the preparation or presented vaterite inclusions (Jessop et al. 2008; Tzeng et al. 2007), and so were discarded. Interpretation of the otolith Sr:Ca life-history transects was possible for 125 specimens, representing 29 different watercourses (and the LDE government hatchery, $n = 8$), distributed over three sectors: 1) South-western Quebec (SWQ), including six stocked creeks and lakes in the upper part of the St. Lawrence River, 2) Quebec City (QC), comprising ten rivers located within 70 km of Quebec City, at the downstream limit of the stocking area, and 3) Eastern Quebec (EQ), consisting of 13 rivers located outside the stocking area (Figure 5.1). Following analysis, one specimen was discarded (see below).

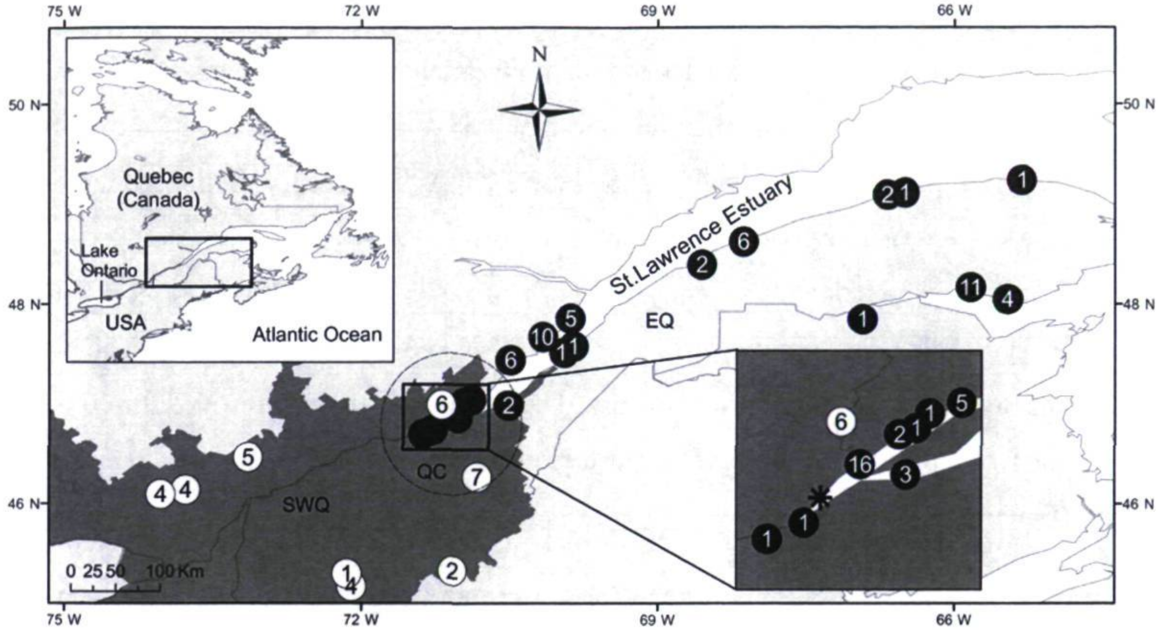

Figure 5.1 Capture locations of the 116 rainbow trout (*Oncorhynchus mykiss*) analysed for otolith microchemistry (the eight fish from the *Lac-des-Écorces* hatchery are not presented). Numbers in the circles represent the sample sizes. Specimens (n = 33) used for determination of the threshold between freshwater and saltwater signatures are shown in white. The area where stocking and farming of rainbow trout is allowed is shown in dark grey. Quebec City is represented by an asterisk. SWQ: South-western Quebec region, QC: Quebec City region (encircled), and EQ: Eastern Quebec region.

Among fish captured inside the stocking area, 41 were *a-priori* known to be freshwater residents. Twenty-one were farmed fish that either came directly from the LDE government hatchery (n = 8) or were captured in lakes shortly after stocking events (SWQ, n = 13). Another twenty specimens were caught upstream of two impassable waterfalls (QC, n = 13) or came from watercourses located far away from the nearest marine habitat (SWQ, n = 7) (Figure 5.1). All these fish were used to establish the threshold demarcating fresh from marine (or brackish) water habitats (thereafter called FW-threshold). Their mean otolith Sr:Ca values varied from 0.327 to 3.684 x 10^{-3}, with an average of 1.517 x 10^{-3}. Mean Sr:Ca + 1 SD was 0.790 to 3.724 x 10^{-3}, with an average of 2.528 x 10^{-3} (Figure 5.2). More than 90% of all Sr:Ca values were less than or equal to 3 x 10^{-3}. To be conservative, we decided to set the FW-threshold at 3.5 x 10^{-3}, which included 96% of the freshwater observations.

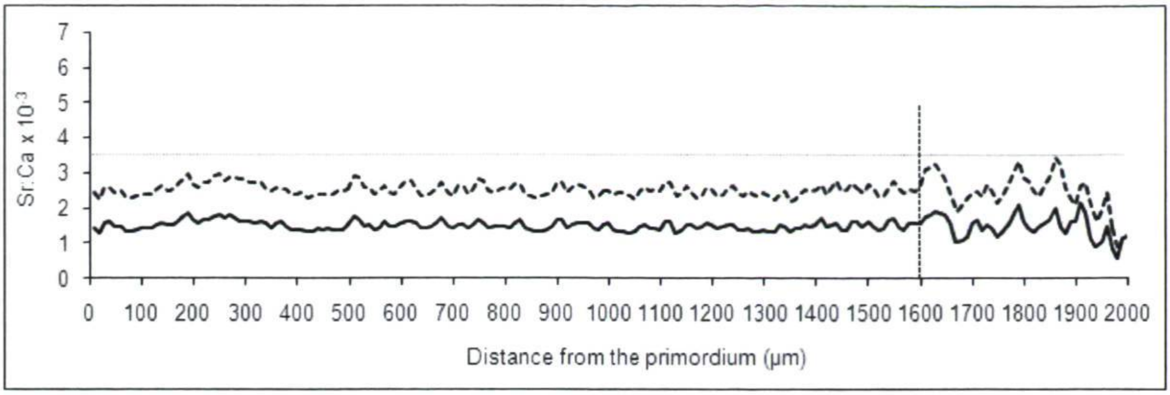

Figure 5.2 Sr:Ca pattern (2-point smoothed averages) of 41 rainbow trout with a known freshwater residence phenotype. The full line corresponds to the mean Sr:Ca values, and the dashed line corresponds to the mean + 1 SD. The threshold of 3.5×10^{-3}, delineating freshwater and saltwater, is shown by a dotted horizontal line. The vertical line represents the distance from the otolith primordium beyond which the number of specimens is less than 30% of the sample.

The phenotype of the 84 remaining rainbow trout (QC and EQ sectors) was determined by two methods. The first method consisted of visually interpreting the otolith Sr:Ca transect of each individual from a point situated 100 µm from the otolith's primordium to the otolith edge. Fish were classified as anadromous (A) – or steelhead – if the 2-point smoothed average curve exceeded the FW-threshold of 3.5×10^{-3} anywhere along the otolith transect from 100 µm outward. Fish were classified as freshwater resident rainbow trout (FW) when all values of the 2-point smoothed average were less than the FW-threshold anywhere along the otolith transect from 100 µm outward. Note that when only one point was located above or under the FW-threshold, it was not taken into account. At distances less than 100 µm from the primordium, Sr:Ca values represented the maternal contribution (C. Donohoe, Institute of Marine Science - UCSC, pers. comm.). If a gravid anadromous female does not stay in a freshwater spawning river for a long period before egg deposition, a marine signal transmitted to the offspring otolith through the egg cytoplasm may be observed near the otolith core (Donohoe et al. 2008; Rieman et al. 1994; Volk et al. 2000; Zimmerman & Reeves 2000, 2002). Fish exhibiting high Sr:Ca values between 0 and 100 µm were therefore classified as the offspring of steelhead. Note that it was not possible to determine the maternal form for two rainbow trout because the Sr:Ca transect did not begin at the otolith primordium.

Despite the fact that visual interpretation of Sr:Ca patterns is common in studies using Sr:Ca otolithometry (e.g. Daverat et al. 2006; Gillanders 2005; Tzeng et al. 2003; Tzeng et al. 2000; Zimmerman & Reeves 2000), the method is quite subjective. More quantitative approaches have been recently proposed to avoid any reader bias (e.g. Hedger et al. 2008). To validate results obtained with the conventional method, we also employed a quantitative approach based on non-parametric smoothing to interpret the otolith Sr:Ca transects. Otolith sequences were smoothed using Generalized Additive Models (GAMS). GAMs were used for modelling the relationship between Sr:Ca ratio and distance from the otolith's primordium because there was no *a priori* reason to choose between the forms of the relationship. Use of GAMs enabled this relationship to be determined from the data (instead of being arbitrarily imposed). GAMs were fitted using the *gam(mgcv)* package of R (Wood 2006), using penalized regression splines. The degree of smoothness of the model term was estimated as part of fitting using generalized cross validation. GAMs were fitted separately to the maternal and offspring parts of the transect sequence. Determination of the transition from maternal to offspring parts of the sequence was based on the fact that the maternal signature could have been a mix of freshwater and saltwater Sr:Ca ratios, but that the initial offspring signature must have been a freshwater Sr:Ca ratio due to spawning in freshwater. The procedure for defining the break was as follows: 1) A distance of 100 μm was defined as the initial break-point between maternal and offspring histories. 2) An offspring GAM was fitted to all parts of the sequence at distances greater than the break-point (thus excluding the maternal history). 3) If the part of the offspring GAM nearest to the primordium showed a saltwater signature (predicted values greater than the FW-threshold), an extra 10 μm was added to the break-point. 4) Steps 2-3 were repeated until the part of the offspring GAM nearest to the core showed a freshwater signal. 5) A maternal GAM was fitted to all parts of the sequence nearer to the primordium than the part of the sequence used to determine the offspring GAM. Otolith histories (maternal or offspring) were defined as being anadromous if any value predicted by the GAM exceeded the FW-threshold.

Comparing interpretations obtained with qualitative and quantitative methods, we found 92% and 87% of concordance for fish phenotypes and maternal forms respectively. Discordant interpretations (n = 18) consisted mainly (83%) of anadromous categorizations according to the visual method as opposed to a freshwater residency classification obtained by the GAM method. Final categorization followed the GAM's interpretation except in cases where obvious evidence (e.g. discordance between signal and capture location of the fish, abnormally low Sr:Ca values for an entire transect) supported the visual method result. Note that one fish classified as anadromous according to both methods was finally removed from the analysis as we suspected an edge effect (Jessop et al. 2002): it presented a sudden saltwater Sr:Ca signal at the very end of the otolith transect, despite being captured in freshwater.

5.4.3. Life-history of established *vs* invading rainbows

Inside the stocking zone, where the majority of captured rainbow trout are believed to be cultured fish, all specimens should originate from a freshwater resident mother and present a freshwater residency phenotype. On the contrary, outside the boundaries of the stocking area, the FW-resident phenotype is expected only among established fish found the two rivers where reproduction has been confirmed (that is, Du Gouffre and Malbaie R). All rainbows captured elsewhere, where the species is not believed to reproduce, were considered as vagrants. They thus should have experienced at least one marine phase representing the migration from their native stream to the river of capture using the St-Lawrence River ($\geq$ 20 PSU in this area, Lecomte & Dodson 2004), a phase that should be reflected along the otolith transect by higher Sr:Ca values. Capture of putative vagrants with a solely freshwater signature would thus suggest that the species is reproducing in more rivers than documented to date. For both established fish and vagrants, the two maternal forms (resident or anadromous) are possible.

5.4.4. Age and size at migration and growth rate

Farmed strains are genetically selected to increase growth rates, and rearing conditions in hatcheries are designed to favour growth. Therefore, growth rates of farmed fish differ to those of fish originating from naturalized populations. Because fish found inside the stocking area limits probably originated in a hatchery, only fish from Eastern Quebec (Charlevoix, Bas-St-Laurent and Gaspesia regions) were kept for size and growth analyses. The age of each remaining specimen (N = 51) was determined by two readers from otolith photographs (obtained after microprobe analyses and otoliths etched with 0.05N HCl) by counting annuli. Given that the locations of the microprobe Sr:Ca measurements were visible on the otolith photos, it was possible to identify the approximate position of each annulus on the Sr:Ca transects, and therefore determine the age of fish at migration in the case of anadromous fish.

To estimate size at migration of steelhead, we back-calculated fish size to the age at habitat switch, as determined from otolith Sr:Ca ratios, according to the "body proportional hypothesis" (BPH) technique (Brisson-Bonenfant 2006; Francis 1990; Jessop et al. 2004). The BPH equation is as follows:

$$\log_{10}L_i = [(c + d\log_{10}O_i)/(c + d\log_{10}O_c)]\log_{10}L_c \qquad (1)$$

where c is the intercept and d is the slope of the body length–otolith radius (BL–OR) regression ($\log_{10}\text{BL} = 1.33 \times \log_{10}\text{OR} + 2.35$; N = 93, $R^2 = 0.82$), L_i and O_i are body length and otolith radius at age i, and L_c and O_c are body length and otolith radius at capture. Otolith radius and distances between annuli and the primordium were measured along the longest radius along the ventral side with image analysis software *Image-Pro Express version 6.0*.

The size-at-age relationship was determined for both anadromous and resident fish in order to compare growth rates between life-history forms. Dates of capture varied among specimens, and current year growth was visible for some fish. To avoid bias, we back-calculated the size of each fish to their last visible annulus (that is, to the spring preceding capture), instead of using size at capture.

5.5. RESULTS

5.5.1. General characteristics of sampled fish

Specimens used for Sr:Ca analyses (excluding fish from the LDE hatchery) showed a wide range of sizes and masses (Table 5.1). The overall sex ratio in our sample was 1.6, with a bias toward females. As expected, this bias was much more pronounced inside the stocking area (SWQ and QC) because when strains used for stocking are not triploid (and hence sterile), they often consisted of *all-female* lineages. Rainbow trout captured outside the stocking area, in Eastern Quebec (EQ), were all believed to be vagrants, except those coming from Du Gouffre and Malbaie Rivers, where natural reproduction is documented. In our sample, the oldest rainbow trout was 9-years old, whereas the youngest one was 1-year old (Table 5.2). On average, fish from the established population were older than those thought to be vagrants.

Table 5.1 Biological characteristics of 116 rainbow trouts captured in Quebec's streams in 2005-2006 and used for otolith microchemistry analyses, including 33 specimens selected to determine the threshold between freshwater and saltwater signatures, but excluding the specimen eliminated because of otolith edge effect. Numbers in parentheses correspond to the *n* used for calculating means when some data were missing. F: female, M: male, I: sex not determined, 3N: triploid farmed fish

Sector of capture	Sex	N	Fork length (mm)		Weight[a] (g)	
			mean	range	mean	range
South-western Quebec (SWQ)	F	10	321	[229 - 406]	513 (9)	[294 - 1361]
	M	3	274	[250 - 323]	223 (2)	[220 - 225]
	I	1	229	-	?	-
	3N	6	287	[210 - 559]	504	[100 - 2381]
Quebec City (QC)	F	17	245 (16)	[119 - 495]	89 (10)	[20 - 291]
	M	7	179	[124 - 260]	69	[24 - 113]
	I	5	229 (3)	[229]	135 (3)	[135]
	3N	16	270 (15)	[232 - 308]	174 (11)	[113 - 340]
Eastern Quebec (EQ) *(outside stocking area)*	F	24	343	[176 - 334]	596 (21)	[63 - 1364]
	M	22	286	[173 - 585]	325 (20)	[54 - 1361]
	I	5	235	[90 - 317]	279 (2)	[227 - 331]

[a] Some fish were weighed after getting defrosted

Table 5.2 Age of 51 rainbow trout found in Eastern Quebec (EQ), according to their region of capture.

Region	N	Mean	Range
Charlevoix			
Du Gouffre and Malbaie R.	16	5.5	[4 - 9]
Other	5	2.8	[2 - 3]
Bas-St-Laurent	10	3.3	[1 - 7]
Gaspesia	20	3.5	[3 - 6]

5.5.2. Life-history patterns: fish phenotype and maternal form

Four main otolith Sr:Ca life-history patterns were observed: i) FW-resident phenotype with a FW-resident maternal form (FW/FW, Figure 5.3a), ii) FW-resident phenotype with an anadromous maternal form (A/FW, Figure 5.3b), iii) anadromous phenotype with a FW-resident maternal form (FW/A, Figure 5.3c), and iv) anadromous phenotype with an anadromous maternal form (A/A, Figure 5.3d). Fish sampled in the stocking area showed the same life history phenotype as their mother whereas this was not the case outside the stocking area in Eastern Quebec (Table 5.3). Among fish sampled in Eastern Quebec, 38% of FW-residents originated from an anadromous mother, whereas 42% of anadromous trout originated from a FW-resident mother.

Occurrence of anadromy varied according to the capture location (Table 5.3, Figure 5.4). Inside the stocking area, that is the Quebec City region, the FW-resident phenotype dominated the sample, and no specimen originated from a steelhead mother. In contrast, outside the stocking area (Eastern Quebec), the signal of anadromy, expressed either by the specimen's phenotype or the maternal form, dominated the sample. Based on a chi-square analysis of the incidence of the saltwater signal as a function of distance from the stocking zone (Charlevoix, Bas-St-Laurent, Gaspesia), the proportion of fish having experienced saltwater increased downstream ($\chi^2 = 8.87$, $N = 51$, d.f. $= 2$, $p = 0.01$). In the more upstream Charlevoix region, where natural reproduction is documented in two rivers, all specimens but one exhibited a FW-resident phenotype, but six (out of 20) appeared to be the offspring of anadromous mothers.

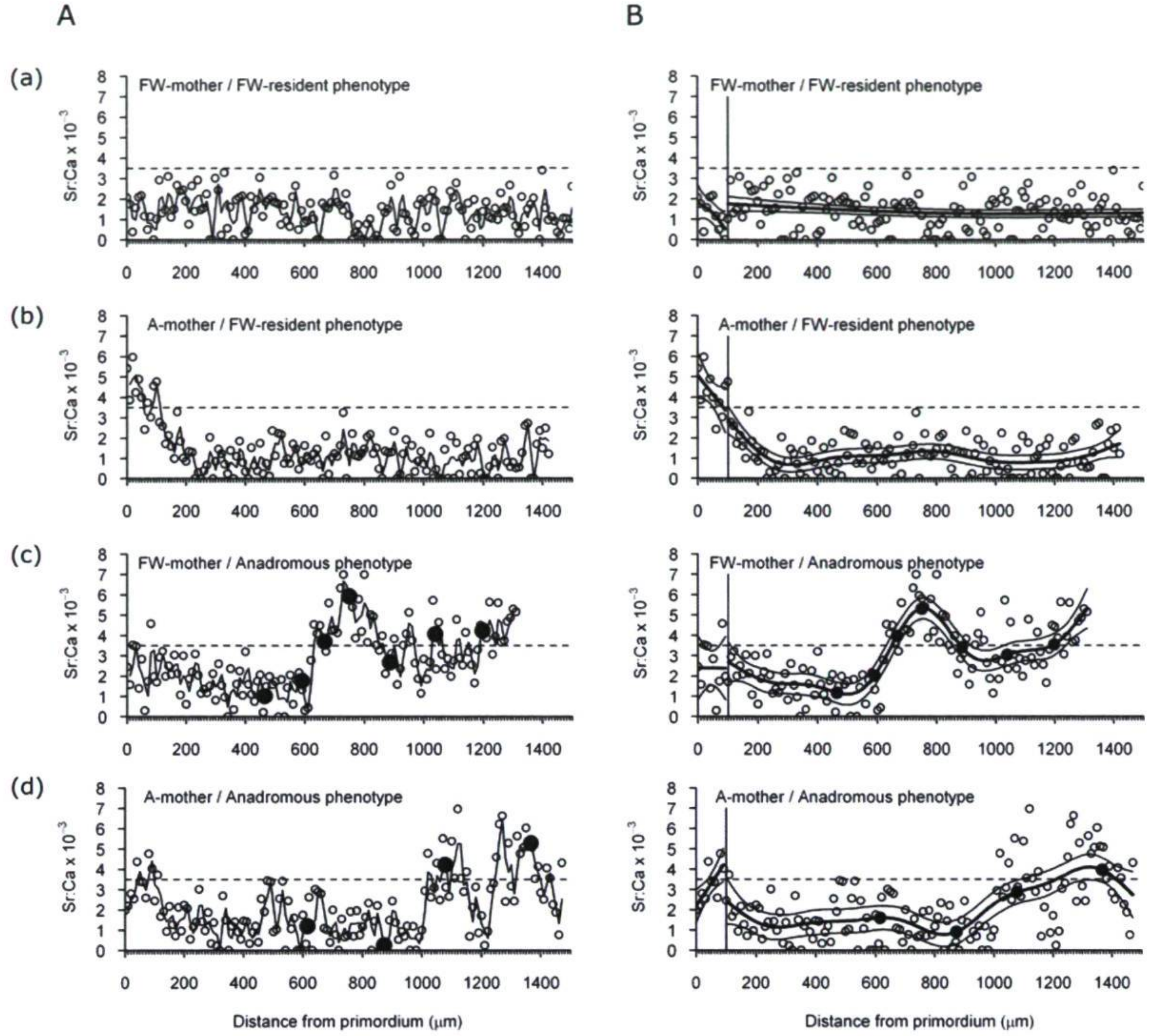

Figure 5.3 Four otolith Sr:Ca life-history patterns observed in 83 rainbow trout (*Oncorhynchus mykiss*) captured in Eastern Quebec, as obtained by the visual interpretation method using the 2-point smoothed averages (A), and the quantitative interpretation method using GAMs (B). Sr:Ca ratios between 0 μm and ~100 μm are associated with the maternal history, whereas Sr:Ca ratios between 100 μm and the otolith edge represent the growing habitats experienced by the fish throughout its life time. Full circles represent the estimated position of each annulus. A-mother: anadromous maternal form, FW-mother: freshwater resident maternal form. The threshold of 3.5 x 10^{-3}, delineating between freshwater and saltwater, is shown by a dotted horizontal line.

Table 5.3 Life-history pattern of 83 rainbow trouts captured in the Quebec City sector and in three different regions of Eastern Quebec, according to their sex. For two specimens, maternal form was not possible to determine. FW: freshwater resident, A: anadromous, F: female, M: male, I: sex not determined (mainly triploid sterile fish).

		Maternal form/Specimen's phenotype						
Region	Sex	FW/FW	A/FW	FW/A	A/A	?/FW	?/A	N
Quebec City	F	11	0	0	0	0	0	32
	M	4	0	0	0	0	0	
	I	17	0	0	0	0	0	
Charlevoix (EQ)	F	8	3	0	0	1	0	21
	M	5	2	1	0	0	0	
	I	0	1	0	0	0	0	
Bas-St-Laurent (EQ)	F	2	2	2	1	0	0	10
	M	0	1	0	0	0	0	
	I	2	0	0	0	0	0	
Gaspesia (EQ)	F	1	2	1	1	0	0	20
	M	5	3	1	3	0	1	
	I	0	0	0	2	0	0	
Total	-	*55*	*14*	*5*	*7*	*1*	*1*	*83*

Most (74%) of the rainbow trout showing either an anadromous phenotype or an anadromous maternal origin were captured in the regions bordering the downstream St. Lawrence Estuary (Bas-St-Laurent and Gaspesia). In these two regions, although we initially surmised no reproduction in these rivers and therefore expected only the anadromous phenotype, 18 rainbow trout showed a FW-resident life-cycle, including two juveniles of 1- and 2-years old.

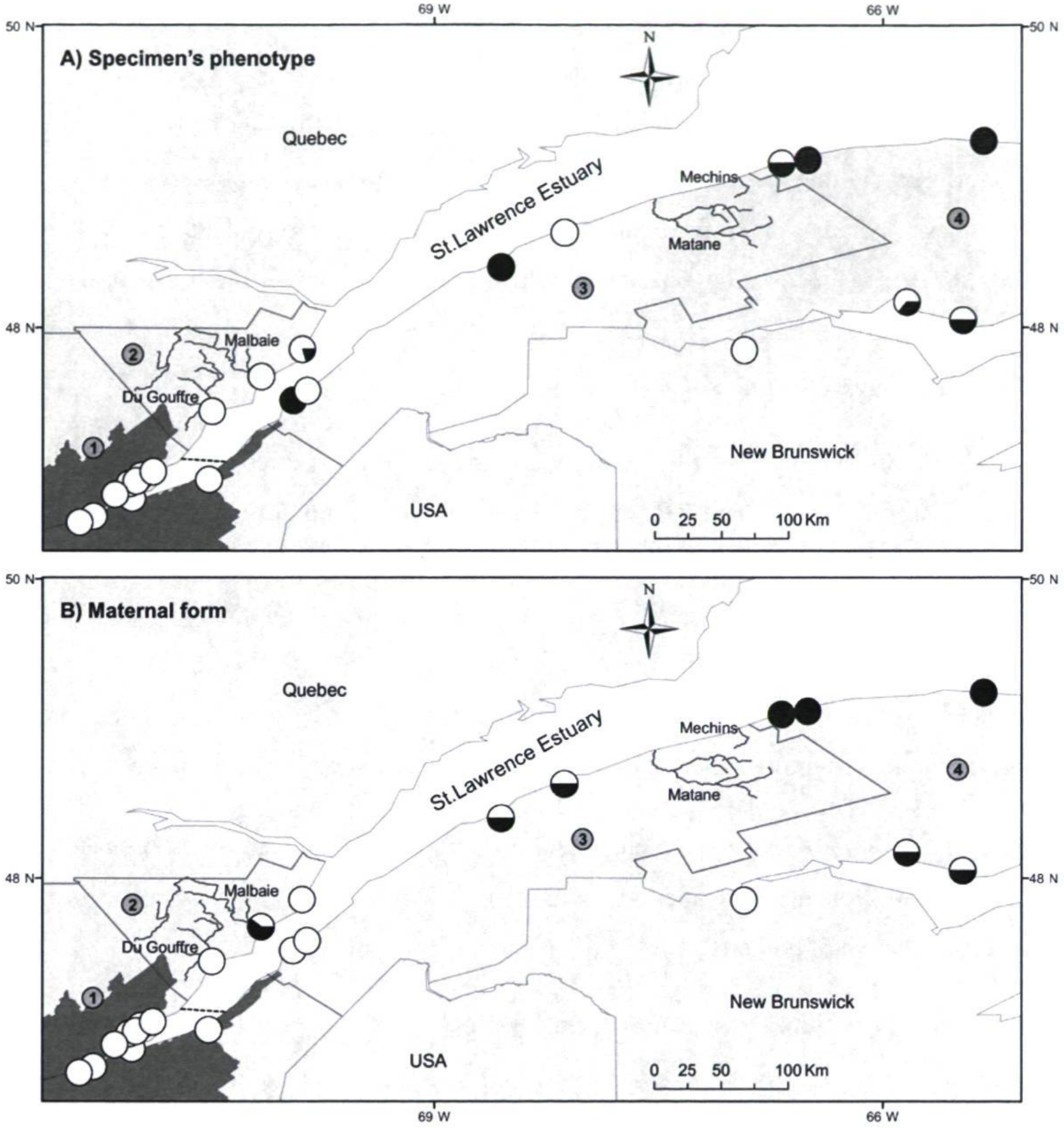

Figure 5.4 Proportion of the anadromy and freshwater(FW)-residency forms in 83 rainbow trout (*Oncorhynchus mykiss*) captured in the Quebec City and Eastern Quebec regions, as determined from the otolith Sr:Ca patterns: A) phenotype of analysed specimens, B) maternal form. Anadromy is shown in black, whereas FW-residency is shown in white. Rivers where natural reproduction has been documented are labelled. The area where stocking and farming of rainbow trout is allowed is shown in dark grey. Approximate limit of the freshwater is indicated by a dashed line. 1: Quebec City region, 2: Charlevoix, 3: Bas-St-Laurent, and 4: Gaspesia.

5.5.3. Characteristics of the anadromous phenotype

Age at first river-to-sea migration (smoltification) Thirteen rainbow trout, all found in Eastern Quebec (that is outside the stocking area), experienced at least one migration into saltwater. For the majority (62%), first movement to the marine habitat occurred at three years of age, whereas 15% first entered in saltwater at 4 years old (Table 5.4). In our sample, three specimens migrated at one and two years of age (Table 5.4). Based on the position of annuli along the Sr:Ca transect, one of these young migrants left freshwater at the very end of the growing season, probably in the fall.

Age at first return to freshwater Several steelhead were captured in estuaries, usually during the same year they had left freshwater, and therefore did not have time to start their migration towards rivers (Table 5.4). It was thus possible to estimate age at freshwater entrance for only seven specimens that experienced at least one complete marine phase. For three of them, the first upstream migration occurred at 4 years old, whereas it occurred one year later for a fourth individual. The three remaining fish were the young seaward migrants mentioned previously and they re-entered freshwater at a younger age.

Multiple migrations Among sampled fish, four experienced a second marine phase (Table 5.4). Three fish (female, male and unknown sex) were probably multispawners according to their age at change of habitat.

Duration of the marine phase Whatever the age of fish at downstream or upstream migration, and regardless of whether this migration was associated with the first or the second marine experience, all steelhead but two returned to freshwater during the growing season following the year of the seaward migration (Table 5.4). One exception was a young migrant that moved to the marine habitat and then returned to freshwater within the same year. The second case was the oldest steelhead of our sample that stayed two years in saltwater during its first marine phase, but only one growing season during its second one, before returning to the river where it was captured.

Table 5.4 Age at migration for 13 anadromous rainbow trout captured in 2006 in Eastern Quebec regions, as revealed by otolith microchemistry. "+" refers to fish age during the growing season (late spring to early fall), "++" refers to fish age at fall, absence of "+" refers to fish age at early spring.

Region	River	ID	Date of capture	Direction of migration	Age at migration	Capture location	Age at capture
Charlevoix	Noire	NO1	June 27	river to sea	0+	river	2+
				sea to river	1		
Bas-St-Laurent	St.Lawrence Estuary	SL1	Sept. 7	river to sea	3	unknown	4++
				sea to river	4+		
	Rimouski	RI1	Oct. 2	river to sea	3	migratory pass	6++
				sea to river	5		
				river to sea	6		
		RI2	Sept. 23	river to sea	3	river mouth	3++
Gaspesia	Sainte-Anne	SA1	June 27	river to sea	3+	river	4+
				sea to river	4		
	Cap-Chat	CC1	July 25	river to sea	4	river mouth	4+
	Bonaventure	BV1	Aug. 28	river to sea	2++	river	4+
				sea to river	3		
				river to sea	3+		
				sea to river	4		
		BV2	Aug. 28	river to sea	4	unknown	5+
	Petite-Cascapedia	PC1	July 2	river to sea	3+	estuary	3+
		PC2	July 2	river to sea	2	estuary	3+
				sea to river	2+		
				river to sea	2++		
		PC3	Aug. 8	river to sea	3	estuary	3+
		PC4	Aug. 8	river to sea	3+	estuary	3+
	Madeleine	MA1	June 5	river to sea	3	river mouth	6
				sea to river	4		
				river to sea	4+		
				sea to river	5+		

Size at migration and growth rate Average fork length (± SD) at the age of the first downstream migration (excluding the youngest migrant NO1) was 265 ± 67 mm (N = 12, range: 168 – 363 mm). When fish first returned to freshwater, they measured 303 ± 89 mm on average (N = 7, range: 157 – 390 mm). When removing younger specimens (NO1 and PC2) that might have been immature at that time, the mean fish length increased to 347 ± 52 mm on average (N = 5, range: 258 – 390 mm). Growth rate (length-at-age) observed for steelhead (excluding NO1) was the same as that for FW-residents (2-factor ANCOVA (age, form, age x form): d.f. = 36, *F* = 28.74, $p > 0.05$, Figure 5.5). However, when size was back-calculated to the most common age for the first freshwater-to-sea migration, that is at the age of 3 years, future steelhead tended to be larger than future FW-residents, but this difference was not significant (268 ± 61 mm *vs* 252 ± 73 mm, Student *t*-test: d.f. = 33, *t*-value = 0.39, p = 0.70). It must be noted however that all back-calculations were based on fish size in spring (at the time of annulus formation). Thus, estimation of size at migration does not take into account the fish's growth during summer, even if it changed habitat later during the growing season.

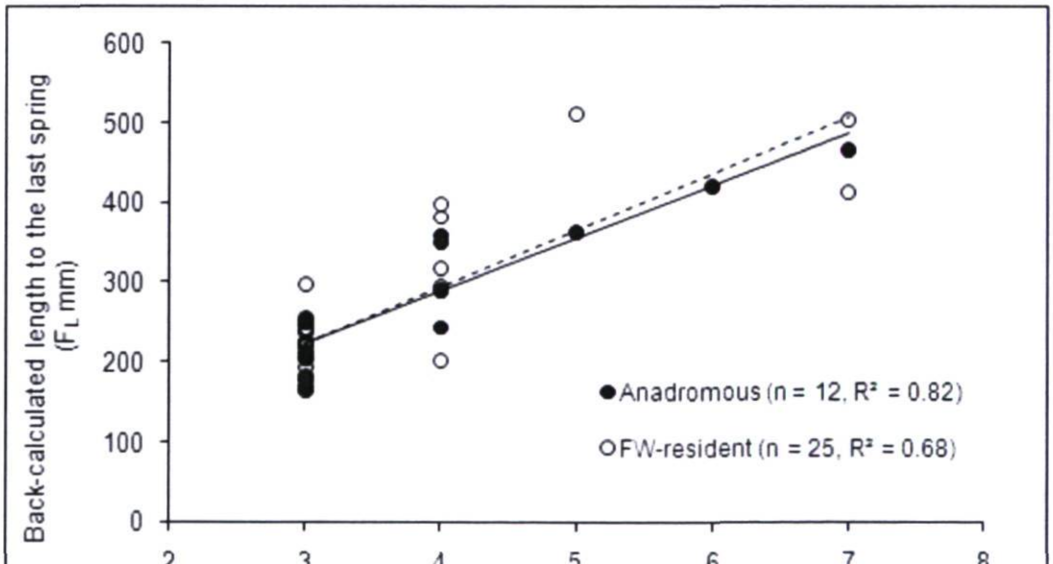

Figure 5.5 Relationship between body length (fork length) and age for 37 anadromous and freshwater(FW)-resident rainbow trout (*Oncorhynchus mykiss*) captured in Eastern Quebec regions in 2005 and 2006.

5.6. DISCUSSION

Rainbow trout is slowly but surely invading Quebec streams, from the upper part of the St. Lawrence River where stocking is allowed, towards rivers located further downstream, outside the limits of the stocking area. The invasion process has led to the establishment of some self-sustaining populations in Eastern Quebec, such as in two rivers of Charlevoix (Du Gouffre and Malbaie), where it forms a genetically distinct population (Chapter 2). Since success of biological invasions usually depends on the presence of long-distance migrants (Begon et al. 1996), anadromy could have promoted the species' dispersion as steelhead can reach streams located far from their native river. Otolith microchemistry analysis performed on specimens captured inside and outside the stocking area revealed that although all fish in the Quebec City region were freshwater residents, both phenotypes (anadromous and freshwater resident) were found in Eastern Quebec. Moreover, the proportion of fish exhibiting the anadromous life cycle increased with the distance from the stocking zone.

5.6.1. Anadromy in the newly established population of Charlevoix

All rainbows captured in the Du Gouffre and Malbaie Rivers, where the species reproduces, exhibited a freshwater resident phenotype. However, 30% of them were produced by anadromous mothers, indicating the presence of an anadromous contingent in this population. The presence of anadromy (as revealed by the maternal form) increases the probability of population dispersal. Furthermore, our results support previous genetic analyses (Chapter 2) and contradict the belief that anadromy among introduced self-sustaining populations of rainbow trout only exists in the Santa Cruz River (Pascual et al. 2001; Riva-Rossi et al. 2004). Moreover, our sampling in Du Gouffre and Malbaie Rivers was not representative of the real spatial and temporal distribution of the species. Specimens were caught during and after the reproduction period, mainly in the streams, and less so at the rivers' mouths. Therefore, capture of resident fish was more probable than anadromous fish that usually stay in the river only for the spawning period. Thus, the proportion of steelhead is probably underestimated. Predominance of freshwater resident rainbows in rivers supporting reproduction could also be related to sport fishing pressure.

Rainbow trout has been fished in Du Gouffre and Malbaie Rivers for many years. Steelhead, being larger than residents, are targeted by fishers, so a decrease in the relative abundance of anadromous trout could be expected, as has been observed in a native population until the adoption of a *catch-and-release* policy (Kostow 2003).

5.6.2. Anadromy and freshwater residency among vagrants

As predicted, anadromy (revealed by fish phenotype and maternal forms) was predominant among vagrants captured in Bas-St-Laurent and Gaspesia regions, and was even probably slightly underestimated because of the capture of a few specimens too young to have undergone smoltification. The invasion process thus appears to be supported by long-distance migrants. However, the presence of freshwater residents was unexpected in these regions, as all the fish were believed to have migrated from populations established upstream in the St. Lawrence River system. The presence of non-migratory fish in these rivers (especially in Gaspesia) and in the Noire River (next to the Malbaie R.), suggests that either there were illegal stocking events, or that the species is reproducing in these streams. Evidence suggests that punctual stockings have no influence on the rainbow trout colonization process (Chapter 2). Thus the spread of established populations may be greater than previously indicated.

5.6.3. Age and size at smoltification

Most of the sampled steelhead exhibited a typical anadromous life cycle, with a first migration towards the marine habitat at approximately 3-years old and measuring ~265 mm. The few younger migrants captured would constitute an exception (see below). The age at smoltification observed in Eastern Quebec is similar to that observed in juvenile steelhead within their native range where they usually spend 2 or 3 years in freshwater before migration (Burgner et al. 1992; Busby et al. 1996). However, Eastern Quebec steelhead appear to leave freshwater at a larger size than North American west coast steelhead (smolt size ~160 mm, (Burgner et al. 1992)). A great variation was found in size at migration, suggesting that migration is more related to age than to size. This contradicts general observations for *O. mykiss* and other salmonids indicating that smolt outmigration is related to a critical size (Brisson-Bonenfant 2006 and references therein; Burgner et al.

1992). However, our results might be biased by small sample size and/or errors associated with the back-calculation method.

5.6.4. Purpose of habitat changes

All anadromous rainbow trout were found in rivers where no reproduction was expected. Therefore, we assumed that when they undertook their first seaward migration, they moved far away downstream of their native stream, never to return, and after a time spent in saltwater they finally entered into a new (non-native) river. The period spent in the marine habitat should not be considered only as a growing period before reproduction, but also as an opportunity to move between rivers. We cannot be certain that migration into non-native rivers is solely for the purpose of reproduction. For example, the specimen captured in the Noire River (located about 30 km downstream of Malbaie River), that experienced precocious down- and upstream migrations, completed its marine phase before the age of two years. It appears unlikely that this fish was mature enough to reproduce. We rather suggest that it might have quickly migrated out of its native river (probably the Malbaie River), simply to switch rivers without necessarily spawning.

It also appears unlikely that the young migrant found in the Petite-Cascapedia River (PC2) was mature enough to reproduce when it returned to freshwater at an age of two years. As for the Noire River fish, its first saltwater incursion was probably related to a habitat change between its native stream and another river, and thus not related to spawning. Consistent with this, the fish underwent a second downstream migration at the end of the same growing season, and when it was captured a year later, it had still not re-entered freshwater (found in the river's estuary).

5.6.5. Age at reproduction

For almost all anadromous fish sampled in this study, the first return to freshwater occurred at 4 years of age. Despite the fact that the first upstream migration might not always be for the purpose of reproduction (especially for fish that migrated at an age of three years or less, see previous section), it seems reasonable to affirm that the age at reproduction for most steelhead in Eastern Quebec is similar to steelhead within their native range, spawning at approximately 4-years old [range: 3 – 5] (Busby et al. 1996; Kostow 2003;

Seamons et al. 2007). However, it should be noted that this conclusion is based on only a few individuals (N = 5) that had time to enter into the river for spawning before being captured.

5.6.6. Multispawning of steelhead

If repeat spawning is frequent among freshwater residents, steelhead multispawners are believed to be generally few in populations of the temperate zone of the North American west coast, with an incidence usually (but not exclusively) less than 10% (Burgner et al. 1992; Busby et al. 1996; Kostow 2003). In our study, three of the 13 fish exhibiting the anadromous life cycle were probably multispawners. Despite our small sample size, we think that the prevalence of multispawners in Eastern Quebec is probably higher than what has been reported in almost all coastal native populations (Narum et al. 2008a), but certainly less than what was observed in the naturalized population of the Santa Cruz River (60%, Pascual et al. 2001). Multispawning can increase the success of invaders since this reproductive mode accelerates effective population growth and ensures genetic variability (Narum et al. 2008a; Riva-Rossi et al. 2007). This impact is enhanced when multispawners are anadromous females, which are known to be much more fecund than resident females (Kostow 2003).

5.6.7. Determination of the phenotype

Although we are unable to identify the life cycle of the fathers of our sampled fish, our results show that the maternal form is not necessarily expressed by its progeny. Within our sample in Eastern Quebec, we found resident rainbow trout with an anadromous maternal origin (38%) and steelhead with a resident maternal origin (42%). This is contrary to what was found by Zimmerman & Reeves (2000) and Donohoe et al. (2008), using a similar approach. However, direct spawning observations, pedigree analyses and breeding experiments have previously demonstrated that both resident and anadromous parents can produce either freshwater resident or steelhead offspring (see references in Kostow 2003). Supporting these observations, population structure analyses conducted on sympatric resident and anadromous forms have shown a lack of strong genetic divergence between life-history forms (Docker & Heath 2003; Heath et al. 2008; Narum et al. 2004; Pascual et al. 2001; Riva-Rossi et al. 2004). Many environmental factors associated with a particular geographic area, such as habitat productivity, migratory hazards, habitat connectivity, or freshwater mortality, have been proposed to explain the occurrence of the two life-history strategies (Kostow 2003 and references therein; Narum et al. 2008b). However, as we found both forms in the same streams, it appears that the adoption of residency or anadromy is the expression of conditional, alternative developmental pathways under the control of threshold traits (Brockman & Taborsky 2008).

We found no difference in growth rate (length-at-age relationship) and size at the age of migration between anadromous and freshwater resident specimens. Based on previous studies on salmonids, we expected that future steelhead would be, just before migration, smaller than future residents (for a same age) (Thériault & Dodson 2003 and references therein), but would thereafter experience a faster growth than freshwater residents (MacCrimmon & Gots 1972; Pascual et al. 2001; Thorpe 1994). The absence of significant differences between the two life-history forms may have been related to purely methodological problems: i) the number of anadromous specimens was low, ii) sizes provided by fishers may have been incorrectly measured, or iii) annuli on otolith's pictures may have been wrongly positioned, or estimated distances between the otolith core and annuli may have been erroneous due to picture precision and unequal otolith grinding. Excluding growth, size-at-age and maternal form, other individual traits, such as sex or condition factor, could have played a role in the adoption of the phenotype. In this study, we found no relation between sex and a particular life-history strategy, as the sex ratio was of 1:1 among anadromous fish. As the mass was not available for many specimen, it was not possible to investigate a potential role of condition factor in the adoption of a phenotype.

5.6.8. Sampling bias and implications for extrapolation

Since the invasion process is still in progress and the number of rainbow trout in many rivers is low, our sampling effort was not systematic but was rather based on voluntary angler returns. As such, some caution is required in applying our conclusions to the situation as a whole. Nevertheless, the presence of consistent patterns within the different river categories (only freshwater residents in all rivers located upstream inside the stocking area (SWQ and QC), dominance of freshwater residents in established populations, and dominance of anadromy in rivers of the Gaspesia and Bas-St-Laurent regions) indicates that our conclusions would probably apply in the case of increased sample sizes and locations. Nevertheless, future studies could focus the sampling efforts on a smaller number of rivers harbouring an abundance of rainbow trout and located at various distances from the established populations and stocking area to validate these preliminary conclusions.

5.6.9. Concluding remarks

As expected, otolith microchemistry analyses demonstrated that the invasion process by rainbow trout in Eastern Quebec is promoted by the presence of anadromous individuals that are able to colonize new rivers following long-distance migrations along the St. Lawrence Estuary corridor. In the newly established population of Charlevoix, anadromy was revealed by the maternal signature, indicating that the Santa Cruz River (Patagonia) is not the only introduced rainbow trout population that has developed an anadromous run. Surprisingly, some specimens with a freshwater resident phenotype were found among putative vagrants, suggesting the existence of unknown self-sustaining populations in Bas-St-Laurent and/or Gaspesia regions. These findings reveal the need for a more rigorous monitoring of the rivers in these regions, in order to monitor and mitigate the establishment of new rainbow trout populations in rivers supporting indigeneous salmonids such as Atlantic salmon (*Salmo salar*) and brook charr (*Salvelinus fontinalis*).

5.7. ACKNOWLEGMENTS

This work was funded by grants from the Natural Sciences and Engineering Research Council of Canada, CIRSA (Centre Interuniversitaire de Recherche sur le Saumon Atlantique), the Fédération Québécoise de la Faune and the Réseau Aquaculture de Québec. We thank our collaborators that helped to collect rainbow trout samples: Ministère des Ressources naturelles et de la faune, Québec Pêche, Fédération québécoise pour le saumon Atlantique, Fédération des gestionnaires de rivières à saumon du Québec, Simon Blanchet, and all ZECs, organisations, sport and commercial fishermen that participated in the sampling campaigns. A special thank to Véronique Thériault and Simon Blanchet for their implication in age determination. We are greatfull to Christopher Donohoe for his advice on the maternal Sr:Ca signature interpretation, and to Rémy Pouliot for his comments on earlier versions of the manuscript.

CHAPITRE 6. CONCLUSION

> *« La perte de biodiversité aquatique causée par l'introduction d'espèces exotiques pour notre bon plaisir doit cesser de toute urgence. Surtout que dans plusieurs pays hôtes, il y a déjà de bonnes espèces pour la pêche sportive.»* – Cambray 2003

L'introduction d'espèces exotiques est l'une des conséquences majeures des activités anthropiques à l'échelle mondiale (Mooney & Cleland 2001). L'incidence des invasions biologiques sur les communautés indigènes est telle qu'elles constituent l'une des principales causes du déclin des espèces et de la biodiversité, après la perte d'habitat (Cambray 2003a). Il n'est donc pas surprenant que l'arrivée de la truite arc-en-ciel, reconnue pour son caractère compétitif, dans la portion est du territoire québécois ait soulevé l'inquiétude des pêcheurs et des gestionnaires de la ressource. Suite aux nombreuses introductions de la truite arc-en-ciel partout dans le monde, les études qui décrivent son impact sur la faune indigène abondent (ex.: références dans Cambray 2003a; et dans Fausch 2007). Au Québec, le saumon atlantique et l'omble de fontaine pourraient être grandement affectés par l'introduction de ce compétiteur. Dans le contexte actuel, où l'on assiste depuis quelques années à un déclin généralisé des stocks de saumon (ICES/CIEM 2008), et où les populations d'omble de fontaine, que l'on croyait très résilientes, commencent à montrer des signes de surexploitation (M. Arvisais, MRNF, comm. pers.), toutes les conditions sont réunies pour que l'introduction de la truite arc-en-ciel ait des impacts importants sur les salmonidés indigènes.

La présente étude avait pour objectif principal de déterminer si la truite arc-en-ciel était en mesure d'envahir avec succès les cours d'eau de l'Est du Québec. L'approche des filtres hiérarchique (Colautti & MacIsaac 2004; Colautti et al. 2004; Kolar & Lodge 2001; Moyle & Marchetti 2006; Quist et al. 2005; Theoharides & Dukes 2007) a été utilisée afin de cibler les divers éléments qui pouvaient favoriser ou freiner le processus d'invasion de la truite arc-en-ciel en fonction des différentes étapes d'une invasion biologique (Theoharides & Dukes 2007; Williamson 1996). Dans le cadre de ce travail, quatre filtres ont été étudiés et ont fait l'objet de chapitres distincts : la pression d'introduction, la résistance abiotique, la résistance biotique et la capacité de dispersion.

6.1. LES FILTRES AUX INVASIONS BIOLOGIQUES : UN VÉRITABLE FREIN POUR LA TRUITE ARC-EN-CIEL?

La survie des individus durant le transit entre l'environnement natif et l'habitat hôte constituait le premier filtre déterminant la capacité d'une espèce à s'introduire. Toutefois, puisqu'au Québec les introductions de truite arc-en-ciel ont été faites volontairement, et donc ont soigneusement été effectuées, cet aspect n'a pas été considéré comme un obstacle. Nous nous sommes plutôt penchés, au deuxième chapitre, sur le filtre associé à la pression d'introduction, ou pression de propagules, qui exige sur un nombre suffisant d'événements d'introduction, de foyers d'introduction et/ou d'individus introduits pour permettre à l'invasion de se produire. Sans avoir fait le survol exhaustif du nombre de spécimens ensemencés dans les divers plans d'eau du sud-ouest de la province au fil des ans, il était néanmoins évident que la pression d'introduction a été très importante au Québec (Figure 1.5). La question était de savoir, parmi toutes ces sources potentielles, laquelle ou lesquelles avaient réellement contribué au processus d'invasion. Nos résultats ont démontré que les populations naturalisées suite aux ensemencements massifs dans le lac Ontario (rivière Ganaraska) et le lac Memphrémagog avaient d'abord permis l'établissement d'une population dans Charlevoix (rivières Du Gouffre et Malbaie), et que de ces trois populations dépend maintenant presque tout le processus de dispersion vers l'aval du système du Fleuve St-Laurent.

Le troisième chapitre traitait de la résistance abiotique, sans doute le principal filtre aux invasions biologiques. En effet, le succès des introductions dépendrait grandement des conditions environnementales prévalant dans le nouvel habitat. Plus les paramètres abiotiques ressemblent aux conditions natales, plus les chances de succès sont grandes (Moyle & Marchetti 2006; Williamson 1996). Fausch et al. (2001) et Fausch (2007) ont démontré que la capacité d'établissement de la truite arc-en-ciel à l'échelle mondiale était particulièrement affectée par le régime hydrologique, surtout par les périodes de crue. Dans son aire de distribution d'origine, c'est durant l'hiver que se produisent les crues les plus importantes. Or au Québec, les inondations surviennent principalement au printemps, durant la période de reproduction de la truite arc-en-ciel. La concordance entre les dates de crues et d'émergence expliquerait l'échec de plusieurs introductions (Fausch et al. 2001). Nous avons voulu savoir si ce paramètre, ou d'autres conditions abiotiques, influençaient l'occurrence de la truite arc-en-ciel dans les rivières de l'Est du Québec. Si la date de la plus forte crue semblait avoir une certaine influence, de même que la température printanière et estivale, c'est la présence de tributaires qui s'est avérée être le facteur le plus important. Ces cours d'eau secondaires, en présentant des débits moins forts et moins variables, pourraient fournir un refuge hydrique pour la truite arc-en-ciel, protégeant la progéniture des crues printanières importantes.

La faune indigène, que ce soit en termes de compétition, de prédation, de parasitisme, de richesse spécifique ou de disponibilité de niches, est considérée comme un troisième filtre aux invasions biologiques. Au quatrième chapitre, nous avons voulu tester l'hypothèse selon laquelle la présence de deux espèces apparentées à la truite arc-en-ciel, soit le saumon atlantique et l'omble de fontaine, nuisait à son établissement en exerçant une forte pression de compétition au stade juvénile. Nos résultats ont démontré que si les salmonidés indigènes étaient en mesure d'offrir une certaine forme de résistance face à la truite arc-en-ciel, ce serait principalement à une grande échelle spatiale (au niveau de la rivière entière). À plus fine échelle, non seulement la truite arc-en-ciel maintient un taux de croissance supérieur à ses deux compétiteurs, mais en plus, lorsqu'elle se trouve en sympatrie avec le saumon et/ou l'omble, elle les force à utiliser un habitat moins optimal et à partager plus intensément les ressources, et ce, même si on ne la retrouve qu'à de faibles densités.

Le dernier filtre aux invasions biologiques, qui fut l'objet du cinquième chapitre, est la capacité de l'espèce à se disperser. Comme chez plusieurs salmonidés, la truite arc-en-ciel présente deux phénotypes distincts : la résidence en eau douce et l'anadromie, c'est-à-dire un cycle de vie impliquant une migration vers l'eau salée durant la période de croissance. Ce dernier mode de vie pourrait permettre à la truite arc-en-ciel d'accroître ses populations par une fécondité plus élevée (en raison d'une plus grande taille des femelles), et de se diffuser efficacement dans le nouvel environnement via les migrations, parfois sur de longues distances, entre l'eau douce et l'eau salée. Or, selon la littérature, il n'y aurait eu qu'une seule population introduite de truite arc-en-ciel ayant développé un contingent anadrome (en Patagonie, Pascual et al. 2001; Riva-Rossi et al. 2004). Nous avons néanmoins testé l'hypothèse selon laquelle la dispersion de la truite arc-en-ciel vers l'est de la province était assurée par des individus anadromes. Tel que prédit, nous avons observé une augmentation de la proportion d'individus anadromes et/ou issus d'une mère anadrome le long d'un gradient ouest-est, illustrant la contribution de ce mode de vie au processus de dispersion de l'espèce. Dans les rivières Malbaie et Du Gouffre toutefois, là où l'espèce se reproduit depuis plusieurs années, le phénotype résident était prépondérant.

En résumé, il semble donc que parmi les quatre filtres étudiés dans le cadre de ce projet de recherche, aucun n'est en mesure d'empêcher l'invasion des rivières de l'Est du Québec par la truite arc-en-ciel : 1) les programmes d'ensemencement intensifs ont permis la naturalisation de populations qui aujourd'hui constituent des sources importantes de migrants, 2) la présence de tributaires dans les rivières à saumon semble diminuer l'impact négatif des crues printanières sur la capacité de colonisation de la truite arc-en-ciel, 3) les habilités compétitrices de la truite arc-en-ciel lui permettent de surpasser la résistance exercée par le saumon atlantique et l'omble de fontaine, et 4) la présence d'individus anadromes assure la propagation de l'espèce.

6.2. VITESSE DE L'INVASION ET EXISTENCE DE POPULATIONS NON DÉTECTÉES

Étant donné l'effort considérable déployé pour introduire la truite arc-en-ciel dans les différentes régions de la portion sud-ouest du Québec et ce, depuis plusieurs décennies, on aurait pu s'attendre à ce que le processus d'invasion ait été plus rapide et que le nombre de populations établies aient été plus considérable. C'est d'ailleurs ce qui a fait croire à certains qu'il n'y avait pas d'invasion du tout.

Peu importe l'espèce, il est commun d'observer un délai entre le moment de l'introduction et la propagation à grande échelle d'une espèce exotique (Fausch 2007; Mooney & Cleland 2001). L'effet de décalage peut être le résultat d'une augmentation normale de la taille et de la distribution d'une population, d'une période d'adaptation au nouvel environnement ou d'un effet de Allee.

Si on regarde plus attentivement l'évolution du processus d'invasion de la truite arc-en-ciel dans les eaux de l'Est du Québec, on constatera qu'en réalité, ce ne fut pas si lent. On se rappellera d'abord que la toute première introduction au Québec a eu lieu il y a plus d'un siècle, soit en 1893-94 (MacCrimmon 1971). Cependant, l'efficacité des programmes d'ensemencements intensifs n'a réellement été observée que vers 1975 (Dumont 1991; Mongeau et al. 1980a; Mongeau et al. 1980b). Moins d'une décennie s'était écoulée qu'on détectait de la reproduction dans les rivières Malbaie (1982) et Du Gouffre (1984) (P. Dulude, Canards Illimités Canada, comm. pers.). À peine quelques années plus tard, Dumont et al. (1988) dressaient le portrait provincial de la situation : la présence de la truite arc-en-ciel avaient été signalée dans 17 rivières situées en dehors du zonage piscicole où son ensemencement est permis. Aujourd'hui, on en dénombre une cinquantaine, la majorité ayant été identifiées entre 2006 et 2008 dans le cadre de ce projet de recherche, grâce notamment à une campagne de sensibilisation menée auprès des pêcheurs sportifs[6]. Le nombre de captures par rivière a par ailleurs fortement augmenté dans certains cas. De plus, entre 2006 et 2010, des événements de reproduction ont été détectés dans de nouvelles rivières, au rythme d'une par année (Les Méchins, Matane et Tortue, auxquelles s'ajoutent maintenant les rivières Sainte-Anne et Nouvelle en Gaspésie, de même que la rivière Jean-Noël dans Charlevoix). Et c'est sans compter les autres populations établies, mais non détectées à ce jour. Dans certaines rivières de l'Est du Québec où la truite arc-en-ciel n'est pas reconnue pour se reproduire, nous avons en effet identifié plusieurs spécimens dont l'origine génétique n'a pu être déterminée (Chapitre 2) et/ou dont la croissance s'est effectuée uniquement en eau douce (Chapitre 5). Ces deux éléments appuient l'hypothèse voulant que d'autres rivières supportent une reproduction naturelle de l'espèce exotique, mais qui n'aurait pas encore été détectée.

En résumé, il aura donc fallu 34 ans seulement (entre 1975 et 2009) à la truite arc-en-ciel pour s'introduire dans une cinquantaine de rivières et s'établir dans une dizaine d'entre elles (en supposant l'existence d'au moins deux populations non encore identifiées). Ce qui signifie *grosso modo* qu'à chaque 3½ ans, cinq nouvelles rivières ont été visitées par

---

[6] En 2010, une truite arc-en-ciel a été enregistrée dans la rivière Sainte-Marguerite, qui se déverse dans la rivière Saguenay. Il s'agit de la première mention de cette espèce dans la région du Saguenay-Lac-Saint-Jean.

l'espèce, dont une supporte desormais une nouvelle population. Vu sous cet angle, il est désormais difficile d'affirmer la quasi-inexistence d'une invasion de la truite arc-en-ciel!

Il aura sans doute fallu quelques années avant que ne débute et s'accélère le processus d'invasion comme tel, pour plusieurs des raisons mentionnées précédemment. Toutefois, il est fort probable qu'une grande partie de la faute soit imputable à notre méconnaissance. En effet, au stade juvénile, la truite arc-en-ciel ressemble à s'y méprendre aux jeunes saumons et ombles, même pour des yeux avertis. De plus, la truite arc-en-ciel anadrome peut être facilement confondue avec un saumon adulte. Il y a donc fort à parier que plusieurs spécimens de truite arc-en-ciel n'ont pas été détectés en raison d'une mauvaise identification de la part des utilisateurs et gestionnaires de la ressource. Et il est d'autant plus facile de passer à côté si l'on ne s'attend pas à la voir là! De plus, les populations récentes ne sont pas aisées à détecter puisque leurs densités sont faibles et qu'elles semblent principalement confinées dans des cours d'eau secondaires.

6.3. À L'HEURE DES CHANGEMENTS CLIMATIQUES

Avec le réchauffement climatique actuel, on peut s'attendre à une augmentation de la température des eaux parallèlement à celle de l'air au cours des prochaines années (Québec 2000). Bien qu'étant une espèce d'eau froide comme les autres membres de la famille des salmonidés, la truite arc-en-ciel est en mesure de tolérer des températures plus élevées que ses cousins québécois (Boughton et al. 2007; Cunjak & Green 1986; Elliott & Hurley 1997; Nelitz et al. 2007; Scott & Crossman 1974). Le réchauffement du climat pourrait donc affecter le processus d'invasion de la truite arc-en-ciel dans l'Est de la province (Rahel et al. 2008). Il s'agit d'un aspect de la problématique que nous avons malheureusement peu abordé dans le cadre de ce projet. Avec une augmentation de la température des rivières, on peut s'attendre à ce que les rivières deviennent plus attrayantes pour la truite arc-en-ciel. C'est d'ailleurs un des facteurs abiotiques qui a été identifié dans le troisième chapitre pour expliquer la présence de l'espèce exotique dans certaines rivières. De plus, la température moyenne des rivières à saumon du Québec se situant actuellement légèrement en deçà de la température optimale pour la truite arc-en-ciel juvénile (Burgner et al. 1992 et voir Chapitre 3), un réchauffement du climat pourrait entraîner une augmentation des performances de l'espèce, tant en termes de croissance, de survie, que d'habilités compétitrices. Ceci, conjugué à une diminution de la performance des espèces indigènes, pourrait non seulement accentuer l'impact négatif de la compétition interspécifique sur les communautés natives, mais également permettre à la truite arc-en-ciel de gagner du terrain. Il a en effet été suggéré que l'invasion des rivières au sud des Appalaches par la truite arc-en-ciel avait été facilitée par le recul des populations natives d'omble de fontaine, qui présentaient, indépendamment de l'arrivée de l'envahisseur, un faible succès reproducteur (Clark & Rose 1997). Ainsi, si nos populations indigènes déclinent en raison du réchauffement climatique, la truite arc-en-ciel s'en verra doublement avantagée.

En plus de la hausse des températures, on peut également s'attendre à une modification du régime de crues. Des hivers plus doux et des printemps plus hâtifs pourraient en effet entraîner un déplacement de la période de crues plus tôt dans l'année. Étant donné que la période de reproduction de la truite arc-en-ciel au Québec a lieu au printemps, une telle modification du régime hydrologique pourrait améliorer la survie des œufs et des alevins qui pour l'heure, semblent souffrir du lessivage des nids au printemps (Fausch et al. 2001).

6.4. RECOMMANDATIONS AUX GESTIONNAIRES

Plusieurs mesures peuvent être entreprises pour contrer l'invasion des rivières de l'Est du Québec par la truite arc-en-ciel. Ces mesures visent essentiellement deux objectifs : 1) empêcher l'établissement de nouvelles populations et 2) réduire, voire éliminer, celles déjà existantes.

6.4.1. Empêcher l'établissement de populations

Le meilleur moyen pour éviter que la truite arc-en-ciel ne s'établisse dans une rivière est d'empêcher son entrée dans le cours d'eau. Il peut s'agir de bloquer physiquement l'accès de la rivière à l'envahisseur, ou de diminuer le nombre de migrants qui pourraient éventuellement accéder à la rivière.

L'utilisation d'une barrière à la migration, jumelée à une passe migratoire, constitue une méthode efficace (Fausch et al. 2009; Peterson et al. 2008), quoique onéreuse, pour empêcher la truite arc-en-ciel d'entrer dans une rivière, surtout lorsqu'elle est située à l'embouchure des rivières. Mais encore faut-il que son fonctionnement (installation et surveillance) couvre l'ensemble de la période où la truite anadrome est susceptible de migrer en eau douce. Dans le cadre de nos campagnes d'échantillonnage (2006 et 2007), des captures ont été rapportées à l'embouchure des rivières entre la mi-mai et la fin septembre. Il faut également que le personnel chargé de permettre le passage des autres poissons vers l'amont soit en mesure d'identifier correctement l'espèce exotique.

Pour réduire le nombre de migrants « à la recherche » d'une rivière, il faut s'attaquer à la source du problème, c'est-à-dire les ensemencements et les populations naturalisées en amont du Fleuve Saint-Laurent. Au Québec, la quasi-totalité des ensemencements de truite arc-en-ciel sont faits avec des femelles stériles (triploïdes) (R. Morin, MAPAQ, comm. pers.). Seul le MRNF et quelques pisciculteurs privés (pour les besoins du MRNF) produisent encore des lots fertiles. La première étape serait donc d'obliger l'utilisation d'individus stériles pour tous les ensemencements, afin de limiter les risques de reproduction. Mais même ainsi, ces risques ne sont pas inexistants puisque jusqu'à 15% des individus peuvent en réalité s'avérer fertiles (R. Morin, MAPAQ, comm. pers.). De plus, bien qu'incapables de se reproduire, les truites stériles peuvent néanmoins compétitionner avec les individus sauvages pour la nourriture, les habitats optimaux et les sites de fraie (surtout les mâles) (Johnson et al. 1986). Ainsi, étant donné les risques écologiques associés à cette pratique, son utilisation ne devrait être que transitoire (Fausch 2007). À long terme, il serait en effet préférable de privilégier l'ensemencement d'espèces indigènes, surtout lorsqu'il s'agit de mettre en valeur la pêche sportive auprès de notre relève québécoise, et de restaurer les plans d'eau où la truite arc-en-ciel est utilisée en remplacement de l'omble de fontaine, dont la survie est compromise par la dégradation de l'habitat.

Les populations des lacs Ontario et Memphrémagog, qui sont vraisemblablement à l'origine de l'invasion de la truite arc-en-ciel dans l'Est du Québec, sont encore aujourd'hui supportées par des ensemencements menés par nos gouvernements voisins. Il serait donc pertinent que le MRNF entreprenne une action concertée avec ses homologues ontariens et états-uniens afin de réduire, ou mieux encore d'arrêter, les déversements de truite arc-en-ciel fertiles dans nos plans d'eau communs. Heureusement, il semble déjà y avoir une volonté en ce sens. Afin de permettre le rétablissement du saumon atlantique (ouananiche), on envisagerait en effet l'arrêt des ensemencements de salmonidés exotiques dans le lac Ontario (R. Bobrowski, OMNR, comm. pers.). Et suite aux résultats obtenus dans le cadre de cette étude, l'État du Vermont songerait à utiliser des lots stériles pour l'ensemencement du lac Memphrémagog (L. Gerardi, Vermont Fish and Wildlife Department, comm. pers.).

6.4.2. Réduire les populations établies

Les quelques populations déjà établies peuvent contribuer substantiellement au processus d'invasion de la truite arc-en-ciel, comme c'est le cas pour la population établie depuis les années '80 dans Charlevoix (Malbaie et Du Gouffre). Il convient donc de réduire au maximum l'abondance de ces populations. Une méthode assez simple pour atteindre cet objectif consisterait à augmenter le prélèvement. Pour ce faire, certaines mesures réglementaires, comme l'augmentation ou l'élimination de la limite de prise et de possession, ou encore l'interdiction de la remise à l'eau, pourraient être envisagées par le MRNF. Dans le cas où les populations sont encore petites et restreintes à des secteurs particuliers de rivières, il pourrait également y avoir du retrait massif par pêche électrique (Moore et al. 1986). Pour les populations bien établies et répandues sur l'ensemble du cours d'eau, l'élimination complète n'est probablement pas possible, mais les densités pourraient en être fortement réduites (Finlayson et al. 2005; Moore et al. 1986; Peterson et al. 2008). Il serait également possible de réduire les effectifs de truite arc-en-ciel en organisant des pêches (sportives) ciblées sur cette espèce.

6.4.3. Travail de sensibilisation

En plus d'agir directement sur l'espèce envahissante, il faut parallèlement impliquer la population (Cambray 2003a, b). Il est en effet primordial que les pêcheurs et les gestionnaires soient sensibilisés à la problématique, car ce sont eux qui se retrouvent sur le terrain, en première ligne. La détection de l'espèce passe par leur vigilance, ils doivent donc être sensibilisés au fait que la truite arc-en-ciel peut être présente dans « leur(s) » rivière(s), qu'il s'agit d'une espèce introduite et qu'elle peut avoir un impact négatif sur les autres espèces. On doit leur indiquer comment l'identifier adéquatement et quoi faire s'ils en observent ou en capturent une. L'enregistrement obligatoire de cette espèce, dans les rivières à saumon par exemple, serait par ailleurs un excellent moyen pour le MRNF de suivre l'avancement de sa dispersion, de statuer sur l'état des populations et d'identifier celles nouvellement établies. En plus de permettre de dresser un meilleur portrait de la situation dans l'Est du Québec, l'implication des utilisateurs de la ressource à cette problématique pourrait permettre de réduire rapidement les abondances (par du retrait volontaire), de faciliter l'acceptation de certaines mesures réglementaires, notamment l'arrêt des ensemencements, et même de réduire (le cas échéant) ou prévenir les déversements illégaux.

6.5. ORIGINALITÉ DE L'ÉTUDE

De très nombreuses études se sont intéressées à l'invasion de la truite arc-en-ciel dans plusieurs régions du globe, au niveau de populations bien établies. Un aspect original de la présente étude était que dans le cas de l'Est du Québec, on étudiait un processus d'invasion qui était non seulement encore en cours, mais surtout qui n'en était qu'à ses débuts. Les mentions de captures étaient donc incomplètes pour certaines régions et certaines périodes, alors que les populations établies étaient peu nombreuses, et leur abondance relativement faible. Certains diront que c'est une chance pour les espèces indigènes. Effectivement. Mais cela peut s'avérer un véritable problème lorsqu'on veut l'étudier! Il n'était toutefois pas envisageable d'attendre que les effectifs augmentent, que la situation se détériore encore davantage, pour mener à bien cette étude. Nous avons donc été obligés de composer avec des approches indirectes ou non conventionnelles pour répondre à certaines questions (ex. Chapitres 3 et 4).

Une autre particularité de ce projet de recherche fut certainement la diversité des méthodes d'analyse utilisées pour répondre à l'ensemble de nos objectifs. À notre connaissance, aucune étude n'avait encore employé simultanément des analyses génétiques, des modélisations, des études d'utilisation d'habitat et l'otolithométrie (microchimie, lectures d'âge et rétro-calculs) pour analyser les différents aspects d'une invasion biologique.

6.6. ORIENTATIONS FUTURES

Advenant que le processus d'invasion de la truite arc-en-ciel se poursuive malgré les actions entreprises pour l'enrayer, les populations établies devraient s'accroître en nombre et en densité. En plus de continuer à faire le suivi des captures, il serait pertinent de dresser un portrait génétique plus complet de la situation, en augmentant le nombre d'individus génotypés par rivière, le nombre de rivières à l'étude et le nombre de populations sources. En plus d'obtenir un portrait plus complet des voies de colonisation, ceci permettrait notamment d'identifier la présence d'une structuration génétique régionale. Il serait également intéressant de vérifier s'il existe une telle structure à l'intérieur même des rivières.

Avec l'augmentation des effectifs, on peut s'attendre à ce que la pression de compétition s'intensifie entre les juvéniles de truite, de saumon et d'omble. On pourrait alors étudier l'impact de la présence de l'espèce exotique à des densités plus élevées, sur une plus grande échelle temporelle et sur davantage de rivières. En plus de regarder l'utilisation de l'habitat, on pourrait entre autre évaluer si la présence de l'envahisseur a un effet sur les taux de croissance des espèces indigènes.

On pourrait donc, de façon générale, pousser encore plus loin les analyses qui ont été réalisées dans le cadre de ce projet. Mais on pourrait également s'attaquer à des aspects complètement différents ou qui n'ont été que brièvement abordés dans cette thèse. Dans quelle proportion les phénotypes sont-ils hérités? Quelle est la contribution du père à ce niveau? Qu'est-ce qui incite certains individus à quitter leur rivière natale pour aller coloniser d'autres cours d'eau? Comment s'effectue la migration entre la rivière natale et celle où l'individu décide de se reproduire : directement ou avec escales, au hasard ou dirigé? Qu'est-ce qui détermine exactement le moment de la migration vers la mer, l'âge ou la taille? La fécondité des femelles et le succès reproducteur sont-ils comparables à ce qui prévaut dans l'aire de distribution d'origine? Est-ce que la truite arc-en-ciel au Québec fraie essentiellement au printemps ou y a-t-il plusieurs périodes de reproduction? Bref, comme dans tout bon projet de recherche, nous avons été en mesure de répondre à certaines questions, mais se faisant, plusieurs autres ont été soulevées.

6.7. MOT DE LA FIN

S'il est une chose que l'on doit retenir, c'est que toutes nos actions de gestion peuvent avoir des conséquences. L'introduction volontaire d'espèces exotiques, comme ce fut le cas pour la truite arc-en-ciel au Québec et un peu partout dans le monde (Cambray 2003b; MacCrimmon 1971), est une pratique des plus courantes. Si les bénéfices socio-économiques qui en découlent sont généralement non négligeables, il n'en demeure pas moins que les conséquences sur les écosystèmes envahis peuvent être très importantes (Ryder & Kerr 1982). Il fut une époque où notre savoir ne nous permettait pas de mesurer toute l'ampleur de ces conséquences. Mais aujourd'hui, avec l'avancement de nos connaissances, la poursuite de telles activités ne saurait être pleinement justifiée, surtout lorsque des impacts négatifs évidents sont à prévoir. En faune aquatique, il serait grand temps que nous cessions de ne considérer que nos propres intérêts de pêcheurs, pour réaliser toute l'importance de préserver l'intégrité écologique de nos plans d'eau (Cambray 2003b). Si, de par notre ignorance, nous avons fait des erreurs dans le passé, notamment avec l'ensemencement d'espèces exotiques, nous avons désormais le devoir de les réparer, autant que faire se peut…

Bibliographie

Aljanabi, S.M. & Martinez, I. 1997. Universal and rapid salt-extraction of high quality genomic DNA for PCR-based techniques. Nucleic Acids Research 25: 4692-4693.

Ayllon, F., Davaine, P., Beall, E. & Garcia-Vazquez, E. 2006. Dispersal and rapid evolution in brown trout colonizing virgin Subantarctic ecosystems. Journal of Evolutionary Biology 19: 1352-1358.

Baxter, C.V., Fausch, K.D., Murakami, M. & Chapman, P.L. 2007. Invading rainbow trout ursurp a terrestrial prey subsidy from native charr and reduce their growth and abundance. Oecologia 153: 461-470.

Beecher, H.A., Johnson, T.H. & Carleton, J.P. 1993. Predicting microdistributions of steelhead (*Oncorhynchus mykiss*) parr from depth and velocity preference criteria: Test of an assumption of the Instream Flow Incremental Methodology. Canadian Journal of Fisheries and Aquatic Sciences 50: 2380-2387.

Begon, M., Harper, J.L. & Townsend, C.R. 1996. Ecology. Individuals populations and communities: 3rd ed, Blackwell Science. 1068 pp.

Belkhir, K., Borsa, P., Chikhi, L., Raufaste, N. & Bonhomme, F. 2004. GENETIX (version 4.05): logiciel sous Window TM pour la génétique des populations. Laboratoire Génome, Populations, Interactions, CNR SUMR 5000, Université de Montpellier II, Montepellier, France.

Benjamin, J.R., Dunham, J.B. & Dare, M.R. 2007. Invasion by nonnative brook trout in Panther Creek, Idaho: roles of local habitat quality, biotic resistance and connectivity to source habitats. Transactions of the American Fisheries Society 136: 875-888.

Blanchet, S. 2007. Interactions compétitives entre le saumon atlantique et la truite arc-en-ciel : aspects écologiques, sélectifs et adaptatifs. PhD Thesis, Département de Biologie. Université Laval, Québec (Québec), Canada.

Blanchet, S., Loot, G., Grenouillet, G. & Brosse, S. 2007. Competitive interactions between native and exotic salmonids: a combined field and laboratory demonstration. Ecology of Freshwater Fish 16: 133-143.

Bøhn, T., Amundsen, P.-A. & Sparrow, A. 2008. Competitive exclusion after invasion? Biological Invasions 10: 359-368.

Boughton, D.A., Gibson, M., Yedor, R. & Kelley, E. 2007. Stream temperature and the potential growth and survival of juvenile *Oncorhynchus mykiss* in a southern California creek. Freshwater Biology 52: 1353-1364.

Bouthillier, L. 1995. La pêche aux salmonidés dans les eaux de la plaine de Montréal : un troisième bilan par le biais des carnets de pêcheurs. Québec, Ministère de l'Environnement et de la Faune du Québec, Service de l'aménagement et de l'exploitation de la faune. Montréal, x + 37 pp.

Boyer, M.C., Muhlfeld, C.C. & Allendorf, F.W. 2008. Rainbow trout (*Oncorhynchus mykiss*) invasion and the spread of hybridization with native westslope cutthroat trout (*Oncorhynchus clarkii lewisi*). Canadian Journal of Fisheries and Aquatic Sciences 65: 658-669.

Brisson-Bonenfant, C. 2006. Stratégie conditionnelle et migration chez le saumon atlantique (*Salmo salar*) juvénile. M.Sc. Thesis. Faculté des Sciences et de Génie, Département de biologie, Université Laval, Québec. 94 pp.

Brockman, H.J. & Taborsky, M. 2008. Alternative reproductive tactics and the evolution of alternative allocation phenotypes. In: Oliveira, R.F., Taborsky, M. & Brockman, H.J., eds. Alternative Reproductive tactics: an integrative approach. Cambridge: Cambridge University Press, pp. 25-51.

Brown, J.E. & Stepien, C.A. 2009. Invasion genetics of the Eurasian round goby in North America: tracing sources and spread patterns. Molecular Ecology 18: 64-79.

Bruno, J.F., Stachowicz, J.J. & Bertness, M.D. 2003. Inclusion of facilitation into ecological theory. TRENDS in Ecology and Evolution 18: 119-125.

Burgner, R.L., Light, J.T., Margolis, L., Okazaki, T., Tautz, A. & Ito, S. 1992. Distribution and origins of steelhead trout (*Oncorhynchus mykiss*) in offshore waters of the North Pacific ocean. International North Pacific Fisheries Commission. Bulletin #51. 73 pp.

Buria, L., Albarino, R., Villanueva, V.D., Modenutti, B. & Balseiro, E. 2007. Impact of exotic rainbow trout on the benthic macroinvertebrate community from Andean-Patagonian headwater streams. Fundamental and Applied Limnology 168: 145-154.

Busack, C.A. & Gall, G.A.E. 1981. Introgressive hybridization in populations of Paiute cutthroat trout (*Salmo clarki seleniris*). Canadian Journal of Fisheries and Aquatic Sciences 38: 939-951.

Busby, P.J., Wainwright, T.C., Bryant, G.J., Lierheimer, L.J., Waples, R.S., Waknitz, F.W. & Lagomarsino, I.V. 1996. Status review of West Coast steelhead from Washington, Idaho, Oregon and California. NOAA Tech. Memo., NMFS-NWFSC-27. U.S. Dept. of Commerce, 261 pp.

Byström, P., Karlsson, J., Nilsson, P., Kooten, T.V., Ask, J. & Olofsson, F. 2007. Substitution of top predators: effect of pike invasion in a subarctic lake. Freshwater Biology 52: 1271-1280.

Cambray, J.A. 2003a. The global impact of alien trout species - a review; with reference to their impact in South Africa. African Journal of Aquatic Science 28: 61-67.

Cambray, J.A. 2003b. Impact on indigenous species biodiversity caused by the globalisation of alien recreational freshwater fisheries. Hydrobiologia 500: 217-230.

Casal, C.M.V. 2006. Global documentation of fish introductions: the growing crisis and recommendations for action. Biological Invasions 8: 3-11.

Chadwick, E.M.P. & Bruce, W.J. 1981. Range extension of steelhead trout (*Salmo gairdneri*) in Newfoundland. Naturaliste Canadien 108: 301-303.

Clark, M.E. & Rose, K.A. 1997. Factors affecting competitive dominance of rainbow trout over brook trout in Southern Appalachian streams: implications of an individual-based model. Transactions of the American Fisheries Society 126: 1-20.

Coghlan Jr, S.M., Cain, G.R. & Ringler, N.H. 2007. Prey selection of subyearling Atlantic salmon and rainbow trout coexisting in a natural stream. Journal of Freshwater Ecology 22: 591-607.

Colautti, R.I., Grigorovich, I.A. & MacIsaac, H.J. 2006. Propagule pressure: a null model for biological invasions. Biological Invasions 8: 1023-1037.

Colautti, R.I. & MacIsaac, H.J. 2004. A neutral terminology to define 'invasive' species. Diversity and Distributions 10: 135-141.

Colautti, R.I., Ricciardi, A., Grigorovich, I.A. & MacIsaac, H.J. 2004. Is invasion success explained by the enemy release hypothesis? Ecology Letters 7: 721-733.

Copp, G.H., Bianco, P.G., Bogutskaya, N.G., Eros, T., Falka, I., Ferreira, M.T., Fox, M.G., Freyhof, J., Gozlan, R.E., Grabowska, J., Kovac, V., Moreno-Amich, R., Naseka, A.M., Penaz, M., Povz, M., Przybylski, M., Robillard, M., Russell, I.C., Stakenas, S., Sumer, S., Vila-Gispert, A. & Wiesner, C. 2005. To be, or not to be, a non-native freshwater fish? Journal of Applied Ichthyology 21: 242-262.

Copp, G.H., Templeton, M. & Gozlan, R.E. 2007. Propagule pressure and the invasion risks of non-native freshwater fishes: a case study in England. Journal of Fish Biology 71 (Supp. D): 148-159.

Corander, J., Waldmann, P. & Sillanpaa, M.J. 2003. Bayesian analysis of genetic differentiation between 24 populations. Genetics 163: 367-374.

Courtenay, W.R. & Taylor, J.N. Year. The exotic ichthyofauna of the contiguous United States with preliminary observations on intranational transplant. Proceedings of the Symposium on stock enhancement in the management of freshwater fish EIFAC Technical Paper #42, Volume 2 : Introductions and Transplantations: 466-487.

Crawford, N.G. 2009. SMOGD: Software for the Measurement of Genetic Diversity. Molecular Ecology Resources. Submitted.

Crossman, E.J. 1991. Introduced freshwater fishes: A review of the North American perspective with emphasis on Canada. Canadian Journal of Fisheries and Aquatic Sciences 48 (Suppl. 1): 46-57.

Crowl, T.A., Townsend, C.R. & McIntosh, A.R. 1992. The impact of introduced brown and rainbow trout on native fish: the case of Australasia. Reviews in Fish Biology and Fisheries 2: 217-241.

Cunjak, R.A. & Green, J.M. 1983. Habitat utilization by brook char (*Salvelinus fontinalis*) and rainbow trout (*Salmo gairdneri*) in Newfoundland streams. Canadian Journal of Zoology 61: 1214-1219.

Cunjak, R.A. & Green, J.M. 1986. Influence of water temperature on behavioral interactions between juvenile brook charr, *Salvelinus fontinalis*, and rainbow trout, *Salmo gairdneri*. Canadian Journal of Zoology 64: 1288-1291.

Currie, R.J., Bennett, A.W. & Beitinger, T.L. 1998. Critical thermal minima and maxima of three freshwater game fish species acclimated to constant temperature. Environnemental Biology of Fishes, 51, 187-200. doi:10.1023/A:1007447417546

Daverat, F., Limburg, K.E., Thibault, I., Shiao, J.-C., Dodson, J.J., Caron, F., Tzeng, W.-N., Iizuka, Y. & Wickström, H. 2006. Phenotypic plasticity of habitat use by three temperate eel species *Anguilla anguilla*, *A. japonica* and *A. rostrata*. Marine Ecology Progress Series 308: 231-241.

Davis, M.A., Grime, J.P. & Thompson, K. 2000. Fluctuating resources in plant communities: a general theory of invasibility. Journal of ecology 88: 528-534.

Dextrase, A.J. & Mandrak, N.E. 2006. Impacts of alien invasive species on freshwater fauna at risk in Canada. Biological Invasions 8: 13-24.

DMTI Spatial. 2005. CanMap Water V2005.3. [computer file]. Markham, Ontario: DMTI Spatial Inc. Available at www.dmtispatial.com.

Docker, M.F. & Heath, D.D. 2003. Genetic comparison between sympatric anadromous steelhead and freshwater resident rainbow trout in British Columbia, Canada. Conservation Genetics 4: 227-231.

Dodson, J.J. 2000. Les risques écologiques potentiels que poserait la culture en mer et l'introduction accidentelle de truites arc-en-ciel dans les rivières à saumon du Québec (particulièrement celles de la Gaspésie). Avis d'expert pour la Société de la faune et des parcs du Québec- Vice-présidence au développement et à l'aménagement de la faune. 36 pp.

Donohoe, C.J., Adams, P.B. & Royer, C.F. 2008. Influence of water chemistry and migratory distance on ability to distinguish progeny of sympatric resident and anadromous rainbow trout (*Oncorhynchus mykiss*). Canadian Journal of Fisheries and Aquatic Sciences 65: 1160-1175.

Drake, M.T. & Taylor, W.W. 1996. Influence of spring and summer water temperature on brook charr, *Salvelinus fontinalis*, growth and age structure in the Ford River, Michigan. Environmental Biology of Fishes 45: 41-51.

Dubé, P., Blanc, J.-M., Chouinard, M. & Noüe, J.d.l. 1991. Triploidy induced by heat shock in brook trout (*Salvelinus fontinalis*). Aquaculture 92: 305-311.

DuBois, R.B., Plaster, S.D. & Rasmussen, P.W. 1989. Fecundity of spring- and fall-run steelhead from two western Lake Superior tributaries. Transactions of the American Fisheries Society 118: 311-316.

Duchesne, P. & Turgeon, J. 2009. FLOCK: a method for quick mapping of admixture without source samples. Molecular Ecology Resources: published online.

Dumont, P. 1991. Les ensemencements de maskinongé, de truite brune et de truite arc-en-ciel dans les eaux de la plaine de Montréal. Proceedings of the Conseil de l'aquiculture et des pêches du Québec. Colloque sur l'ensemencement: 30-42.

Dumont, P., Bergeron, J.F., Dulude, P., Mailhot, Y., Rouleau, A., Ouellet, G. & Lebel, J.-P. 1988. Introduced salmonids: where are they going in Quebec watersheds of the Saint-Laurent River? Fisheries 13: 9-17.

Elliott, J.M. & Hurley, M.A. 1997. A functional model for maximum growth of Altantic salmon parr, *Salmo salar*, from two populations in northwest England. Fonctional Ecology 11: 592-603.

Elton, C.S. 1958. The ecology of invasions by animals and plants. The University of Chicago Press. 181 pp.

Englund, R.A. & Polhemus, D.A. 2001. Evaluating the effects of introduced rainbow trout (*Oncorhynchus mykiss*) on native stream insects on Kauai Island, Hawaii. Journal of Insect Conservation 5: 265-281.

Fausch, K.D. 1988. Tests of competition between native and introduced salmonids in streams: what have we learned? Canadian Journal of Fisheries and Aquatic Sciences 45: 2238-2246.

Fausch, K.D. 1998. Interspecific competition and juvenile Atlantic salmon (*Salmo salar*): on testing effects and evaluating the evidence across scales. Canadian Journal of Fisheries and Aquatic Sciences 55(Suppl.1): 218-231.

Fausch, K.D. 2007. Introduction, establishment and effects of non-native salmonids: considering the risk of rainbow trout invasion in the United Kingdom. Journal of Fish Biology 71 (Supp. D): 1-32.

Fausch, K.D. 2008. A paradox of trout invasions in North America. Biological Invasions 10: 685-701.

Fausch, K.D., Rieman, B.E., Dunham, J.B., Young, M.K. & Peterson, D.P. 2009. Invasion versus isolation: trade-offs in managing native salmonids with barriers to upstream movement. Conservation Biology 23: 859-870.

Fausch, K.D., Taniguchi, Y., Nakano, S., Grossman, G.D. & Townsend, C.R. 2001. Flood disturbance regimes influence rainbow trout invasion success among five Holarctic regions. Ecological Applications 11: 1438-1455.

Felsenstein, J. 2004. PHYLIP (Phylogeny Inference Package) version 3.6. Distributed by the author. Department of Genome Sciences, University of Washington. Seatle.

Finlayson, B., Somer, W., Duffield, D., Propst, D., Mellison, C., Pettengill, T., Sexauer, H., Nesler, T., Gurtin, S., Elliot, J., Partridge, F. & Skaar, D. 2005. Native inland trout restoration on national forests in the Western United States: time for improvement? Fisheries 30: 10-19.

Francis, R.I.C.C. 1990. Back-calculation of fish length: a critical review. Journal of Fish Biology 36: 883-902.

Friedland, K.D., Reddin, D.G. & Kocik, J.F. 1993. Marine survival of North American and European Atlantic salmon: effects of growth and environment. ICES Journal of Marine Science 50: 481-492.

García-Berthou, E. 2007. The characteristics of invasive fishes: what has been learned so far? Journal of Fish Biology 71 (Supp. D): 33-55.

Gard, R. & Flittner, G.A. 1974. Distribution and abundance of fishes in Sagehen Creek, California. Journal of Wildlife Managegement, 38, 347-358.

Garside, E.T. & Tait, J.S. 1958. Preferred temperature of rainbow trout (*Salmo gairdneri* Richardson) and its unusual relationship to acclimation temperature. Canadian Journal of Zoology, 36, 563-567.

Gatz, A.J., Sale, M.J. & Loar, J.M. 1987. Habitat shifts in rainbow trout: competitive influences of brown trout. Oecologia 74: 7-19.

Gibson, R.J. 1978. The behavior of juvenile Atlantic salmon (*Salmo salar*) and brook trout (*Salvelinus fontinalis*) with regard to temperature and to water velocity. Transactions of the American Fisheries Society 107: 703-712.

Gibson, R.J. 1981. Behavioural interactions between coho salmon (*Oncorhynchus kisutch*), Atlantic salmon (*Salmo salar*), brook trout (*Salvelinus fontinalis*) and steelhead trout (*Salmo gairdneri*) at the juvenile fluviatile stages. Canadian Technical Report of Fisheries and Aquatic Sciences : 1029. v + 116 pp.

Gillanders, B.M. 2005. Otolith chemistry to determine movements of diadromous and freshwater fish. Aquatic Living Resources 18: 291-300.

GISD. 2005. Global Invasive Species Database. *Oncorhynchus mykiss*. Available from: http://www.issg.org/database/species/ecology.asp?si=103&fr=1&sts=sss&lang=EN [Accessed 26th August 2009].

Godby, N.A., Rutherford, E.S. & Mason, D.M. 2007. Diet, feeding rate, growth, mortality, and production of juvenile steelhead in a Lake Michigan tributary. North American Journal of Fisheries Management 27: 578-592.

Goren, M. & Galil, B.S. 2005. A review of changes in the fish assemblages of Levantine inland and marine ecosystems following the introduction of non-native fishes. Journal of Applied Ichthyology 21: 364-370.

Goudet, J. 1995. FSTAT (vers. 1.2): a computer program to calculate F-statistics. Journal of Heredity 86: 485-486.

Greig, C. & Banks, M.A. 1999. Five multiplexed microsatellite loci for rapid response run identification of California's endangered winter chinook salmon. Animal genetics 30: 318-320.

Griffiths, R.W., Schloesser, D.W., Leach, J.H. & Kovalak, W.P. 1991. Distribution and dispersal of the zebra mussel (*Dreissena polymorpha*) in the Great Lakes region. Canadian Journal of Fisheries and Aquatic Sciences 48: 1381-1395.

Gross, R., Gum, B., Reiter, R. & Kühn, R. 2004. Genetic introgression between Arctic charr (*Salvelinus alpinus*) and brook trout (*Salvelinus fontinalis*) in Bavarian hatchery stocks inferred from nuclear and mitochondrial DNA markers. Aquaculture International 12: 19-32.

Grover, J.P. 1997. Resource competition. Chapman and Hall Ed. 342 pp.

Guay, J.C., Boisclair, D., Leclerc, M. & Lapointe, M. 2003. Assessment of the transferability of biological habitat models for Atlantic salmon parr (*Salmo salar*). Canadian Journal of Fisheries and Aquatic Sciences 60: 1398-1408.

Gunn, J.S., Harrowfield, I.R., Proctor, C.H. & Thresher, R.E. 1992. Electron microprobe analysis of fish otoliths - evaluation of techniques for studying age and stock discrimination. Journal of Experimental Marine Biology and Ecology 158: 1-36.

Hänfling, B. 2007. Understanding the establishment success of non-indigenous fishes: lessons from population genetics. Journal of Fish Biology 71 (Supp. D): 115-135.

Hansen, L.P. & Quinn, T.P. 1998. The marine phase of the Atlantic salmon (*Salmo salar*) life cycle, with comparisons to Pacific salmon. Canadian Journal of Fisheries and Aquatic Sciences 55 (Suppl. 1): 104-118.

Hansen, L.P. & Windsor, M.L. 2006. Interactions between aquaculture and wild stocks of Atlantic salmon and other diadromous fish species: science and management, challenges and solutions. ICES Journal of Marine Science 63: 1159-1161.

Hasegawa, K. & Maekawa, K. 2006. The effects of introduced salmonids on two native stream-dwelling salmonids through interspecific competition. Journal of Fish Biology 68: 1123-1132.

Hasegawa, K., Yamamoto, T., Murakami, M. & Maekawa, K. 2004. Comparison of competitive ability between native and introduced salmonids: evidence from pairwise contests. Ichthyological Research 51: 191-194.

Hastings, A., Cuddington, K., Davies, K.F., Dugaw, C.J., Elmendorf, S., Freestone, A., Harrison, S., Holland, M., Lambrinos, J., Malvadkar, U., Melbourne, B.A., Moore, K., Taylor, C. & Thomson, D. 2005. The spatial spread of invasions: new developments in theory and evidence. Ecology Letters 8: 91-101.

Hayes, K.R. & Barry, S.C. 2008. Are there any consistent predictors of invasion success? Biological Invasions 10: 483-506.

Hearn, W.E. & Kynard, B.E. 1986. Habitat utilization and behavioral interaction of juvenile Atlantic salmon (*Salmo salar*) and rainbow trout (*S. gairdneri*) in tributaries of the White River of Vermont. Canadian Journal of Fisheries and Aquatic Sciences 43: 1988-1998.

Heath, D.D., Bettles, C.M., Jamieson, S., Stasiak, I. & Docker, M.F. 2008. Genetic differentiation among sympatric migratory and resident life history forms of rainbow trout in British Columbia. Transactions of the American Fisheries Society 137: 1268-1277.

Heath, D.D., Pollard, S. & Herbinger, C. 2001. Genetic structure and relationships among steelhead trout (*Oncorhynchus mykiss*) populations in British Columbia. Heredity 86: 618-627.

Hedger, R.D., Atkinson, P.M., Thibault, I. & Dodson, J.J. 2008. A quantitative approach for classifying fish otolith strontium:calcium sequences into environmental histories. Ecological Informatics 3: 207-217.

Hengeveld, R. 1989. Dynamics of biological invasions: Chapman and Hall Editors. 160 pp.

High, B., Peery, C.A. & Bennett, D.H. 2006. Temporary staging of Columbia River summer steelhead in coolwater areas and its effect on migration rates. Transactions of the American Fisheries Society, *135*, 519-528. doi:10.1577/T04-224.1

Hitt, N.P., Frissell, C.A., Muhlfeld, C.C. & Allendorf, F.W. 2003. Spread of hybridization between native westslope cutthroat trout, *Oncorhynchus clarki lewisi*, and nonnative rainbow trout, *Oncorhynchus mykiss*. Canadian Journal of Fisheries and Aquatic Sciences 60: 1440-1451.

Hornik, K. 2007. The R FAQ, http://CRAN.R-project.org/doc/FAQ/R-FAQ.html, ISBN 3-900051-08-9

Hosmer, D.W. & Lemeshow, S. 1989. Applied logistic regression, Wiley, New York.

Hutchinson, G.E. 1959. Homage to Santa Rosalia or Why are there so many kinds of animals? The American Naturalist 93: 145-159.

ICES/CIEM. 2008. What's happening to Atlantic salmon? http://www.ices.dk.

Jacot Guillarmod, A. 1979. Water weeds in Southern Africa. Aquatic Botany 6: 377-391.

Jeschke, J.M. & Strayer, D.L. 2006. Determinants of vertebrate invasion success in Europe and North America. Global Change Biology 12: 1608-1619.

Jeschke, J.M. & Strayer, D.L. 2008. Are threat status and invasion success two sides of the same coin? Ecography 31: 124-130.

Jessop, B.M., Shiao, J.-C., Iizuka, Y. & Tzeng, W.N. 2002. Migratory behaviour and habitat use by American eels *Anguilla rostrata* as revealed by otolith microchemistry. Marine Ecology Progress Series 233: 217-229.

Jessop, B.M., Shiao, J.C., Iizuka, Y. & Tzeng, W.N. 2004. Variation in the annual growth, by sex and migration history, of silver American eels *Anguilla rostrata*. Marine Ecology Progress Series 272: 231-244.

Jessop, B.M., Shiao, J.C., Iizuka, Y. & Tzeng, W.N. 2008. Prevalence and intensity of occurrence of vaterite inclusions in aragonite otoliths of American eels *Anguilla rostrata*. Aquatic Biology 2: 171-178.

Johnson, J.H. 1980. Production and growth of subyearling Coho salmon, *Oncorhynchus kisutch*, Chinook salmon, *Oncorhynchus tshawytscha*, and steelhead *Salmo gairdneri*, in Orwell Brook, tributary of Salmon River, New York. Fishery Bulletin 78: 549-554.

Johnson, O.W., Dickhoff, W.W. & Utter, F.M. 1986. Comparative growth and development of diploid and triploid Coho Salmon, *Oncorhynchus kisutch*. Aquaculture 57: 329-336.

Jost, L. 2008. G_{ST} and its relatives do not measure differentiation. Molecular Ecology 17: 4015-4026.

Kareiva, P. 1990. Population dynamics in spatially complex environments: theory and data. Philosophical Transactions of the Royal Society of London B 330: 175-190.

Keeley, E.R. 2000. An experimental analysis of territory size in juvenile steelhead trout. Animal Behaviour 59: 477-490.

Kerr, S.J. & Lasenby, T.A. 2000. Rainbow trout stocking in inland lakes and streams: An annoted bibliography and literature review. Fish and Wildlife Branch, Ontario Ministry of Natural Resources, Peterborough, Ontario. 220 pp. + annexes pp.

Kiesecker, J.M., Blaustein, A.R. & Miller, C.L. 2001. Transfer of a pathogen from fish to amphibians. Conservation Biology 15: 1064-1070.

Kimura, M. & Weiss, G.H. 1964. The stepping-stone model of populations structure and the decrease of genetic correlation with distance. Genetics 49: 561-576.

Kohler, C.C. & Courtenay, W.R. 1986. American Fisheries Society position on introduction of aquatic species. Fisheries 11: 39-42.

Kolar, C.S. & Lodge, D.M. 2001. Progress in invasion biology: predicting invaders. Trends in Ecology and Evolution 16: 199-204.

Korsu, K., Huusko, A. & Muotka, T. 2008. Ecology of alien species with special reference to stream salmonids. Boreal Environment Research 13: 43-52.

Kostow, K. 2003. Factors that influence evolutionarily significant unit boundaries and status assessment in a highly polymorphic species, *Oncorhynchus mykiss*, in the Columbia Basin. Information Report #2003-04. Oregon Department of Fish and Wildlife and NOAA Fisheries, 122 pp.

Krueger, C.C. & May, B. 1991. Ecological and genetic effects of salmonid introductions in North America. Canadian Journal of Fisheries and Aquatic Sciences 48 (Suppl. 1): 66-77.

Langella, O. 1999. Populations version 1.2.30 Distributed by the author, CNRS UPR9034, France.

Larson, G.L. & Moore, S.E. 1985. Encroachment of exotic rainbow trout into stream populations of native brook trout in the southern Appalachian Mountains. Transactions of the American Fisheries Society 114: 195-203.

Laurenson, L.B.J. & Hocutt, C.H. 1985. Colonisation theory and invasive biota: the Great Fish River, a case study. Environmental Monitoring and Assessment 6: 71-90.

Laurenson, L.B.J., Hocutt, C.H. & Hecht, T. 1989. An evaluation of the success of invasive fish species of the Great Fish River. Journal of Applied Ichthyology 1: 28–34.

Lecomte, F. & Dodson, J.J. 2004. Role of early life-history constraints and resource polymorphism in the segregation of sympatric populations of an estuarine fish. Evolutionary Ecology Research 6: 631-658.

Lecomte, F. & Dodson, J.J. 2005. Distinguishing trophic and habitat partitioning among sympatric populations of the estuarine fish *Osmerus mordax* Mitchill. Journal of Fish Biology 66: 1601-1623.

Lefler, K., Gál, J. & Demeter, G. 2006. Effect of water temperature on the embryonic development and hatching results of rainbow trout (*Oncorhynchus mykiss*). Magyar Állatorvosok Lapja, 128, 565-569.

Legendre, V., Mongeau, J.-R., Leclerc, J. & Brisebois, J. 1980. Les Salmonidés des eaux de la Plaine de Montréal. 1. Historique, 1534-1977. Ministère du Loisir, de la Chasse et de la Pêche, Service de l'Aménagement et de l'Exploitation de la Faune, Rapport Technique #06-27. 280 pp.

Leprieur, F., Beauchard, O., Blanchet, S., Oberdorff, T. & Brosse, S. 2008. Fish invasion in the world's river systems: When natural processes are blurred by human activities. PLoS Biology 6: 404-410.

Levine, J.M. 2000. Species diversity and biological invasions: relating local process to community pattern. Science 288: 852-854.

Lodge, D.M. 1993. Biological invasions: Lessons for ecology. Trends in Ecology and Evolution 8: 133-137.

Lowe, S., Browne, M., Boudjelas, S. & Poorter, M.D. 2007. 100 Espèces Exotiques Envahissantes parmi les plus néfastes au monde. Une sélection de la Global Invasive Species Database (GISD): Publié par le Groupe de spécialistes des espèces envahissantes (Invasive Species Specialist Group-ISSG), de la Commission de la Sauvegarde des Espèces (CSE) de l'Union Mondiale pour la Nature (UICN). 12 pp.

MacArthur, R. & Levins, R. 1964. Competition, habitat selection, and character displacement in a patchy environment. Zoology 51: 1207-1210.

MacCrimmon, H.R. 1971. World distribution of rainbow trout (*Salmo gairdneri*). Journal of Fisheries and Research Board of Canada 28: 663-704.

MacCrimmon, H.R. & Gots, B.L. 1972. Rainbow trout in the Great Lakes. Ministry of Natural Resources, Ontario. 66 pp.

MacIsaac, H.J., Grigorovich, I.A. & Ricciardi, A. 2001. Reassessment of species invasions concepts: Great Lakes basin as a model. Biological Invasions 3: 405-416.

MacKenzie, D.I., Nichols, J.D., Royle, J.A., Pollock, K.H., Bailey, L.L. & Hines, J.E. 2006. Occupancy estimation and modeling: Inferring patterns and dynamics of species occurrence. Elsevier, San Diego CA.

Magoulick, D.D. & Wilzbach, M.A. 1998. Are native brook charr and introduced rainbow trout differentially adapted to upstream and downstream reaches? Ecology of Freshwater Fish 7: 167-175.

MAPAQ. 2005. Les zones piscicoles du Québec. Agriculture, Pêcheries et Alimentation du Québec, Québec, Canada.

McCann, J.A. 1984. Preface. In: Stauffer, W.R.C.a.J.R., ed. Distribution, Biology, and Management of Exotic Fishes. pp. ix-x.

McLean, J.E., Bentzen, P. & Quinn, T.P. 2003. Differential reproductive success of sympatric, naturally spawning hatchery and wild steelhead trout (*Oncorhynchus mykiss*) through the adult stage. Canadian Journal of Fisheries and Aquatic Sciences 60: 433-440.

McLean, J.E., Bentzen, P. & Quinn, T.P. 2004. Differential reproductive success of sympatric, naturally spawning hatchery and wild steelhead, *Oncorhynchus mykiss*. Environmental Biology of Fishes 69: 359-369.

Mellina, E. & Rasmussen, J.B. 1994. Occurrence of zebra mussel (*Dreissena polymorpha*) in the intertidal region of the St. Lawrence Estuary. Journal of Freshwater Ecology 9: 81-84.

Mitro M.G., Zale A.V. and Rich B.A., 2003. The relation between age-0 rainbow trout (*Oncorhynchus mykiss*) abundance and winter discharge in a regulated river. Canadian Journal of Fisheries and Aquatic Sciences, *60*, 135-139. doi:10.1139/f03-006

Moles, A.T., Gruber, M.A.M. & Bonser, S.P. 2008. A new framework for predicting invasive plant species. Journal of Ecology 96: 13-17.

Molony, B. 2001. Environmental requirements and tolerances of rainbow trout (*Oncorhynchus mykiss*) and brown trout (*Salmo trutta*) with special reference to Western Australia: A review. Fisheries Research Report of Western Australia, n°130.

Mongeau, J.-R. & Brisebois, J. 1982. Ce qu'il advient des truites ensemencées dans les eaux de la plaine de Montréal, d'après les expériences d'étiquetage et de recapture, de 1977 à 1981 inclusivement. Ministère du Loisir, de la Chasse et de la Pêche, Service de l'Aménagement et de l'Exploitation de la Faune. Montréal., 47 pp.

Mongeau, J.-R., Courtemanche, A., Massé, G. & Vincent, B. 1974. Cartes de répartition géographique des espèces de poissons au sud du Québec, d'après les inventaires ichthyologiques effectués de 1963 à 1972. Ministère du Tourisme, de la Chasse et de la Pêche, Province de Québec. Direction de la Chasse et de la Pêche, Service de l'Aménagement de la Faune. Rapport spécial #4. 92 pp.

Mongeau, J.-R., Leclerc, J. & Brisebois, J. 1980a. La répartition géographique des poissons, les ensemencements, la pêche sportive et commerciale, les frayères et la bathymétrie du fleuve Saint-Laurent dans le Bassin de La Prairie et les Rapides de Lachine. Ministère du Loisir, de la Chasse et de la Pêche, Service de l'Aménagement et de l'Exploitation de la Faune. Montréal, 145 pp.

Mongeau, J.-R., Legendre, V., Leclerc, J. & Brisebois, J. 1980b. Les salmonidés des eaux de la plaine de Montréal. 2. Biométrie, biogéographie, 1970-1975, et registre des pêches, 1941-1976. Ministère du Loisir, de la Chasse et de la Pêche, Service de l'Aménagement et de l'Exploitation de la Faune. Montréal, 139 pp.

Mooney, H.A. & Cleland, E.E. 2001. The evolutionary impact of invasive species. PNAS 98: 5446-5451.

Moore, S.E., Larson, G.L. & Ridley, B. 1986. Population control of exotic rainbow trout in streams of a natural area park. Environmental Management 10: 215-219.

Moore, S.E., Ridely, B. & Larson, G.L. 1983. Standing crops of brook trout concurrent with removal of rainbow trout from selected streams in Great Smoky Mountains National Park. North American Journal of Fisheries Management 3: 72-80.

Morin, P.J. 1999. Community Ecology. Blackwell Science. 424 pp.

Morris, D.B., Richard, K.R. & Wright, J.M. 1996. Microsatellites from rainbow trout (*Oncorhynchus mykiss*) and their use for genetic study of salmonids. Canadian Journal of Fisheries and Aquatic Sciences 53: 120-126.

Mouillot, D., Stubbs, W., Faure, M., Dumay, O., Tomasini, J.A., Wilson, J.B. & Chi, T.D. 2005. Niche overlap estimates based on quantitative functionnal traits: a new family of non-parametric indices. Oecologia 145: 345-353.

Moyle, P.B. & Light, T. 1996. Biological invasions of fresh water: empirical rules and assembly theory. Biological Conservation 78: 149-161.

Moyle, P.B. & Marchetti, M.P. 2006. Predicting invasion success: freshwater fishes in California as a model. BioScience 56: 515-524.

Mullins, C.C. Year. Proceedings of the Newfoundland and Labrador region salmonid stock assessment meeting, November 2003. Proceedings of the DFO Canadian Science Advisory Secretariat, Proceeding Series 2003/035: 19-20.

Narum, S.R., Contor, C., Talbot, A. & Powell, M.S. 2004. Genetic divergence of sympatric resident and anadromous forms of *Oncorhynchus mykiss* in the Walla Walla River, U.S.A. Journal of Fish Biology 65: 471-488.

Narum, S.R., Hatch, D., Talbot, A.J., Moran, P. & Powell, M.S. 2008a. Iteroparity in complex mating systems of steelhead *Oncorhynchus mykiss* (Walbaum). Journal of Fish Biology 72: 45-60.

Narum, S.R., Zendt, J.S., Graves, D. & Sharp, W.R. 2008b. Influence of landscape on resident and anadromous life history types of *Oncorhynchus mykiss*. Canadian Journal of Fisheries and Aquatic Sciences 65: 1013-1023.

Needham, P.R. & Behnke, R.J. 1962. The origin of hatchery rainbow trout. The Progressive Fish-Culturist: 156-158.

Nei, M. 1987. Molecular evolutionary genetics. New York: Columbia University Press.

Nelitz, M.A., MacIsaac, E.A. & Peterman, R.M. 2007. A science-based approach for identifying temperature-sensitive streams for rainbow trout. North American Journal of Fisheries Management 27: 405-424.

O'Reilly, P.T., Hamilton, L.C., McConnell, S.K. & Wright, J.M. 1996. Rapid analysis of genetic variation in Atlantic salmon (*Salmo salar*) by PCR multiplexing of dinucleotide and tetranucleotide microsatellites. Canadian Journal of Fisheries and Aquatic Sciences 53: 2292-2298.

Ojaveer, H., Leppäkoski, E., Olenin, S. & Ricciardi, A. 2002. Ecological impact of Ponto-Caspian invaders in the Baltic Sea, European inland water and the Great Lakes : an inter-ecosystem comparison. *In*: Invasive Aquatic Species of Europe, E. Leppäkoski et al. Ed. Kluwer Academic Publishers, pp. 412-425.

Olden, J.D. & Rooney, T.P. 2006. On defining and quantifying biotic homogenization. Global Ecology and Biogeography 15: 113-120.

Olsen, J.B., Bentzen, P. & Seeb, J.E. 1998. Characterization of seven microsatellite loci derived from pink salmon. Molecular Ecology 7: 1087-1089.

Orizaola, G. & Brana, F. 2006. Effect of salmonid introduction and other environmental characteristics on amphibian distribution and abundance in mountain lakes of northern Spain. Animal Conservation 9: 171-178.

Ostberg, C.O. & Rodriguez, R.J. 2006. Hybridization and cytonuclear associations among native Westslope cutthroat trout, introduction rainbow trout, and their hybrids within the Stehikin River Drainage, North Cascades National Park. Transactions of the American Fisheries Society 135: 924-942.

Paetkau, D., Calvert, W., Stirling, I. & Strobeck, C. 1995. Microsatellite analysis of population structure in Canadian polar bears. Molecular Ecology 4: 347-354.

Paetkau, D., Slade, R., Burden, M. & Estoup, A. 2004. Genetic assignment methods for the direct, real-time estimation of migration rate: a simulation-based exploration of accuracy and power. Molecular Ecology 13: 55-65.

Parks, S.D.E. 2001. Trypanotolerance in West African Cattle and the Population Genetic Effects of Selection [Ph.D. thesis], University of Dublin.

Pascual, M.A., Bentzen, P., Riva-Rossi, C.M., Mackey, G., Kinnison, M.T. & Walker, R. 2001. First documented case of anadromy in a population of introduced rainbow trout in Patagonia, Argentina. Transactions of the American Fisheries Society 130: 53-67.

Pelletier, S. 1985. Inventaire ichtyologique (pêche à l'électricité) de la rivière Du Gouffre. Août - Septembre 1984. Rapport technique.: Ministère du Loisir, de la Chasse et de la Pêche. Direction régionale de Québec. Service de l'aménagement et de l'exploitation de la faune, 15 pp.

Peterson, D.P., Rieman, B.E., Dunham, J.B., Fausch, K.D. & Young, M.K. 2008. Analysis of trade-offs between threats of invasion by nonnative brook trout (*Salvelinus fontinalis*) and intentional isolation for native westslope cutthroat trout (*Oncorhychus clarkii lewisi*). Canadian Journal of Fisheries and Aquatic Sciences 65: 557-573.

Piry, S., Alapetite, A., Cornuet, J.-M., Paetkau, D., Beaudoin, L. & Estoup, A. 2004. GENECLASS2: A software for genetic assignment and first-generation migrant detection. Journal of Heredity 95: 536-539.

Platts, W.S. Year. Validity of methodologies to document stream environments for evaluating fishery conditions. Proceedings of the Proceedings of the Symposium and Specialty Conference on Instream Flow vol. 2: 267-284.

Porter, T.R. Year. Observations of rainbow trout (*Oncorhynchus mykiss*) in Newfoundland 1976 to 1999. Proceedings of the DFO Canadian Science Advisory Secretariat, Proceeding Series 2000/043: 9 pp.

Pritchard, J.K., Stephens, M. & Donnelly, P. 2000. Inference of population structure using multilocus genotype data. Genetics 155: 945-959.

Québec. 2000. Plan d'action québécois 2000-2002 sur les changements climatiques. Envirodoq : ENV2000-0173. 41 pp.

Quist, M.C., Rahel, F.J. & Hubert, W.A. 2005. Hierarchical faunal filters: an approach to assessing effects of habitat and nonnative species on native fishes. Ecology of Freshwater Fish 14: 24-39.

Rahel, F.J., Bierwagen, B. & Taniguchi, Y. 2008. Managing aquatic species of conservation concern in the face of climate change and invasive species. Conservation Biology 22: 551-561.

Rannala, B. & Mountain, J.L. 1997. Detecting immigration by using multilocus genotypes. Proceedings of the National Academy of Sciences USA 94: 9197-9221.

Raymond, M. & Rousset, F. 1995. GENEPOP (Version 1.2): Population genetics software for exact tests and ecumenicism. The Journal of Heredity 86: 248-249.

Reed, S.J.B. 1993. Electron Microprobe Analysis, 2nd Edition: Cambridge University Press, Cambridge. 326 pp.

Ricciardi, A. 2003. Predicting the impacts of an introduced species from its invasion history: an empirical approach applied to zebra mussel invasions. Freshwater Biology 48: 972-981.

Ricciardi, A. 2005. Facilitation and synergistic interactions between introduced aquatic species. *In*: Invasive alien species, a new synthesis. Mooney HA et al. Ed. 368 pp.

Ricciardi, A. 2006. Patterns of invasion in the Laurentian Great Lakes in relation to changes in vector activity. Diversity and Distributions 12: 425-433.

Ricciardi, A. & Atkinson, S.K. 2004. Distinctiveness magnifies the impact of biological invaders in aquatic ecosystems. Ecology Letters 7: 781-784.

Ricciardi, A. & Kipp, R. 2008. Predicting the number of ecologically harmful exotic species in an aquatic system. Diversity and Distributions 14: 374-380.

Ricciardi, A. & MacIsaac, H.J. 2000. Recent mass invasion of the North American Great Lakes by Ponto-Caspian species. TRENDS in Ecology and Evolution 15: 62-65.

Ricciardi, A. & Mottiar, M. 2006. Does Darwin's naturalization hypothesis explain fish invasions? Biological Invasions 8: 1403-1407.

Richards, C.L., Bossdorf, O., Muth, N.Z., Gurevitch, J. & Pigliucci, M. 2006. Jack of all trades, master of some? On the role of phenotypic plasticity in plant invasion. Ecology Letters 9: 981-993.

Rieman, B.E., Myers, D.L. & Nielsen, R.L. 1994. Use of otolith microchemistry to discriminate *Oncorhynchus nerka* of resident and anadromous origin. Canadian Journal of Fisheries and Aquatic Sciences 51: 68-77.

Riva-Rossi, C., Pascual, M.A., Babaluk, J.A., García-Asorey, M. & Halden, N.M. 2007. Intra-population variation in anadromy and reproductive life span in rainbow trout introduced in the Santa Cruz River, Argentina. Journal of Fish Biology 70: 1780-1797.

Riva-Rossi, C.M., Lessa, E.P. & Pascual, M.A. 2004. The origin of introduced rainbow trout (*Oncorhynchus mykiss*) in the Santa Cruz River, Patagonia, Argentina, as inferred from mitochondrial DNA. Canadian Journal of Fisheries and Aquatic Sciences 61: 1095-1101.

Robitaille, J.A., Pomerleau, C. & Paulhus, P.J. 1987. Analyse sommaire des captures de la pêcherie expérimentale de l'Aquarium du Québec, de 1971 à 1986. Ministère du Loisir, de la Chasse et de la Pêche du Québec. Direction de la faune aquatique et Direction régionale de Québec. Rapp. tech. 87-02. vi + 54 pp.

Rodríguez, M.A. 1995. Habitat-specific estimates of competition in stream salmonids: a field test of the isodar model of habitat selection. Evolutionary Ecology 9: 169-184.

Rose, G.A. 1986. Growth decline in subyearling brook trout (*Salvelinus fontinalis*) after emergence of rainbow trout (*Salmo gairdneri*). Canadian Journal of Fisheries and Aquatic Sciences 43: 187-193.

Ryder, R.A. & Kerr, S.R. 1982. Reducing the risk of fish introductions: A rational approach to the management of integrated coldwater communities. Proceedings of the Symposium on stock enhancement in the management of freshwater fish EIFAC Technical Paper #42, Volume 2 : Introductions and Transplantations: 510-533.

SAS. 2001. SAS v9. Language Guide, SAS Institute Inc. Release 6.03. Cary, N.C.

Sax, D.F., Stachowicz, J.J. & Gaines, S.D. 2005. Species invasions: insights into ecology, evolution and biogeography. 495 pp.

Scott, D. & Irvine, J.R. 2000. Competitive exclusion of brown trout *Salmo trutta* L., by rainbow trout *Oncorhynchus mykiss* Walbaum, in lake tributaries, New Zealand. Fisheries Management and Ecology 7: 225-237.

Scott, W.B. & Crossman, E.J. 1974. Poissons d'eau douce du Canada. Office des recherches sur les pêcheries du Canada, Ottawa. Bulletin 184: 1026 p.

Scribner, K.T., Gust, J.R. & Fields, R.L. 1996. Isolation and characterization of novel salmon microsatellite loci: cross-species amplification and population genetic applications. Canadian Journal of Fisheries and Aquatic Sciences 53: 833–841.

Seamons, T.R., Bentzen, P. & Quinn, T.P. 2007. DNA parentage analysis reveals inter-annual variation in selection: results from 19 consecutive brood years in steelhead trout. Evolutionary Ecology Research 9: 409-431.

Shea, K. & Chesson, P. 2002. Community ecology theory as a framework for biological invasions. TRENDS in Ecology and Evolution 17: 170-176.

Shigesada, N. & Kawasaki, K. 1997. Biological invasions: theory and practice: Oxford Series in Ecology and Evolution. 205 pp.

Shigesada, N., Kawasaki, K. & Takeda, Y. 1995. Modeling stratified diffusion in biological invasions. The American Naturalist 146: 229-251.

Simberloff, D. & Von Holle, B. 1999. Positive interactions of nonindigenous species: invasional meltdown? Biological Invasions 1: 21-32.

Sotiropoulos, J.C., Nislow, K.H. & Ross, M.R. 2006. Brook trout, *Salvelinus fontinalis*, microhabitat selection and diet under low summer stream flows. Fisheries Management and Ecology 13: 149-155.

Soto, D., Arismendi, I., González, J., Sanzana, J., Jara, F., Jara, C., Guzman, E. & Lara, A. 2006. Southern Chile, trout and salmon country: invasion patterns and threats for native species. Revista Chilena de Historia Natural 79: 97-117.

Spies, I.B., Brasier, D.J., O'Reilly, P.T.L., Seamons, T.R. & Bentzen, P. 2005. Development and characterization of novel tetra-, tri-, and dinucleotide microsatellite markers in rainbow trout (*Oncorhynchus mykiss*). Molecular Ecology Notes 5: 278-281.

Stauffer, J.R. 1984. Colonization Theory Relative to Introduced Populations. *In*: Distribution, Biology, and Management of Exotic Fishes. Walter R. Courtenay and Jay R. Stauffer Ed. pp. ix-x.

Stohlgren, T.J., Binkley, D., Chong, G.W., Kalkhan, M.A., Schell, L.D., Bull, K.A., Otsuki, Y., Newman, G., Bashkin, M. & Son, Y. 1999. Exotic plant species invade hot spots of native plant diversity. Ecological Monographs 69: 25-46.

Theoharides, K.A. & Dukes, J.S. 2007. Plant invasion across space and time: factors affecting nonindigenous species success during four stages of invasion. New Phytologist 176: 256-273.

Thériault, V. & Dodson, J.J. 2003. Body size and the adoption of a migratory tactic in brook charr. Journal of Fish Biology 63: 1144-1159.

Thorpe, J.E. 1994. Salmonid fishes and the estuarine environment. Estuaries 17: 76-93.

Tilman, D. 1982. Resource competition and community structure. 296 pp.

Tzeng, W.-N., Chang, C.-W., Wang, C.-H., Shiao, J.-C., Iizuka, Y., Yang, Y.-J., You, C.-F. & Lozys, L. 2007. Misidentification of the migratory history of anguillid eels by Sr/Ca ratios of vaterite otoliths. Marine and Freshwater Research 348: 285-295.

Tzeng, W.-N., Iizuka, Y., Shiao, J.C., Yamada, Y. & Oka, H.P. 2003. Identification and growth rates comparison of divergent migratory contingents of Japanese eel (*Anguilla anguilla*). Aquaculture 216: 77-86.

Tzeng, W.-N., Wang, C.H., Wickström, H. & Reizenstein, M. 2000. Occurence of the semi-catadromous European eel *Anguilla anguilla* in the Baltic Sea. Marine Biology 137: 93-98.

Volk, E.C., Blakley, A., Schroder, S.L. & Kuehner, S.M. 2000. Otolith chemistry reflects migratory characteristics of Pacific salmonids: Using otolith core chemistry to distinguish maternal associations with sea and freshwaters. Fisheries Research 46: 251-266.

Volpe, J.P., Anholt, B.R. & Glickman, B.W. 2001. Competition among juvenile Atlantic salmon (*Salmo salar*) and steelhead (*Oncorhynchus mykiss*): relevance to invasion potential in British Colombia. Canadian Journal of Fisheries and Aquatic Sciences 58: 197-207.

Vondracek, B. & Longanecker, D.R. 1993. Habitat selection by rainbow trout *Oncorhynchus mykiss* in a California stream: implications for the instream flow incremental methodology. Ecology of Freshwater Fish 2: 173-186.

Waters, T.F. 1983. Replacement of brook trout by brown trout over 15 years in a Minnesota stream: production and abundance. Transactions of the American Fisheries Society 112: 137-146.

Weir, B.S. & Cockerham, C.C. 1984. Estimating *F*-statistics for the analysis of population structure. Evolution 38: 1358-1370.

Welcomme, R.L. 1984. International Transfers of Inland Fish Species. In: Stauffer, W.R.C.a.J.R., ed. Distribution, Biology, and Management of Exotic Fishes. pp. 22-40.

Whitworth, W.E. & Strange, R.J. 1983. Growth and production of sympatric brook and rainbow trout in an Appalachian stream. Transactions of the American Fisheries Society 112: 469-475.

Whoriskey Jr., F.G., Naiman, R.J. & Heinermann, P.H. 1981. Steelhead trout (*Salmo gairdneri*) on the North shore of the Gulf of St. Lawrence, near Sept-Îles, Québec. Canadian Journal of Fisheries and Aquatic Sciences 38: 245-246.

Williamson, M. 1996. Biological Invasions. Chapman and Hall Ed. 244 pp.

Williamson, M.H. & Fitter, A. 1996. The characters of successful invaders. Biological Conservation 78: 163-170.

Wood, S.N. 2006. Generalized additive models: an introduction with R: Chapman and Hall/CRC. 416 pp.

Zimmerman, C.E. 2005. Relationship of otolith strontium-to-calcium ratios and salinity: experimental validation for juvenile salmonids. Canadian Journal of Fisheries and Aquatic Sciences 62: 88-97.

Zimmerman, C.E. & Reeves, G.H. 2000. Population structure of sympatric anadromous and nonanadromous *Oncorhynchus mykiss*: evidence from spawning surveys and otolith microchemistry. Canadian Journal of Fisheries and Aquatic Sciences 57: 2152-2162.

Zimmerman, C.E. & Reeves, G.H. 2002. Identification of steelhead and resident rainbow trout progeny in the Deschutes River, Oregon, revealed with otolith microchemistry. Transactions of the American Fisheries Society 131: 986-993.

Appendix A: Univariate statistics for geomorphological variables

Se référer au Chapitre 3 : Abiotic variables accounting for presence of the exotic rainbow trout (*Oncorhynchus mykiss*) in Eastern Quebec Rivers

Table A1. Results of the univariate analyses on untransformed geomorphological variables. Three variables (Sin, Dam and SZD) do not respect the Hosmer and Lemeshow criteria fixed at $P < 0.25$ (in bold) to be included in a multivariate model.

Variable	Test for variance equality		Student test		
	F value	P > F	Method	T value	P > T
MS	1.21	0.55	Pooled	2.96	< 0.01
Sin	1.92	0.03	Satterthwaite	-1.19	0.24
MinE	2.29	< 0.01	Satterthwaite	-0.90	**0.37**
MaxE	1.76	0.06	Pooled	-3.24	< 0.01
Len	1.40	0.29	Pooled	-3.47	< 0.01
STrib	3.64	< 0.01	Satterthwaite	-4.97	< 0.01
LTrib	5.22	< 0.01	Satterthwaite	-6.23	< 0.01
Dam	1.38	0.32	Pooled	-0.16	**0.87**
SZD	1.05	0.85	Pooled	0.71	**0.48**

Table A2. Transformation of the geomorphological variables for which the relationship with the logit was not linear. The mention 'na' appears for excluded variables (refer to Annexe A1). No transformation was necessary for the PCs (either in geomorphological or climatic models)

Variable	Form of the relation	Transformation
MS	quadratic	MS MS^2
Sin	linear	•
MinE	null	na
MaxE	linear	•
Len	linear	•
STrib	linear	•
LTrib	linear or categoric[§]	• [0], [1-2] and [3+] [0] and [1+]
Dam	null	na
SZD	null	na

[§] It was not clear which type of relation was the most significant, therefore we tested all (untransformed data and two categorizations)

Appendix B: Analyses of the rivers' detectability

Se référer au Chapitre 3 : Abiotic variables accounting for presence of the exotic rainbow trout (*Oncorhynchus mykiss*) in Eastern Quebec Rivers

Table B1. Description of the two variables used to evaluate the influence of the detection effort (targetted on Atlantic salmon) on the rainbow trout prevalence in 44 rivers located in Eastern Quebec. P-values indicate significant univariate relationships with the presence of the exotic fish species.

Variable	Abbreviation	Category	Description	Fisher p-value
Monitoring effort	Mo_Ef	[0]	No effort	< 0.01
		[1]	Presence of counting fence and/or visual counting by snorkelling	
Fishing effort	Fi_Ef	[0]	No salmon fishing-day from 1984 to 2008	< 0.01
		[1]	1 - 1000 salmon fishing-days from 1984 to 2008	
		[2]	1001 - 5000 salmon fishing-days from 1984 to 2008	
		[3]	5001 - 10 000 salmon fishing-days from 1984 to 2008	
		[4]	10 001 - 50 000 salmon fishing-days from 1984 to 2008	
		[5]	> 50 000 salmon fishing-days from 1984 to 2008	

Table B2. Significance and coefficients of the detection effort variables when included in the two most significant geomorphological models presented in Table 3.2. Climatic model is not used since its contribution to explain the rainbow trout prevalence was marginal when compared to the geomorphological models.

Model ID[a]	Variables	Khi2 p-value	β estimate (SE)
When the "monitoring effort" variable is added			
G1	LTrib	< 0.01	0.95 (0.29)
	Mo_Ef[1 vs 0]	0.08	1.62 (0.93)
G2	LTrib[1-2 vs 0]	0.03	2.74 (1.27)
	LTrib[3+ vs 0]	< 0.01	3.85 (1.11)
	Mo_Ef[1 vs 0]	0.06	1.86 (0.98)
When the "fishing effort" variable is added			
G1	LTrib	0.03	0.88 (0.40)
	Fi_Ef[1 vs 0]	0.98	-10.21 (339.70)
	Fi_Ef[2 vs 0]	0.15	2.34 (1.63)
	Fi_Ef[3 vs 0]	0.74	0.61 (1.82)
	Fi_Ef[4 vs 0]	0.05	3.40 (1.72)
	Fi_Ef[5 vs 0]	0.96	13.09 (288.70)
G2	LTrib[1-2 vs 0]	0.17	2.30 (1.67)
	LTrib[3+ vs 0]	0.02	3.64 (1.58)
	Fi_Ef[1 vs 0]	0.98	-9.60 (339.70)
	Fi_Ef[2 vs 0]	0.13	2.67 (1.74)
	Fi_Ef[3 vs 0]	0.58	1.03 (1.86)
	Fi_Ef[4 vs 0]	0.04	3.61 (1.74)
	Fi_Ef[5 vs 0]	0.97	13.68 (330.30)

[a] In reference to IDs presented in Table 3.2

Appendix C: Sampled rivers and fish features

Se référer au Chapitre 4 : Biotic resistance as fact or fiction; interspecific competition between introduced and native juvenile salmonid species at an early invasive stage

Table C1. Features of the nine rivers sampled in 2007 and 2008 in Eastern Quebec, Canada. "Study" rivers supported a rainbow trout population whereas no rainbow trout were captured "control" rivers. *Onmy*: rainbow trout, *Sasa*: Atlantic salmon, *Safo*: brook charr, "++": abundant captures, "+": some captures, "0": absence of the species.

River	Sampling starting date	Type	Species composition			Sampling scale		Nb of stations resampled in 2008
						Large	Small	
			Onmy	*Sasa*	*Safo*	nb stations	nb stations/ nb transects	
Calway	June 18, 2007	control	0	0	++	18	$3 / 5^a$	0
Tortue	August 7, 2008	study	++	0	++	-	$3 / 6^b$	NA
Du Gouffre	July 2, 2007	study	+	++	++	25	3 / 9	2
Malbaie	July 9, 2007	study	++	++	+	15	3 / 9	3
Petit-Saguenay	July 16, 2007	control	0	++	+	11	3 / 9	0
Trois-Pistoles	July 23, 2007	control	0	0	+	9	$2^c / 6$	0
Sud-Ouest	July 30, 2007	control	0	+	+	11	3 / 9	0
Matane	August 11, 2007	study	+	++	+	19	3 / 9	2
Mechins	August 6, 2007	study	++	0	++	14	3 / 9	3

[a] In one station, we sampled a single transect of 39 unities. In a second station, we sampled only two transects

[b] Only two transects by station

[c] One station was abandoned since really few salmonids were captured in that river

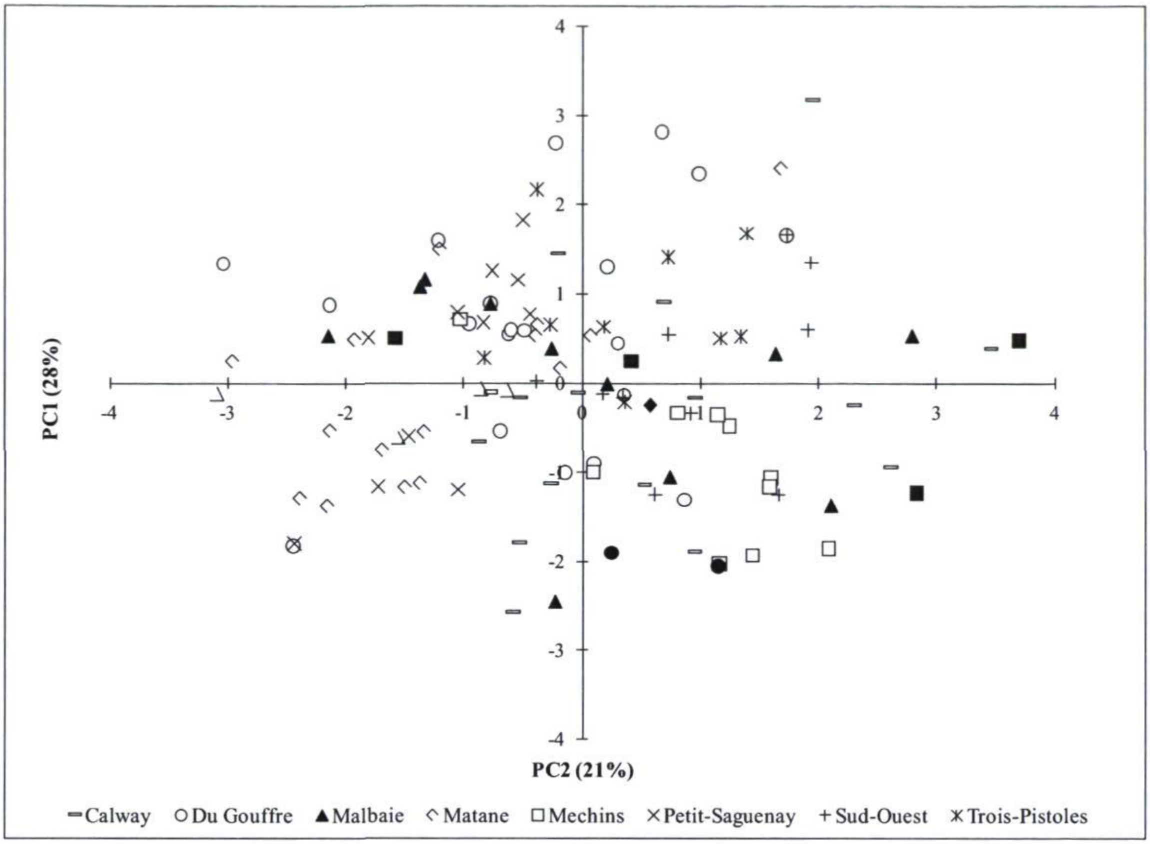

Figure C2. Spatial position of the stations according to the two first axes of the principal componant analysis (PCA) performed on habitat variables. Filled symbols represent stations where rainbow trout has been found.

Table C3. Body size and mass of gut content of salmonids included in the diet comparison analyses. Different letters indicate a significative difference ($p < 0.05$) in size or food mass between species within a river.

River	Species	N	Fork length (mm)		Gut content (g)	
			mean (± SD)		mean (± SD)	
Du Gouffre	rainbow trout	9	57 (± 5)	ab	0.0242 (± 0.0140)	b
	brook charr	10	67 (± 17)	a	0.0776 (± 0.0716)	a
	Atlantic salmon	9	49 (± 15)	b	0.0145 (± 0.0058)	b
Malbaie	rainbow trout	7	59 (± 35)	c	0.1089 (± 0.1140)	c
	brook charr	7	71 (± 19)	c	0.1267 (± 0.1893)	c
	Atlantic salmon	10	65 (± 4)	c	0.0382 (± 0.0256)	c
Matane	rainbow trout	12	38 (± 2)	d	0.0189 (± 0.0092)	d
	brook charr	13	59 (± 10)	e	0.0743 (± 0.0749)	e
	Atlantic salmon	10	44 (± 4)	f	0.0333 (± 0.0183)	de
Mechins	rainbow trout	10	40 (± 4)	g	0.0143 (± 0.0117)	f
	brook charr	10	48 (± 5)	h	0.0155 (± 0.0131)	f