SOPHIE LENORMAND

ÉVOLUTION DE L'ANADROMIE ET STRATÉGIE DE REPRODUCTION CHEZ L'OMBLE DE FONTAINE (*SALVELINUS FONTINALIS*)

Thèse
présentée
à la Faculté des études supérieures
de l'Université Laval
pour l'obtention
du grade de Philosophiae Doctor (Ph.D.)

Doctorat en biologie
FACULTÉ DES SCIENCES ET DE GÉNIE
UNIVERSITÉ LAVAL
QUÉBEC

AVRIL 2003

National Library
of Canada

Acquisitions and
Bibliographic Services

395 Wellington Street
Ottawa ON K1A 0N4
Canada

Bibliothèque nationale
du Canada

Acquisisitons et
services bibliographiques

395, rue Wellington
Ottawa ON K1A 0N4
Canada

Your file Votre référence
ISBN: 0-612-82692-9
Our file Notre référence
ISBN: 0-612-82692-9

Canada

UNIVERSITÉ
LAVAL

Faculté des études supérieures

ATTESTATION

Ce 24e jour du mois de mars de 2003, les personnes soussignées, en leur qualité de membres du jury de la thèse de Madame Sophie Lenormand, ont assisté à la soutenance de cette thèse.

NOMS	UNIVERSITÉ	SIGNATURE
LOUIS BERNATCHEZ	LAVAL	
Julian Dodson	LAVAL	
JEREMY MCNEIL	LAVAL	
Steve McCormick	Univ. Massachusetts	

SIGNATURE DU PRÉSIDENT DE LA SOUTENANCE

FES-53a (08-01)

Résumé

Dans certaines populations, la sélection naturelle favorise le maintien de plusieurs phénotypes alternatifs. Comment une diversité de tactiques de reproduction peut-elle évoluer sous les pressions sélectives reste à l'heure actuelle une des questions centrales de la biologie de l'évolution. Chez les salmonidés, deux tactiques majeures sont observées : l'anadromie, caractérisée par une migration depuis la rivière natale vers l'eau salée, et la résidence en eau douce. L'expression de ces tactiques est plastique et dépend de la croissance et des perspectives de croissance des individus en eau douce. Cette étude, basée sur la population d'ombles de fontaine de la rivière Sainte-Marguerite, Saguenay, Québec, visait à mieux comprendre l'existence et le maintien de ces tactiques alternatives chez les salmonidés, ainsi qu'à mettre en évidence certains des facteurs qui influencent l'évolution de l'anadromie. L'échantillonnage d'ombles résidants et anadromes, un suivi de la pêche sportive et un programme de marquage-recapture ont permis d'évaluer les conséquences de l'expression de l'anadromie ou de la résidence sur le cycle vital et le succès reproducteur des individus. Les patrons de migration des ombles anadromes ont souligné l'évolution conjointe du comportement migratoire et du cycle vital anadrome. L'analyse du cycle vital des individus anadromes et des individus résidants a mis en évidence l'existence d'un compromis entre croissance et survie associé à l'expression de l'anadromie ou de la résidence. L'utilisation de l'habitat estuarien accélérait la croissance des individus mais au prix d'une mortalité élevée. La résidence en eau douce était associée à une faible croissance mais une survie supérieure jusqu'à la reproduction. En eau douce, les facteurs environnementaux, tels que la compétition intra et interspécifique, peuvent influencer les opportunités de croissance et donc les perspectives de reproduction des individus qui adoptent la résidence. Cependant, nous avons observé qu'une isolation géographique relativement récente (35 ans) peut changer la norme de réaction des individus à ces opportunités de croissance et conduire à une reproduction en eau douce malgré une faible croissance. Une forte héritabilité du comportement migratoire et/ou des traits qui régulent les besoins énergétiques des individus pourraient expliquer la disparition du comportement anadrome dans des communautés qui ont été isolées. De façon générale, l'existence d'un compromis entre croissance et survie en eau douce et en milieu marin, la variabilité environnementale et une sélection dépendante de la fréquence des tactiques exprimées pourrait prévenir une spécialisation vers la résidence ou l'anadromie et favoriser le maintien de la plasticité phénotypique des populations à l'égard de la migration.

Abstract

In some populations, natural selection favours the maintenance of several alternative phenotypes. How a diversity of reproductive tactics evolves under natural selection remains a central issue of evolutionary biology. In salmonids, two major tactics are observed: anadromy, characterized by a migration from the natal river to salt water, and freshwater residency. The expression of these tactics is plastic and depends on individuals' growth and scope of growth in fresh water. This study, based on the brook charr population of the Sainte-Marguerite River, Saguenay, Québec, aimed at a better understanding of the existence and the maintenance of alternative tactics in salmonids, and at highlighting some of the factors involved in the evolution of anadromy. Combining samplings of resident and anadromous charr, a creel census and a mark-recapture experiment, we assessed the consequences, in terms of life-history and life-time reproductive success, of expressing anadromy or freshwater residency. Migratory patterns of anadromous charr emphasized the co-evolution of migratory behaviour and life-history. The life-history of anadromous and resident charr highlighted the existence of a trade-off between growth and survival, associated with the expression of anadromy or of residency. The use of estuarine areas enhanced growth but increased risks of mortality. Freshwater residency was associated with a poor growth but a much better survival to reproduction. In fresh water, environmental factors, such as intra- and inter-specific competition, may influence growth opportunities, and hence, reproductive prospects of individuals that adopt residency. However, we observed that a relatively recent geographical isolation (35 years) can change the reaction norm of individuals to growth opportunities and lead to a reproduction in fresh water in spite of poor growth. A high heritability of migratory behaviour and/or of traits regulating energy requirements of individuals could explain the disappearance of anadromous behaviour in isolated communities. Overall, the existence of a trade-off between growth and survival in fresh water and in estuarine areas, environmental variability and frequency-dependent selection may prevent a specialization towards anadromy or residency and favour the maintenance of phenotypic plasticity with regard to migration.

Avant-propos

Cette étude a été réalisée dans le cadre du programme de recherche inter-universitaire intitulé «L'anadromie chez l'omble de fontaine (*Salvelinus fontinalis*) et sa relation dans le partage de la productivité de l'écosystème avec le saumon atlantique (*Salmo Salar*) : implications pour la gestion ». Trois projets complémentaires ont été menés au sein du bassin hydrographique de la rivière Sainte-Marguerite, affluent du Saguenay, Québec, de 1998 à 2001. Le premier (Université McGill) visait à estimer la productivité des écosystèmes dulçaquicole et estuarien ainsi que l'efficacité alimentaire de l'omble de fontaine dans ces deux milieux. Le second (Université de Montréal) a analysé le réseau trophique et évalué la répartition des ressources présentes en eau douce. Enfin, l'étude présentée ici faisait partie du dernier projet (Université Laval), s'intéressant plus particulièrement à l'évolution de l'anadromie chez l'omble de fontaine (importance de la croissance au cours des jeunes stades de vie dans l'expression de la résidence ou l'anadromie, description des patrons de migration, évaluation des paramètres du cycle vital et du succès reproducteur des individus résidants et anadromes).

Cette étude faisait également partie des programmes de recherche du CIRSA (Centre Interuniversitaire de Recherche sur le Saumon Atlantique) et de Québec-Océan (ex GIROQ).

Remerciements

Julian Dodson m'a encadrée, m'a fait bénéficier de son expérience, de ses connaissances et de la richesse de ses réflexions. Il sait transmettre à ses étudiants son dynamisme et favorise leur intégration dans la communauté scientifique internationale, leur donnant ainsi des atouts majeurs pour progresser dans leur domaine. Je le remercie très chaleureusement de m'avoir accueillie dans son laboratoire, de m'avoir offert un si beau sujet de recherche, de tout ce qu'il m'apporté au cours de ces dernières années mais aussi de sa gentillesse et de sa confiance.

Cyrille Barrette, Louis Bernatchez et Jeremy McNeil ont également suivi l'avancement de cette thèse, à différentes étapes. Je leurs suis extrêmement reconnaissante pour le temps qu'ils ont investi, pour leurs précieux conseils et leurs réflexions sur le sujet.

Stephen McCormick a accepté de participer à l'évaluation de ce travail et cela me fait particulièrement plaisir. Ses recherches sont une importante contribution à nos connaissances sur l'omble de fontaine et les salmonidés, et ont éclairé plusieurs aspects de cette étude.

Pierre Magnan m'a appris à lire les otolithes d'omble de fontaine et Kevin McCann m'a initiée à la modélisation et l'utilisation de MATLAB. Francis Bérubé m'a très souvent dépannée en programmation. Qu'ils soient assurés de toute ma reconnaissance pour avoir grandement facilité ma tâche.

Parmi ceux qui m'ont fait avancer par leurs connaissances et leurs réflexions, je tiens également à remercier Nadia Aubin-Horth, Vincent Castric et Dany Garant pour toutes les discussions enrichissantes.

Bien que très loin de l'autre côté de l'Atlantique, Marc Legendre, qui m'a fait découvrir la biologie des poissons et la recherche au sein de l'IRD, a toujours été présent, quelque part, dans le travail de terrain, les analyses de données et l'expression des résultats. Je le remercie du fond du cœur pour tout ce qu'il m'a appris et pour m'avoir donné l'envie de continuer.

Jérôme Lazard, du CIRAD, et Dominique Ombredane, de l'ENSA de Rennes, m'ont également toujours soutenue dans la voie que j'avais choisie. Je n'oublierai jamais leur gentillesse et tous les efforts qu'ils ont faits pour moi.

La réussite de cette étude tenait à deux choses : l'échantillonnage et le marquage d'un nombre suffisant d'ombles de fontaine, la recapture d'un nombre suffisant de poissons étiquetés. Je tiens donc à exprimer ma plus profonde gratitude envers toutes les personnes dont les efforts ont permis de remplir la première condition : Simon Bilodeau-Gauthier, André Boivin, Vincent Castric, Félix Charlebois, Mathieu Desgagnés, Jean-Martin Fréchette, Steve Gaouette, Cindy Garneau, Nico Jomphe, Marie-Claude Landry-Pelchat, Christian Langlois, Kristin Lunn, Jean-Guillaume Marquis, Annie Ménard, Caroline Mimeault, Geneviève Morinville, Pierre-Alexandre Paradis, Claude Poirier, Louis-Vincent Saint-Hilaire-Gravel, Joselito Savard, Véronique Thériault, Simon Trépanier et beaucoup d'autres… L'appui de la ZEC Sainte-Marguerite, l'excellente collaboration des pêcheurs du Saguenay et du Club de Pêche de la Sainte-Marguerite a rempli la deuxième moitié du contrat. Un grand merci à tous.

Si j'étais dans mon élément sur le Saguenay, je n'avais que très peu d'expérience en eau vive, milieu qu'il m'a fallu apprivoiser au cours de mes premières années de terrain. Simon Trépanier a été mon guide sur les ruisseaux, m'a appris l'art des trappes et m'a initiée à la pêche électrique, avec tout le savoir-faire qui le caractérise. Je le remercie pour ce précieux cadeau et pour sa gentillesse à mon arrivée au Québec et au CIRSA.

Sur quatre ans et demi passés au Québec, j'ai résidé deux ans à la station de recherche du CIRSA, dans des conditions qui ne pouvaient que favoriser la réussite de la partie « terrain » de cette étude. Je tiens donc à remercier ceux qui ont fait et qui font du CIRSA un centre de recherche dynamique, efficace et où il fait bon vivre, et tout spécialement, Julian Dodson, un directeur scientifique plein d'énergie, Dany Bussières, qui a assuré le démarrage du centre, Françoise Colombani, dont l'efficacité en tant que nouveau gérant n'est plus à prouver, et sur place, André Boivin, l'homme de toutes les situations, Albertine Gauthier, Collette Dufour et Collette Gauthier qui étaient là pour prendre soin de moi pendant mes séjours à Sacré-Cœur.

Je voudrais également souligner l'efficacité et la gentillesse de Michèle Carignan, qui a réglé nombre de mes problèmes administratifs à l'université, s'est adaptée aux aléas de ma rédaction, de mon dépôt initial et de la présentation de mon séminaire… avec le sourire.

Parce qu'un entourage sympathique prend toute son importance quand on s'investit dans un doctorat, je tiens à remercier Nadia Aubin-Horth, Frédéric Lecomte et Stéphane Plourde, qui m'ont accueillie au sein du laboratoire Dodson, Véronique Thériault, qui a été bien plus que ma partenaire de terrain, Dany Garant, pour tous les bons souvenirs au CIRSA et à Québec, Gesche Winkler et Hidetaka Yoneyama dont la gentillesse m'a beaucoup touchée, ainsi que tous les autres étudiants des laboratoires Dodson et Bernatchez avec qui j'ai passé de bons moments.

Claude Poirier m'a mis une canne à mouche entre les mains et c'est l'un des plus beaux cadeaux qu'il m'a fait. Je n'oublierai jamais sa prévenance et sa gentillesse à mon égard, les parties de pêche et les soirées qui ont embelli mes automnes.

Outre leur investissement au cours de cette étude, Francis Bérubé, André Boivin, Steve Gaouette et Annie Ménard m'ont offert leur amitié, synonyme d'un précieux soutien moral. Qu'ils soient assurés de toute ma reconnaissance pour toutes les fois où ils ont été *là* et de ma plus profonde affection peu importent les distances qui nous sépareront.

Enfin, en cette fin de thèse, je tiens tout particulièrement à remercier mes parents dont la gentillesse et l'appui inconditionnel ont grandement facilité toutes ces années d'étude.

Cette étude n'aurait pas pu être réalisée sans le soutien financier du Gouvernement du Canada (CRSNG et Parc Marin du Saguenay – Saint-Laurent), du Gouvernement du Québec (FAPAQ), de la Fondation de la Faune du Québec, de tous les autres partenaires du CIRSA Inc., ainsi que de Québec-Océan (ex GIROQ).

à Marie, Éva, Léo, Diran, Tiago, Meven,
Charlotte, Alexanne, Ewen et Marcel(le ?),

Table des matières

Liste des tableaux

Liste des figures

1. Introduction

> "Evolutionary biologists… want to understand why things are different, not why they are the same. They want to understand what causes diversity. Much of their thinking is colored by this concentration on the causes of variation." (Stearns 2000).

1.1. Stratégie et tactiques de reproduction

La sélection naturelle favorise souvent un seul phénotype dans une population donnée, considéré alors comme le meilleur phénotype ou phénotype optimal pour cette population. Cependant, de nombreux organismes présentent des phénotypes alternatifs, au niveau de leur morphologie, de leur comportement ou encore de leur cycle vital, et ces variantes peuvent être observées au sein de la même population. Les exemples (passés en revue dans Roff 1996) incluent la présence ou l'absence de structures morphologiques d'attaque et de défense (p.e. Moczek et al. 2002) et le dimorphisme des ailes (Zera et Denno 1997 et p.e. Roff et Fairbairn 1993) chez les insectes, les dimorphismes trophiques chez les amphibiens et les poissons (p.e. Snorrason et al. 1994), l'adoption de différents comportements reproducteurs (Lank et al. 1995, Emlen 1997, Henson et Warner 1997, Zamudio et Sinervo 2000, Taborsky 2001, Kurdziel et Knowles 2002), la métamorphose ou la paedomorphose chez les amphibiens (p.e. Whiteman 1994), la migration ou la résidence chez les insectes (Roff et Fairbairn 1991), les oiseaux (Lundberg 1987 et p.e. Adriaensen et Dhondt 1990) et les poissons (Jonsson et Jonsson 1993). Comment une telle diversité phénotypique évolue t-elle sous les pressions sélectives reste à l'heure actuelle une des questions majeures de la biologie de l'évolution.

Dans certains cas, un polymorphisme génétique pourrait être responsable du polymorphisme phénotypique. La présence de différents allèles à un même locus serait notamment à l'origine de certains polymorphismes de couleur (Roff 1996 et, p.e., Lank et al. 1995). Les rares exemples documentés de phénotypes alternatifs directement associés à un polymorphisme génétique incluent également la taille à la première reproduction (et le comportement reproducteur associé) chez le poisson porte-épée, *Xiphophorus nigrensis* (Ryan et al. 1992). Le maintien de ces stratégies alternatives implique l'égalité des fitness (valeurs sélectives) des différents phénotypes déterminés génétiquement, qui pourrait reposer sur une sélection dépendante de la fréquence des stratégies considérées (plus une stratégie devient rare, plus sa valeur sélective augmente, et inversement (Maynard-Smith 1982)).

Si une sélection dépendante de la fréquence peut expliquer le maintien d'un polymorphisme génétique, elle pourrait également expliquer le maintien de l'expression de phénotypes alternatifs à partir d'un seul et même génotype, à des fréquences où les fitness associés à ces phénotypes seraient identiques. Cependant, l'existence de stratégies mixtes (stratégies permettant l'expression de tactiques alternatives, à la différence de stratégies alternatives où un génotype correspond à une seul phénotype) où les fitness associés aux tactiques alternatives sont égaux (Maynard-Smith 1982), n'a jamais été clairement démontrée par des études empiriques (Gross 1996).

Il semble en effet que les phénotypes alternatifs observés en milieu naturel soient souvent associés à des fitness inégaux (Dominey 1984, Gross 1996 et, p.e., Brockmann et al. 1994, Foote et al. 1997 mais voir Sato 1998). Il semble également que, dans des populations où plusieurs tactiques peuvent être exprimées par l'ensemble des individus (monomorphisme génétique pour l'expression des tactiques), cette expression soit souvent régulée par la taille, la croissance ou l'état physiologique des individus à un moment précis de leur ontogénie (p.e. Lundberg 1987, Metcalfe 1998, Kurdziel et Knowles 2002, Moczek et al. 2002). Ces observations ont favorisé l'essor d'un troisième concept expliquant le maintien de phénotypes alternatifs dans une même population, appelé communément « stratégie conditionnelle » et résumé dans Gross et Repka (1998) (mais voir également Levins 1963, Maynard-Smith 1982, Dominey 1984, Caro et Bateson 1986, Hazel et al. 1990, Roff 1996, Hunt et Simmons 2001). Tous les individus ont la capacité d'exprimer les différentes tactiques observées dans la population. L'expression de l'une ou l'autre de ces tactiques par un individu donné dépend de son « état » à une certaine période de sa vie et la tactique exprimée résulte en un fitness supérieur pour cet individu. Une stratégie conditionnelle suppose l'existence d'un point de transition à un « état » seuil (cas simple impliquant seulement deux tactiques alternatives), en-dessous duquel les individus exprimeront une tactique et au-dessus duquel, ils en exprimeront une autre.

Bien que la stratégie conditionnelle soit une forme discrète de plasticité phénotypique adaptative (*sensu* Houston et McNamara 1992), elle n'exclut pas une composante héréditaire du trait sous-jacent à l'expression des différentes tactiques (voir Roff 1996). Des études théoriques ont montré que l'héritabilité (des tactiques ou du trait sous-jacent) n'empêche pas des tactiques alternatives associées à des fitness inégaux d'être maintenues en équilibre stable (Hazel et al. 1990, Gross et Repka 1998 mais voir également Hazel et Smock 2000). Une stratégie conditionnelle n'exclut pas non plus l'existence d'une sélection dépendante de la fréquence des tactiques exprimées, qui stabiliserait les fréquences d'expression de ces tactiques (Gross 1996 et p.e. Gross 1991, Hutchings et Myers 1994 et voir également Roff 1998).

1.2. Évolution de l'anadromie chez les salmonidés

1.2.1. Anadromie et tactiques de reproduction alternatives chez les salmonidés

Les salmonidés anadromes naissent en eau douce mais quittent leur rivière natale, après quelques mois à quelques années, pour gagner le milieu marin (McDowall 2001). La (ou les) période(s) de croissance en eau salée dure(nt) également de quelques mois à quelques années, selon les espèces, et les retours en eau douce sont motivés soit par un événement reproducteur soit par des changements environnementaux saisonniers, dans le cas des populations à migration estuarienne ou côtière (Randall et al. 1987).

Si l'anadromie n'est pas spécifique aux salmonidés, elle est reconnue comme l'un des traits caractéristiques de cette famille. Cependant, la migration apparaît facultative chez de nombreuses espèces. Premièrement, certaines populations dont les fondateurs étaient anadromes ont évolué vers un cycle vital entièrement en eau douce. Les cas les plus extrêmes, comme la manifestation immédiate de la résidence en eau douce chez des stocks anadromes transplantés dans un nouvel environnement, suggèrent que les individus anadromes constituant les stock d'origine étaient capables d'exprimer avec succès la tactique résidante (McDowall 2001). Ensuite, dans de nombreuses populations exprimant l'anadromie, une partie des individus se reproduit sans avoir jamais migré vers l'eau salée (Jonsson et Jonsson 1993). L'exemple le plus connu est peut-être celui des mâles précoces chez le saumon atlantique, *Salmo salar* (voir Fleming 1996). Leur cycle vital en eau douce, caractérisé par une maturité sexuelle avancée et une petite taille à la reproduction (relativement aux mâles anadromes), est associé à un tactique de reproduction furtive, leur permettant de féconder les œufs des femelles anadromes sans participer à la compétition intra-sexuelle pour accéder à ces dernières. Cependant, chez d'autres espèces comme les ombles (*Salvelinus*), la truite brune (*Salmo trutta*), la truite fardée (*Oncorhynchus clarki*), la truite arc-en-ciel (*O. mykiss*) et le saumon sockeye (*O. nerka*), la forme résidante peut être observée aussi bien chez les femelles que chez les mâles (Jonsson et Jonsson 1993).

1.2.2. Facteurs potentiellement impliqués dans l'évolution de l'anadromie chez les salmonidés

La migration des salmonidés leur permettrait d'accéder à des ressources alimentaires supérieures (Northcote 1978, Gross et al. 1988) et/ou d'éviter certains risques spécifiques aux rivières – par exemple ceux associés la formation des glaces ou à une forte réduction des débits (Nikolskii 1963). La croissance des salmonidés est généralement beaucoup plus élevée en eau salée qu'en eau douce (Hutchings et Morris 1985, Gross 1987, et, p.e., Jonsson 1985, Morita 2001). La fécondité des poissons augmentant généralement avec la taille (Wootton 1998), chez les femelles, forte croissance est synonyme de fécondité élevée (Hutchings et Morris 1985, Gross 1987 et, p.e., Jonsson 1985, Morita et Takashima 1998). Chez les deux sexes, une taille supérieure constitue un avantage dans les compétitions territoriales au moment de la reproduction (Dodson 1997). Cependant, les poissons anadromes affectent d'importantes ressources énergétiques dans les déplacements, l'adaptation à l'eau salée et le maintien de la capacité physiologique à réguler leur pression osmotique en eau salée et en eau douce. De plus, la mortalité due à la prédation et aux maladies est susceptible d'atteindre des niveaux beaucoup plus élevés en milieu marin qu'en milieu dulçaquicole (Jonsson et Jonsson 1993 et p.e. Dieperink et al. 2002 pour la prédation). Les individus résidants en eau douce ne bénéficient pas des avantages, en terme de croissance, associés à l'anadromie, mais n'en subissent pas les coûts, ce qui est un avantage en soi. Leur cycle de vie est caractérisé par une faible croissance mais aussi par une survie élevée. Un compromis entre croissance et survie pourrait donc jouer un rôle majeur dans le maintien des deux tactiques résidante et anadrome au sein d'une même population (voir Moran 1992, Roff 1996, Mangel et Stamps 2001).

De nombreuses études suggèrent la présence d'un mécanisme conditionnel régulant l'expression de la migration dans les populations partiellement anadromes, basé sur la taille, la croissance (ou les perspectives de croissance) en eau douce au stade juvénile (Jonsson et Jonsson 1993 et p.e. Jonsson 1985, Metcalfe 1998, Forseth et al. 1999, Rikardsen et Elliott 2000, Thériault 2001, Morinville et Rasmussen 2003). Et bien que des parents résidants puissent produire des descendants anadromes, et vice-versa (voir Jonsson et Jonsson 1993), une héritabilité de certains traits liés à la croissance (p.e. taux métaboliques et efficacité de croissance, voir Forseth et al. 1999), ou de la croissance elle-même (p.e. Garant et al. 2002), pourrait expliquer une certaine héritabilité de la tactique exprimée (p.e. Nordeng 1983). De plus, comme il a été dit plus haut, le contexte théorique de la stratégie conditionnelle n'exclut pas la présence d'une sélection dépendante de la fréquence, et celle-ci pourrait agir comme facteur stabilisateur des proportions d'individus résidants et migrateurs dans les populations de salmonidés partiellement anadromes (p.e. Hutchings et Myers 1994).

Enfin, l'anadromie est une forme de dispersion et les forces agissant sur l'évolution de la dispersion - stochasticité démographique, variabilité spatiale, sélection de parentèle, dépression de consanguinité (passées en revue dans Castric 2002; voir aussi Clobert et al. 2001) - pourraient également agir sur l'évolution de l'anadromie.

1.3. Co-évolution de la migration et du cycle vital anadrome

Les patrons de migration d'une population ne sont pas aléatoires. La migration implique un ensemble de comportements spécialisés, apparus par sélection naturelle (Dingle 1980). Chaque changement d'habitat doit donc tendre vers la maximisation du fitness des individus migrateurs (voir Krebs et Davis 1993). C'est la différence entre les bénéfices et les coûts associés à un changement d'habitat, propres à un contexte environnemental donné, qui va modeler les patrons de migration d'une population (voir, par exemple, Gross 1987 dans le cas de la diadromie). Cependant, les coûts et les avantages immédiats associés à un changement d'habitat peuvent différer selon la taille des individus (Werner et Gilliam 1984). Par exemple, chez les salmonidés, les risques de stress osmotique (Hoar 1976, McCormick et Saunders 1987), de prédation et de maladies (Marschall et al. 1998) diminuent avec la taille. Le type de proies associées à un habitat particulier est également susceptible de convenir plus spécialement à une taille d'individus donnée (Keeley et Grant 2001). De plus, même dans un cas hypothétique où mortalité et croissance ne dépendraient pas directement de la taille, les modèles dynamiques d'écologie comportementale prévoient que les bénéfices (en terme de fitness) de tout acte comportemental peuvent varier avec l'âge, la taille et l'état physiologique des individus au moment où cet acte est entrepris (McNamara et Houston 1986, Mangel et Clark 1986, Ludwig et Rowe 1990). Une prédiction majeure dérive de ces modèles : les individus de valeur reproductive supérieure (par exemple, les juvéniles proches de la maturité sexuelle, les adultes de grande taille et en bonne condition) devraient adopter des comportements plus prudents parce qu'ils ont moins à gagner en augmentant encore leur valeur reproductive (par un accroissement en taille) qu'à perdre s'ils devaient mourir avant la reproduction (Clark 1994). Dans une population donnée, les patrons de migration sont donc susceptibles de changer en fonction de l'âge, de la taille et de la condition des individus. Le comportement migratoire et les paramètres du cycle vital devraient alors évoluer de façon conjointe, pour former des stratégies adaptatives qui procurent des avantages sélectifs dans un contexte environnemental spécifique (Hutchings et Morris 1985). L'analyse du cycle vital de populations migratrices est donc indissociable de l'analyse de leurs patrons de migration.

1.4. L'omble de fontaine, cycles de vie et problématique

L'omble de fontaine, *Salvelinus fontinalis*, est un salmonidé indigène du nord-est de l'Amérique du Nord (MacCrimmon et Campbell 1969). Dans de nombreuses rivières ouvertes sur les eaux estuariennes, cette espèce se présente sous les deux formes que l'on peut observer chez les salmonidés : la forme résidante, dont la vie entière se déroule en eau douce, et la forme anadrome, qui se reproduit en eau douce mais effectue des migrations entre l'eau douce et l'eau salée au stade juvénile et au stade adulte (Power 1980). La résidence en eau douce est observée chez les mâles et chez les femelles (Power 1980 et, p.e., Castonguay et al. 1982, Doyon et al. 1991).

Comme chez deux autres salmonidés typiquement polymorphes, l'omble chevalier, *Salvelinus alpinus*, et la truite brune, *Salmo trutta* (Northcote 1992 et p.e. Hindar et al. 1991), les formes résidante et anadrome d'omble de fontaine présentes dans un même cours d'eau peuvent appartenir à un seul et même pool génique (Jones et al. 1997, Castric 2002). Les déplacements de la forme anadrome sont généralement de courte durée (2 à 4 mois) et se limitent aux aires estuariennes et côtières proches de la rivière d'origine (White 1940, Wilder

1952, Smith et Saunders 1958, Power 1980 et références incluses, Dutil et Power 1980, Castonguay et al. 1982, Montgomery et al. 1990, Doyon et al. 1991, Lesueur 1993). La reproduction a lieu à l'automne mais les adultes entament leur montaison vers les sites de fraie dès l'été. Les ombles de fontaine anadromes atteignent généralement la maturité sexuelle durant leur deuxième ou troisième saison de croissance en eau salée et sont souvent itéropares (Power 1980). On observe cependant des différences majeures entre les populations. L'âge à la première dévalaison varie de un à sept ans (Randall et al. 1987). Et, bien que l'exploitation des zones estuariennes ait lieu généralement durant l'été, une variété de mouvements saisonniers ont été décrits à travers l'aire de répartition de *S. fontinalis* (passés en revue dans LeJeune 1987). L'importante variabilité des cycles de vie et des comportement observés chez l'omble de fontaine font de cette espèce un excellent modèle pour explorer la relation entre contexte environnemental, comportement migratoire et cycle vital.

Pour comprendre la problématique de l'évolution de l'anadromie chez l'omble de fontaine, il faut remettre ces observations récentes dans une perspective historique. La dernière colonisation du nord de l'aire de répartition de l'omble de fontaine date d'après le retrait final des calottes de glace ayant occupé cette zone durant la dernière période glaciaire, il y a environ 10 000 ans (Power 2001). Cette colonisation, discutée par Castric (2002), a donc été entreprise par des individus anadromes en provenance du sud. Ces individus ont fondé des populations où, à l'heure actuelle, s'expriment à la fois l'anadromie et la résidence. Les questions qui se posent aujourd'hui sont donc les suivantes : quels facteurs ont favorisé le développement (ou simplement l'expression) de la résidence en eau douce dans des populations dont les fondateurs étaient anadromes ? Dans le sud de l'aire de répartition de l'omble de fontaine, la tactique anadrome a presque entièrement disparue. Dans le nord de l'aire de répartition de l'espèce, les deux tactiques (résidence et anadromie) sont-elles en équilibre stable ou en évolution vers une stratégie basée sur la seule résidence en eau douce, comme dans les populations les plus anciennes (voir Castric 2002) ? Quels sont les facteurs qui peuvent favoriser le maintien de ces deux tactiques alternatives ?

L'objectif de cette thèse était d'explorer ces questions chez la population d'omble de fontaine de la rivière Sainte-Marguerite, Saguenay, Québec et, à partir de ce modèle, de mettre en évidence certains des facteurs clés dans l'évolution de l'anadromie chez les salmonidés. En outre, l'omble de fontaine anadrome est un poisson de plus en plus populaire auprès des pêcheurs sportifs. L'établissement de plans de gestion durable des populations exploitées nécessite une meilleure compréhension des patrons de migration et du cycle vital de cette espèces, ainsi que l'identification des facteurs qui peuvent favoriser ou défavoriser le maintien de l'anadromie dans ces populations.

1.5. Évolution de l'anadromie et stratégie de reproduction chez l'omble de fontaine : comment les individus maximisent-ils leur fitness par l'expression de l'anadromie ou de la résidence ?

Les mécanismes proximaux régulant l'expression de l'anadromie chez l'omble de fontaine de la rivière Sainte-Marguerite sont analysés par Thériault (2001) et Morinville et Rasmussen (2003). Une faible efficacité de croissance (des coûts métaboliques élevés), éventuellement associée à une faible croissance en eau douce, favorise une migration vers la zone estuarienne. Le projet de recherche présenté ici était axé sur les conséquences de l'expression de l'anadromie ou de la résidence sur le cycle vital et le succès reproducteur des individus ou, autrement dit, sur la façon dont les individus migrateurs et les individus résidants maximisent leur fitness par l'expression de l'anadromie ou de la résidence. L'étude du cycle de vie des ombles anadromes a été basée sur un échantillonnage direct au moment de la dévalaison et durant les périodes de croissance en estuaire, un suivi de la pêche sportive et un grand programme de marquage-recapture, en collaboration avec les pêcheurs sportifs. Les ombles résidants ne sont pas exploités et ont été échantillonnés directement dans trois tributaires de la rivière Sainte-Marguerite.

L'optimisation de la tactique anadrome ne peut être considérée que comme l'optimisation conjointe du cycle vital des individus anadromes et de leur patrons de migration, dans un contexte environnemental spécifique (voir ¶ 1.3). Cette étude avait donc pour premier objectif (Chapitre 2) de décrire les patrons de migration de la population d'ombles de fontaine de la rivière Sainte-Marguerite et de tester l'hypothèse selon laquelle les mouvements saisonniers des ombles anadromes changent en fonction de leur âge, de leur stade de maturité, de leur taille et de leur condition, et des opportunités et des contraintes environnementales spécifiques à leur aire de migration, la rivière Saguenay. Plus spécifiquement, nous avons voulu si vérifier si une augmentation de la valeur reproductive des ombles anadromes avec leur croissance en estuaire étaient associée à l'adoption de comportements migratoires moins risqués (voir Clark 1994). En outre, cette première partie était d'une importance primordiale d'un point de vue méthodologique. L'analyse du cycle vital d'une population en mouvement permanent peut être facilement biaisée par les lieux et les périodes d'échantillonnage de cette population. Il fallait donc savoir où et quand se trouvaient telle classe d'âge, telle classe de taille ou tel stade de vie avant d'analyser des échantillons obtenus en différents lieux et à différentes périodes de l'année. Enfin, la description des patrons de migration d'une population exploitée dans différents habitats en fonction de la saison, comme l'est la population étudiée, constitue un outil de gestion indispensable.

Comme chez de nombreuses populations de salmonidés (Randall et al. 1987), tous les ombles de fontaine anadromes de la Sainte-Marguerite n'entreprennent pas leur première migration au même âge. Si la croissance et la mortalité augmentent simultanément à l'entrée en estuaire, le moment de la migration est susceptible d'avoir un effet majeur sur la taille à un âge donné et la survie jusqu'à la reproduction, et donc sur le cycle vital et le succès reproducteur des individus anadromes. Dans le cadre théorique de la stratégie conditionnelle exposé ci-dessus, ce n'est pas la migration en soi qui doit être considérée comme une tactique alternative à la résidence mais les cycles de vie associés à une migration à un âge donné qui doivent être considérés comme autant de tactiques alternatives, au même titre que la résidence. Dans le chapitre 3, nous avons exploré les conséquences sur le cycle vital et le succès reproducteur d'une migration précoce ou d'une migration plus tardive. Notre principal objectif était de tester l'hypothèse selon laquelle 1) les migrants les plus jeunes maximisent leur fitness en maximisant leur croissance et en se reproduisant à une âge inférieur et/ou une taille supérieure, relativement aux migrants plus âgés et 2) les migrants plus âgés maximisent leur fitness en maximisant leur survie, relativement aux migrants plus jeunes, parce qu'ils bénéficient d'une meilleure survie à la dévalaison du fait de leur taille supérieure (Jonsson and Jonsson 1993, Økland et al. 1993). Explorer cette interaction entre âge à la migration, cycle de vie et succès reproducteur constituait la meilleure occasion d'entrevoir les liens les plus ténus entre les opportunités et les contraintes associées au comportement anadrome, l'expression de ce comportement et la valeur sélective de cette expression. Les résultats obtenus donnent une base empirique pour discuter des facteurs qui peuvent favoriser le maintien de différents âges à la migration au sein d'une même population.

Enfin, qu'ils soient intrinsèques aux individus ou environnementaux, les facteurs qui régulent l'expression de la résidence en eau douce devraient être principalement ceux qui affectent la façon dont certains individus peuvent maximiser leur succès reproducteur en restant en eau douce. Dans le quatrième chapitre, nous sommes intéressés à l'effet de l'isolation géographique, de la compétition intra- et inter-spécifique et des fluctuations environnementales sur le cycle de vie d'ombles résidants, parmi des communautés différant par leur tendance à la migration. Nous avons comparé le cycle vital des ombles de trois tributaires de la rivière Sainte-Marguerite, en deux années différentes. Un de ces tributaires est isolé du reste de la rivière depuis 35 ans et aucune dévalaison d'ombles juvéniles n'y est observée à l'heure actuelle. Les deux autres tributaires sont caractérisés par une montaison d'ombles anadromes et par la présence de juvéniles de saumon atlantique (*Salmo salar*). La dévalaison d'ombles juvéniles est plus importante dans le tributaire présentant les plus grandes opportunités de compétition inter-spécifique Notre premier objectif était d'évaluer si les ombles du ruisseau isolé ne migrent parce que 1) les perspectives de croissance sont supérieures dans ce tributaire (voir Morita et al. 2000) ou 2) parce qu'une sélection « de bord d'abîme » (les individus qui ont dévalé après l'isolation n'ont jamais pu revenir et contribuer aux générations suivantes) a eu pour conséquence la perte du comportement anadrome et/ou modifié la norme de réaction des ombles face à leur perspectives de croissance en eau douce i.e. leur seuil de croissance pour la maturation sexuelle en eau douce est différent de celui des ombles des deux autres tributaires. Notre deuxième objectif était de tester l'hypothèse selon laquelle les ombles du ruisseau caractérisé par la dévalaison la plus importante ont de plus faibles opportunités de croissance et de plus faibles perspectives de reproduction en tant que résidents en eau douce. Deux années d'échantillonnage ont permis d'évaluer si la variabilité environnementale peut avoir un effet sur le succès reproducteur des ombles résidants, une fois qu'ils ont exprimé la tactique résidante.

2. Seasonal and ontogenetic patterns in the migration of anadromous brook charr (*Salvelinus fontinalis*).

Sophie Lenormand, Julian J. Dodson and Annie Ménard

2.1. Résumé

Les patrons de migration de l'omble de fontaine anadrome de la rivière Sainte-Marguerite, Québec, Canada, ont été étudiés dans le but d'explorer l'hypothèse voulant que le comportement migratoire des individus change en fonction de la taille lors de la période critique de la première dévalaison mais aussi lors des mouvements saisonniers ultérieurs, car les individus de taille supérieure se doivent d'adopter des comportements moins risqués pour protéger leurs atouts reproductifs. La première dévalaison se déroulait sur un mois, au printemps, mais les migrants les plus petits descendaient la rivière en dernier et semblaient retarder leur migration vers le large. Tel que prédit, les patrons de migration des ombles changeaient au cours de leur ontogénie et, plus les poissons grandissaient et augmentaient leur valeur reproductive, plus ils adoptaient des comportements prudents. Les juvéniles d'âge en mer 0 restaient en estuaire jusqu'en octobre et passaient l'hiver hors de leur rivière natale. Les juvéniles d'âge en mer 1 regagnaient leur rivière natale plus tôt à l'automne et une partie d'entre y passaient l'hiver. Les adultes (une partie des migrants d'âge en mer 1 et les migrants d'âge en mer supérieur) entreprenaient leur migration vers les sites de fraie de juillet à septembre, les plus grands plus tôt que les plus petits. Les géniteurs dévalaient à nouveau après la reproduction ou passaient l'hiver en rivière. Les différences environnementales associées à la situation géographique peuvent expliquer les variations des patrons de migration et du cycle vital qui sont observées entre les populations d'ombles de fontaine, mettant en évidence l'évolution conjointe du comportement anadrome et du cycle vital.

2.2. Abstract

Migration patterns of anadromous brook charr from the Sainte-Marguerite River, Québec, Canada, were investigated to explore the hypothesis that migratory behaviour of individuals changes according to size during the critical period of first downstream migration, when survival is likely to be related to size, but also during subsequent seasonal movements, as larger fish should be more averse to risk in order to protect their reproductive assets. First downstream migration occurred over a month in spring but smaller charr migrated last and seemed to delay offshore migration. As predicted, migratory patterns of charr changed through ontogeny and, as fish grew and accumulated fitness assets, they adopted more conservative behaviours. Sea age 0 juveniles stayed in estuarine areas until October and over-wintered outside their natal river. Sea age 1 juveniles returned to their natal river earlier in the fall and part of them over-wintered there. Adults (part of sea age 1 migrants and older migrants) undertook their upstream migration to spawning areas from July to September, larger ones moving earlier than smaller ones. Post-spawners either migrated downstream or over-wintered in the river. Environmental differences related to geographical location may be responsible for the variation of migration patterns and life-histories observed among brook charr populations, emphasizing the co-evolution of anadromous behaviour and life-history.

"being killed greatly decreases future fitness." (Lima and Dill 1990)

2.3. Introduction

Migration involves specialized behaviours that have arisen through natural selection (Dingle 1980). Therefore, migrants are expected to maximize their fitness by changing habitats when appropriate (Krebs and Davis 1993). From this evolutionary perspective, Gross (1987) developed a model for understanding diadromy in fish: individuals would migrate if "the growth and survivorship advantages of utilizing a second habitat, plus the cost of moving between habitats,... exceed the advantages of staying in only one habitat for the same period of time". As far as anadromy in salmonids is concerned, though moving to salt water involves energetic costs, osmotic stress and a higher predation risk than in fresh water, the fitness payoff of migration to sea results from an enhanced growth rate in a richer feeding area (Jonsson and Jonsson 1993).

Salmons (*Oncorhyncus gorbuscha*, *O. keta*, *O. kisutch*, *O. masou*, *O. nerka*, *O. tshawytscha* and *Salmo salar*) undertake only two transitions between fresh and salt water before reproduction: one at smolting and another when mature individuals return to reproduce. However, in many charrs (*Salvelinus*) and trouts (e.g. *Oncorhyncus clarki*, *Salmo trutta*) populations, fish move back and forth between their natal rivers and estuarine areas at the juvenile and adult stages (Randall et al 1987). As in salmon, some of their movements are clearly ontogenetic in nature. There is first a downstream migration, whose timing depends on size and growth rate (e.g. Økland et al. 1993, Rikardsen et al. 1997, Thériault 2001) and an upstream migration to spawning areas. Other movements are related to seasonal changes affecting the habitats they exploit. Juveniles and adults tend notably to over-winter in their natal river (Randall et al. 1987). According to the model of Gross (1987), such observations imply that the growth/mortality trade-off constraining anadromy is altered by seasonal changes.

The immediate advantages and costs of staying in a given habitat may vary with individual body size (Werner and Gilliam 1984). In salmonids, a common example of size-dependent costs of migration to salt water is the migratory or post-migratory size-selective mortality observed in several species (references in Bohlin et al. 1996). Moreover, even in the absence of size-dependent effects on growth or mortality, dynamic models suggest that life-time fitness benefits of any behavioural act may depend on individuals' age, size or physiological state at the time that act is performed (McNamara and Houston 1986, Ludwig and Rowe 1990, Clark 1994). Namely, individuals with greater reproductive value (e.g. juveniles close to size at maturity, adults with a large size and in good condition) should be more averse to risk predation because they would gain less from a given absolute increase in assets relative to what they would lose if caught by a predator (Clark 1994). Therefore, we would expect that the migratory behaviour of salmonids carrying out seasonal movements changes according to individuals' age (or sea age, age since migration, when growth is more a function of sea age than of total age), maturity stage, size and condition.

Though this issue has never been studied as such, there is some evidence that seasonal migrations differ according to individuals' size in several charr and trout populations. For instance, larger individuals return to fresh water sooner than smaller ones (e.g. Castonguay et al. 1982, Dempson and Green 1985, Jonsson 1985, Gulseth and Nilssen 2000). The work of Castonguay et al. (1982) also suggested that smaller brook charr (*Salvelinus fontinalis*), corresponding to migrants-of-the-year, do not return to the Saint-Jean River at the end of the summer growing season. If such size or age-dependent patterns exist, their study is of major importance for the protection and enhancement of salmonid populations. First, the identification of life stages exposed to exploitation according to area and time of year is an obvious pre-requisite to the establishment of successful local management plans. Moreover, the effectiveness of conservation policies relies on a good understanding of the evolution of salmonid life-history, which is intimately connected with anadromy. Life-history traits and migratory behaviour should co-evolve to form adaptive strategies which convey selective advantages in specific environmental settings (Hutchings and Morris 1985). Ontogenetic patterns in the migration of salmonid populations would represent optimal behavioural paths towards the maximization of fitness and may provide interesting insights into the evolution of anadromy.

The brook charr is native to eastern North America where it is one of the most popular game fishes. Like many salmonids, it may exist as migratory and freshwater resident forms that differ in life-history patterns (Power 1980). Marine movements of anadromous brook charr are of short duration (2-4 months) and seem to be limited to estuarine and coastal regions nearby their natal river (Power 1980 and references therein, Castonguay et al. 1982, Montgomery et al. 1990). Reproduction takes place in the fall but adults start their upstream migration during the summer. Anadromous brook charr usually mature during their second or third growing season in salt water and multiple spawning is common (Power 1980). There are, however, significant differences between populations. Ages at first downstream migration range from one to seven years (Randall et al. 1987). Although exploitation of estuarine areas usually takes place during the summer, a variety of seasonal movements has been described throughout the *S. fontinalis* distributional range (for a review, see Lejeune 1987). The extensive life-history and behavioural differences observed in brook charr makes this species a particularly interesting model to explore the relationship between anadromous behaviour and the evolution of life-history (see Dodson 1997).

In the present study, we tested the hypothesis that migratory behaviour of anadromous brook charr changes according to size during the critical period of first downstream migration (when survival is likely to be related to size) but also during subsequent seasonal movements, as larger fish should be more averse to risk in order to protect their reproductive assets. Migratory patterns were investigated combining a monitoring of first downstream migration, direct sampling in estuarine areas, creel census and a mark-recapture experiment, in collaboration with anglers. Seasonal movements were analysed according to sea age, maturity stage and size of individuals. We predicted that, as migrants grow, they should opt for more conservative behaviours.

2.4. Materials and methods

2.4.1. Study Area

The Sainte-Marguerite River (48°27' N, 69°95' W; Figure 2-1) empties into the Saguenay Fjord, 25 km upstream from its confluence with the Saint-Lawrence maritime estuary (Québec, Canada). It is divided in two main branches: the Principal branch and the

North-East branch; each is 100 km long, approximately 25 m wide and drains an area of 1 000 km^2. Daily flows range between 10 m^3.s^{-1} (February) and 430 m^3.s^{-1} (May). The river is ice-covered from December to April. Maximum observed water temperature during the study was 25°C (July). In addition to brook charr, the river also contains Atlantic salmon (*Salmo salar*) and, to a lesser extent, longnose and white sucker (*Catastomus catastomus* and *C. commersoni*), longnose dace (*Rhinichthys cataractae*), fallfish (*Semolitus corporalis*) and American eel (*Anguilla rostrata*). Predators of anadromous charr present in the river are merganser (*Mergus merganser*), mink (*Mustela vison*), osprey (*Pandion haliaetius*) and river otter (*Lutra canadiensis*).

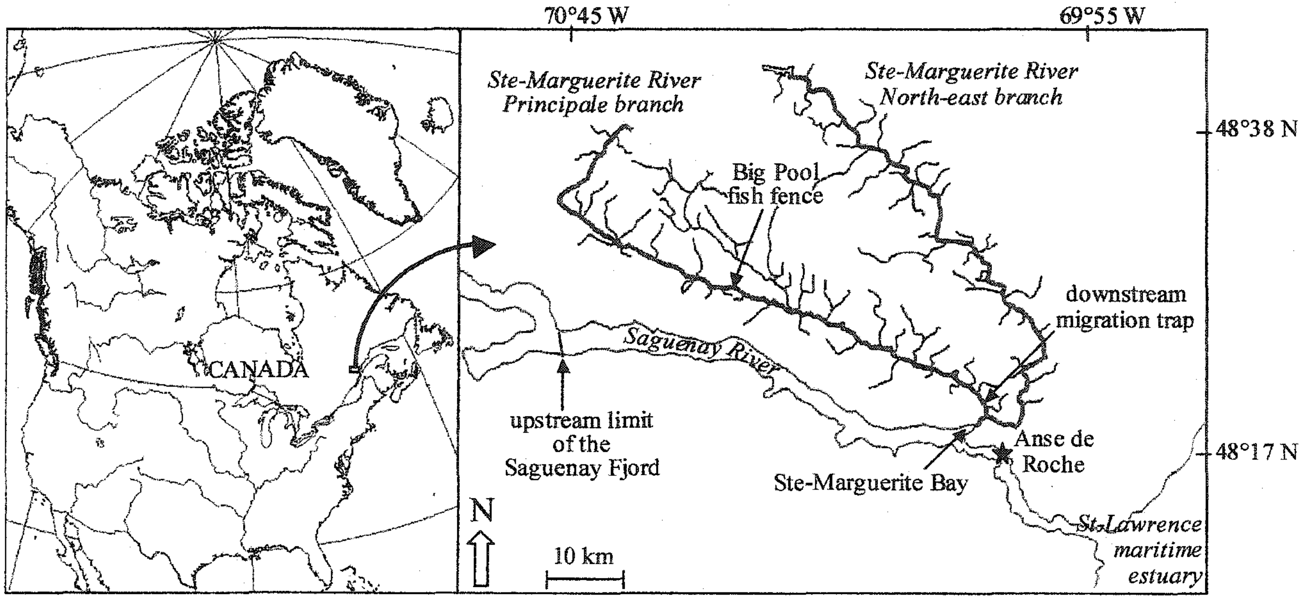

Figure 2-1. Location of the Sainte-Marguerite/Saguenay river system and of sampling sites.

Anadromous charr migrate to the Sainte-Marguerite River estuary which forms a large shallow bay named the Sainte Marguerite Bay. From there, they have access to the Saguenay River (Figure 2-1). The 100 km downstream part of the Saguenay River (the Saguenay Fjord), under tidal influence, is a mixing zone between fresh water from upstream and salt water from the Saint-Lawrence maritime estuary. In a sub-arctic fjord such as the Saguenay, fresh water inputs are considerable and show important fluctuations. From May to October, a very strong thermo-haline stratification is observed. The water column is divided into a thin mixed layer (5-10 m) of warm (5-15°C), brackish (0-18 PSU (practical salinity units)) water and a thick (up to 275 m), underlying layer of cold and saline water (< 0.5°C, > 26 PSU at 15 m). In the fall, as surface temperature decreases, exchanges between the two layers increase and salinity at the surface rises to 22 PSU in November. During the ice-cover period (December to April), surface temperature stays around 0°C and surface salinity stabilizes at low values (under 7 PSU *vs.* 20 PSU at 10 m). From mid-March to the beginning of May (ice-melt period), the increase of freshwater inputs and surface water temperature gradually restores the summertime thermo-haline stratification (Chassé and Côté 1991 and references therein).

The Saguenay River is characterized by a low primary production but high densities of zooplankton (Drainville 1970). At least 410 species of marine benthic invertebrates are present in the fjord (ZIP-Saguenay 1998). Among them, amphipods (Gammaridae), mysids and polychaetes probably constitute major prey items for juvenile anadromous brook charr, as observed in other estuaries (White 1940, Gaudreault et al. 1982). Fish populations are also relatively diverse, with 76 species recorded to date. Common prey of large (more than 25 cm) anadromous charr are present: smelt (*Osmerus mordax*), sticklebacks (*Gasterosteus aculeatus* and *Pungitius pungitius*) and sand lances (*Ammodytes* spp.). High productivity and abundance of large prey (large invertebrates and fish) are two factors that may explain the fast growth of salmonids in the sea, relative to river systems (Keeley and Grant 2001). Thus, as in many estuaries, the Saguenay should constitute a better feeding habitat than charrs' natal river, especially in winter when prey are still abundant in the former area. However, mortality of anadromous charr migrating to the Saguenay is much higher than mortality of freshwater resident charr from the Sainte-Marguerite River (Chapter 3, Chapter 4), indicating that the estuary is a more risky habitat than the river. Potential predators of anadromous charr in the Saguenay are cormorant (*Phalacrocorax auritus*), heron (*Ardea herodias*), loon (*Gavia immer*), merganser (*Mergus merganser*), osprey (*Pandion haliaetius*), harbor seal (*Phoca vitulina*) and Greenland shark (*Somniosus microcephalus*).

2.4.2. Sampling and mark-recapture experiment

Anadromous brook trout were sampled and tagged at different life-stages during four years (1998-2001). In 1999 and 2000, descending charr were caught by an Alaskan trap (1 cm mesh) set on the Principal branch of the Sainte-Marguerite River, at 7 km from the river's mouth (Figure 2-1). Monitoring started just after the ice break-up period, when discharge was beginning to decrease and ended when catches had been minor (less than 20 fish per day) for 10 consecutive days. The trap covered one third of the river and caught at least 1 000 charr every year. Fish were measured (fork length (FL), to the nearest mm). Twelve percent of total catches in 1999 and 10% in 2000 were sacrificed for laboratory analyses (see below). The rest of the fish were marked with clear, individually labelled T-bar anchor tags (Floy FF-94), providing that their fork length was greater than 75 mm. Tag retention was tested in aquarium on 20 fish ranging from 75 mm and 132 mm FL. No tag loss, mortality or serious injury was observed after 3 months.

In the Sainte-Marguerite Bay, sampling and tagging of anadromous juveniles was carried out by approximately weekly hauls of a 40-m beach seine (0.5 cm mesh, 1.5 m deep) in September and October 1998, from the beginning of May until mid-October in 1999 and 2000, and in May 2001. All the fish caught by seining were measured; recaptures were recorded and untagged fish were marked with T-bar tags (Floy FF-94). In July 1999, we took two additional seine samples in a deeper, colder and more saline area of the Saguenay Fjord, Anse de Roche (Figure 2-1), where several migrants-of-the-year had been recaptured by anglers. Every year, anadromous spawners were sampled during their upstream migration by inserting a trap into the Big Pool (Figure 2-1) fish fence (wire covered by a net, 4 cm mesh). The fence only operates in July and serves to delay the upstream migration of Atlantic salmon for conservation purposes. An additional seine haul (5 cm mesh) was made at the same location at the end of August to complete the sampling. All fish were measured and those that were not recaptures were tagged with T-bar tags (Floy FD-94).

Fishing for anadromous charr is permitted in the Saguenay River (including Sainte-Marguerite Bay) all year long and in the Sainte-Marguerite River, from June 15 to October 31. Tag returns from the sport fishery were encouraged with a 5 $ cash reward and the opportunity to participate in an annual draw for prizes. In 1998, 1999 and 2000, we completed the mark-recapture experiment by a creel census in the Sainte-Marguerite River and the Sainte-Marguerite Bay. Two registration stations were operated, at 30 km upstream on the river and at the river's mouth. Catches were measured and weighed. In the fall, future or post-spawners were identified according to external signs of maturation (hooknose, orange to black belly and sperm outflow by abdominal stripping in males; dilation of urogenital papilla and egg outflow by abdominal stripping in females). Sub-samples of fish were dissected for more detailed analysis (see below) on a regular basis. In winter, as angling is forbidden in the Sainte-Marguerite River, we made two additional samplings under ice cover, using four rods baited with worms and corn : in the downstream pools of the Sainte-Marguerite, on 20 February 2000 and 31 January 2001, and at the river mouth, on 1 and 16 February 2001. All the fish caught were sacrificed for laboratory analysis.

Charr that had been sacrificed or sampled from anglers (tagged fish and sub-samples of untagged fish) were measured, weighed and classified with respect to sex and maturity stage (Nikolskii 1963). Stomach contents were analysed for a related study (conducted by Geneviève Morinville and Joe Rasmussen, McGill University, Montreal). Sagittal otoliths were removed, cleaned and fastened to glass slides with a clear mounting adhesive at its melting point (50°C). After hardening of the adhesive, total age and age at downstream migration were read under a binocular microscope, using reflected light. Age at downstream migration was determined at the first major increase of annulus width (Figure 2-2). This method was tested on fish that were recaptured after growth in salt water but which had been tagged during their downstream migration (i.e. fish for which sea age was already known): 95% of 545 fish (528) were successfully re-classified based on sea age.

2.4.3. Data analysis

First downstream migration was characterized according to age and body size of migrating charr. Seasonal migratory patterns were analysed according to sea age, maturity stage and body size of migrants. Differences in length between two groups were tested by two-tailed Student t-test when data met the required assumptions and by Mann-Whitney U test otherwise. Proportions were compared by chi-square test (using Yate's correction for continuity when some expected frequencies became less than 10).

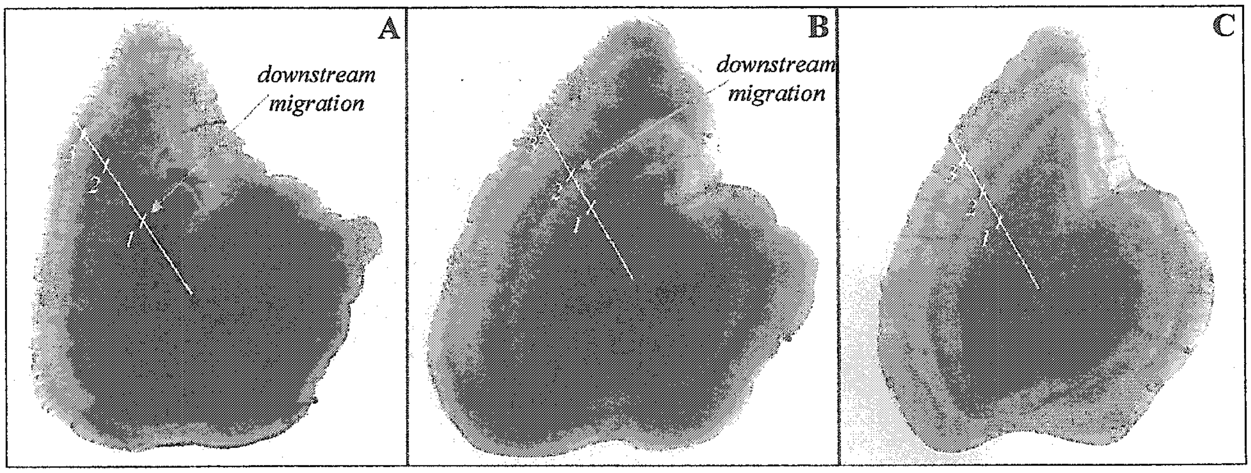

Figure 2-2. Left sagittal otolith of age 3 brook charr caught in the Sainte-Marguerite River (Big Pool, July 2000) with different migratory patterns: A) charr having migrated at age 1, B) charr having migrated at age 2 and C) freshwater resident charr. Downstream migration is characterized by a major increase of annulus width. Numbers in italics indicate beginning of year *n*. Otoliths B and C were enlarged relative to otolith A to enhance comparisons.

2.5. Results

2.5.1. First downstream migration

The monitoring of downstream migration in 1999 and 2000 resulted in the capture of 1483 and 1019 migrants-of-the-year, respectively. Sub-samples of 178 fish in 1999 and 92 in 2000 were used for age determination. According to the temporal distributions of catches in the trap (Figure 2-3), we probably missed the onset of downstream migration in 1999. However, the first significant catches of first-time migrants in Sainte-Marguerite Bay (SMB) started four days after the trap was installed in the river and included tagged in the trap. Therefore, the migration peak we observed on the first day of monitoring was most likely the first one. In both years, the out-migration of brook charr was concentrated over a month (Figure 2-3). Migration time (days after first day of monitoring) decreased with length of migrating charr (1999, slope = -0.116, $R^2 = 0.07$, $p < 0.0001$ and 2000, slope = -0.083, $R^2 = 0.05$, $p < 0.0001$), indicating that larger fish migrated earlier than smaller ones.

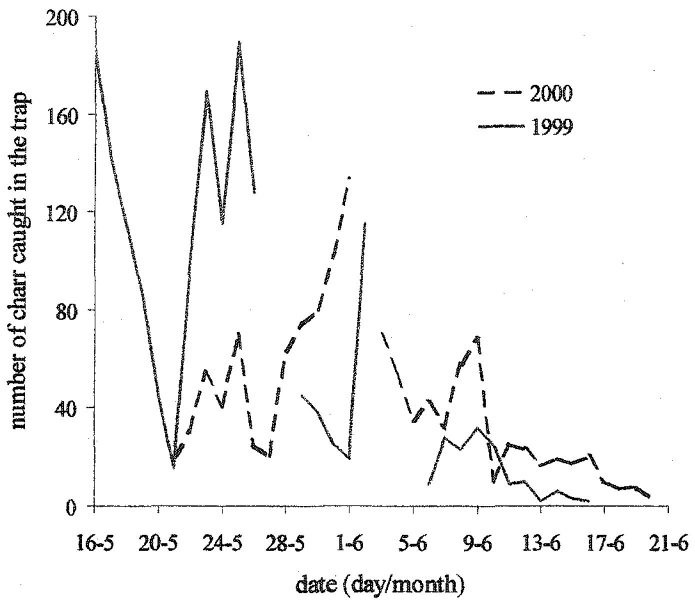

Figure 2-3. Number of emigrating brook charr caught per day set on the Principale branch trap of the Sainte-Marguerite River, Québec, in 1999 and 2000. Absences of data points correspond to days where traps were not in function due to high water flow.

There was no significant difference in the length of emigrating charr between 1999 and 2000 samplings (Figure 2-4): 1999, mean length = 111.8 mm and 2000, mean length = 112.4 mm, Mann-Whitney U test, $z = -1.19$, $p = 0.23$. Charr belonged to three age classes : 1+ (29% of migrants in 1999 and 26% in 2000), 2+ (68% of migrants in 1999 and 69% in 2000) and exceptionally 3+. Fish migrating at age 2 were significantly bigger than fish migrating at age 1 (1999, 2+ length ± S.D. = 118,4 ± 14,7 mm and 1+ length = 89.0 ± 9.8 mm, $t = -14.8$, $p < 0.001$; 2000, 2+ length = 114.5 ± 16.2 mm and 1+ length = 91.0 ± 10.8 mm, $t = -7,33$, $p < 0.0001$). None of the sampled fish showed any signs of a previous reproduction.

When they entered the SMB, migrants-of-the-year (sea age 0 migrants) could be easily distinguished from migrants of greater sea age because of almost no over-lap between length distributions of sea age 0 and sea age 1 charr: by the third week of May 1999 and 2000, more than 97% of charr that had migrated the previous spring (sea age 1) had a fork length greater than 155 mm (seine sampling, 1999, n = 43, 2000, n = 49) while more than 99% of new migrants had a fork length smaller than 155 mm (Figure 2-4).

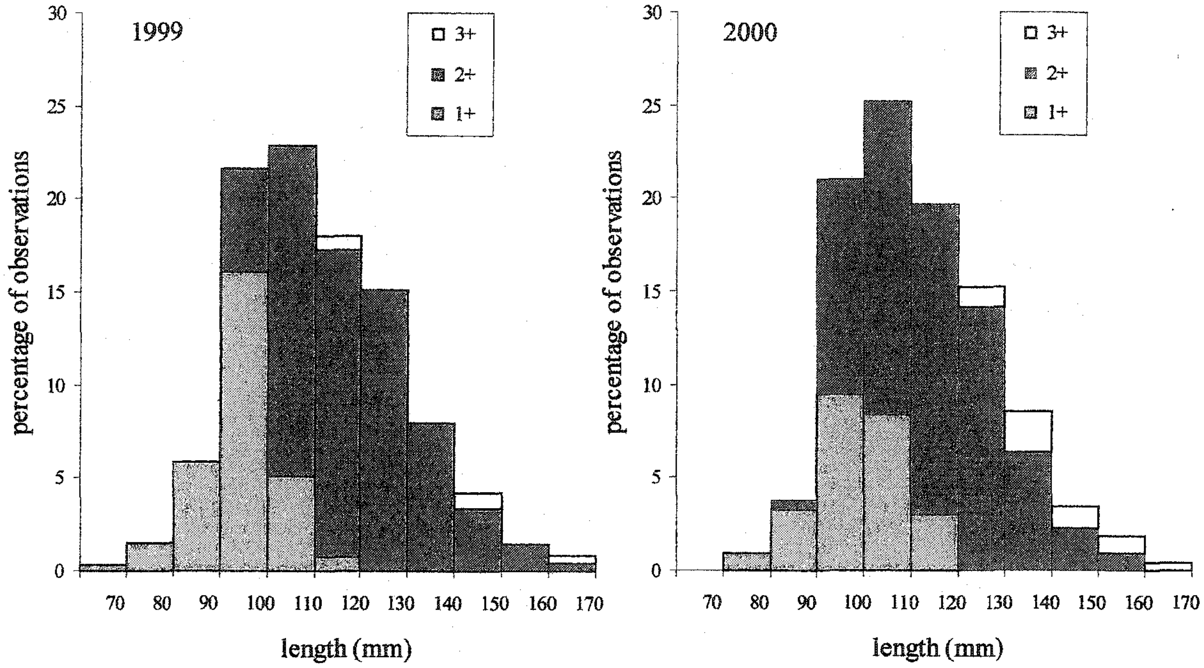

Figure 2-4. Fork length frequencies of all emigrating brook charr caught in the trap set from mid-May to mid-June on the Sainte-Marguerite River, Québec, in 1999 (n=1483) and 2000 (n=1019), and distribution of ages in length classes according to the relative frequencies of age classes in each length class (sacrifices, 1999, n = 178 and 2000, n = 92).

2.5.2. The tagging program

A total of 8412 charr were marked with T-bar tags from September 1998 until August 2001. We recaptured 1262 (15.0%) of these fish during subsequent samplings. Anglers from the Sainte-Marguerite River (SMR) and the Saguenay River reported 1402 catches of tagged fish (16.7%) prior to December 2001. Only three charr were recaptured in estuarine areas out of the Saguenay Fjord. These fish were caught in the Saint-Lawrence River, at less than 20 km from the Saguenay River mouth. We did not observe any effect of tagging on growth: length distributions of fish tagged at migration and recaptured one year later did not differ significantly from length distribution of untagged fish of the same sea age (May 2000, untagged charr, n = 29, length ± S.D. = 230.7 ± 42.4 and tagged charr, n = 39, length = 235.6 ± 30.6, t = 0.56, p = 0.58; May 2001, untagged charr, n = 29, length = 220.7 ± 36.3 and tagged charr, n = 49, length = 225.5 ± 22.6, t = -0.73, p = 0.47). In addition, no size-specific mortality due to tagging was detected: length distributions, at the time of downstream migration, of fish recaptured one year after migration did not differ significantly from length distributions revealed by downstream migration monitoring (Mann-Whitney U test, 1999 downstream migration, 54 recaptures in 2000, p = 0.87 and 2000 downstream migration, 34 recaptures in 2001, p = 0.54). The latter observation also shows the complete absence of size-specific mortality following downstream migration.

2.5.3. Temporal evolution of catches and recaptures of tagged fish, according to sea age, maturity stage and body size

2.5.3.1. Spring

Temporal patterns of beach seine catches in SMB were similar in all four years with respect to the presence or absence, and size of migrants. Analysis of the evolution of the length of anadromous charr caught in the bay, on a weekly basis, from May to October 1999 and 2000 (when sampling was the most extensive) revealed that the largest fish were found at the end of April/beginning of May, just after the ice-melt (Figure 2-5). Sampling of anglers' captures (n = 14, length ± S.D. = 386.1 ± 64.2 mm, Figure 2-6) and analysis of recaptures (Table 2-1) showed that these charr were mainly migrants of sea ages ≥ 2 (more than 90% of sampled fish and of tag returns in early spring 1999 and 2000). Most of these fish were caught directly at the river mouth and all had the characteristics of kelts which had over-wintered in the river after spawning (dark colour, low condition factor, frailty, white flesh, empty and contracted stomachs). All sea age 3 migrants but only 5 out of 12 sea age 2 migrants were identified as spawners from the previous year (hook nose in males, well developed but flabby gonads, presence of a few remaining ovulated eggs in females) and recaptures included fish tagged on the spawning grounds. At the same period, charr of sea ages ≥ 2 were also recaptured in the upstream part of the Saguenay River (essentially in fresh water, Table 2-1), but were more silvery in colour and in better condition.

From mid-May to the beginning of June 1999 and mid-May to mid-June 2000, we observed a progressive decrease in the length of charr present in the SMB (Figure 2-5), related to successive shifts in sea age structure. Firstly, the decrease of maximum observed length in seine hauls corresponded to a progressive disappearance of the oldest migrants in anglers' captures (Figure 2-6) and recaptures (Table 2-1). Secondly, this period included peak catches of sea age 1 and 2 charr in the SMB (Figure 2-6 and Table 2-1). Before the third week of May, sea age 1 migrants were almost exclusively recaptured in the Saguenay River, upstream from the SMB (Table 2-1). Anglers from the SMB call charr that arrive by mid-May "blue trout" because of their silver-blue colour. They are also characterized by their orange flesh, originating from intensive feeding on marine crustaceans (Geneviève Morinville, McGill University, Montreal, personal communication). Lastly, by the third week of May, migrants-of-the-year entered the bay, which induced a decrease in the mean length of charr caught by seining.

2.5.3.2. Summer

Significant numbers of migrants-of-the-year were caught by seining in the SMB every week from the third week of May until the last week of July (Figure 2-5). However, tag returns showed that some sea age 0 charr left the SMB as soon as the first week of June, migrating to upstream or downstream areas of the Saguenay Fjord (Table 2-1). Migrants-of-the-year sampled at Anse de Roche (Figure 2-1) on July 1 and 2, 1999 were significantly larger than migrants-of-the-year sampled in the SMB on 4 July 1999 (Anse de Roche, $n = 83$, mean length = 143.2 and SMB, $n = 96$, mean length = 132.0, Mann-Whitney U test, $z = 3.27$, $p = 0.001$). As smaller migrants were not large enough to be targeted by anglers in June and July, we could not use recaptures from the sport-fishery to compare the length at tagging of charr that migrated first to deeper, colder and more saline areas of the Saguenay Fjord with the length of charr that stayed longer in the SMB.

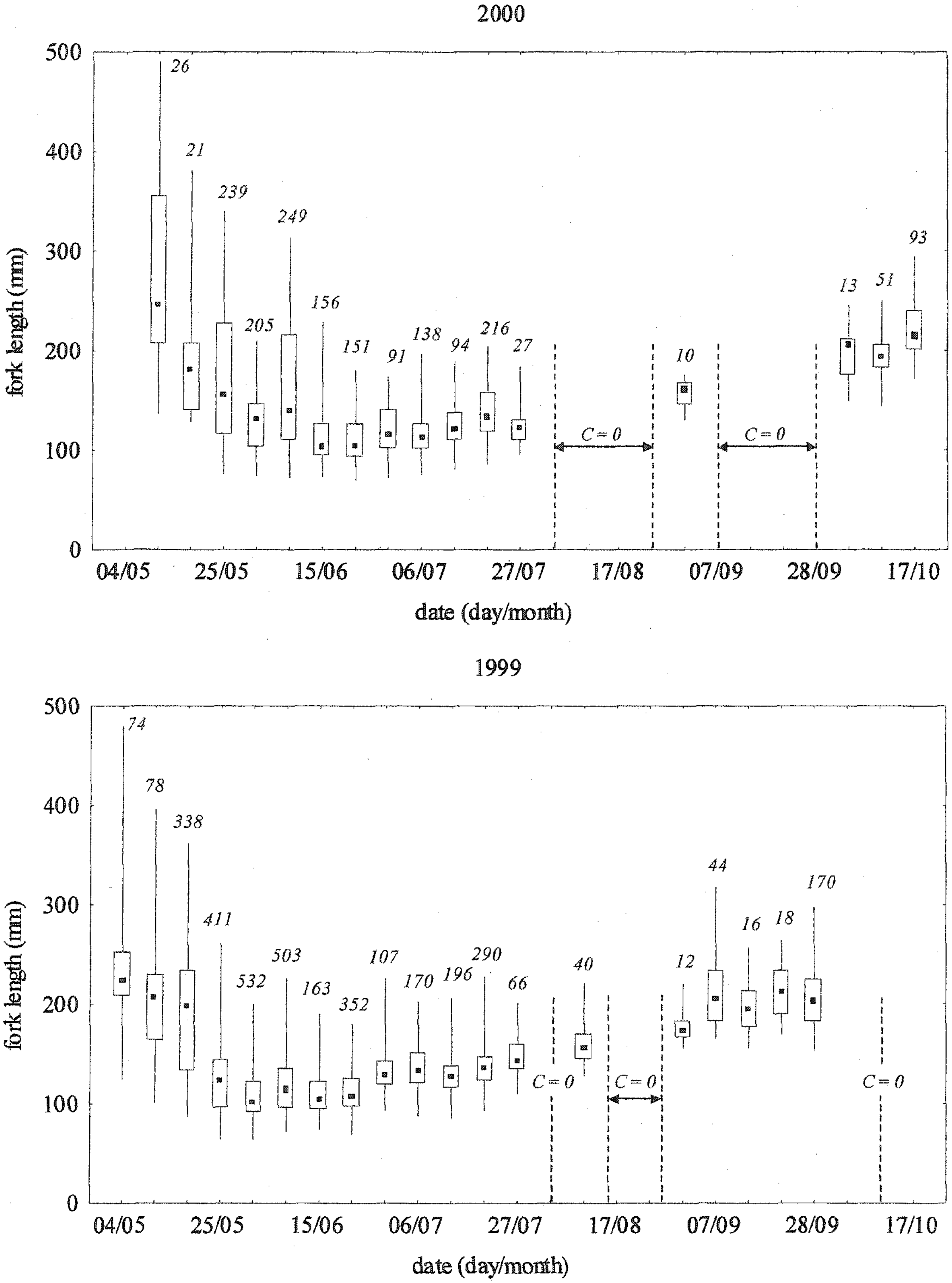

Figure 2-5. Temporal evolution of length (median, 25-75% range, total range) of brook charr caught by seining in the Sainte-Marguerite Bay, Québec, in 1999 and 2000, on a weekly basis. Numbers in italics are the numbers of charr caught per week (fishing effort was increased when catches were low).“ C = 0 ” indicate that no fish could be caught though fishing effort was maximal.

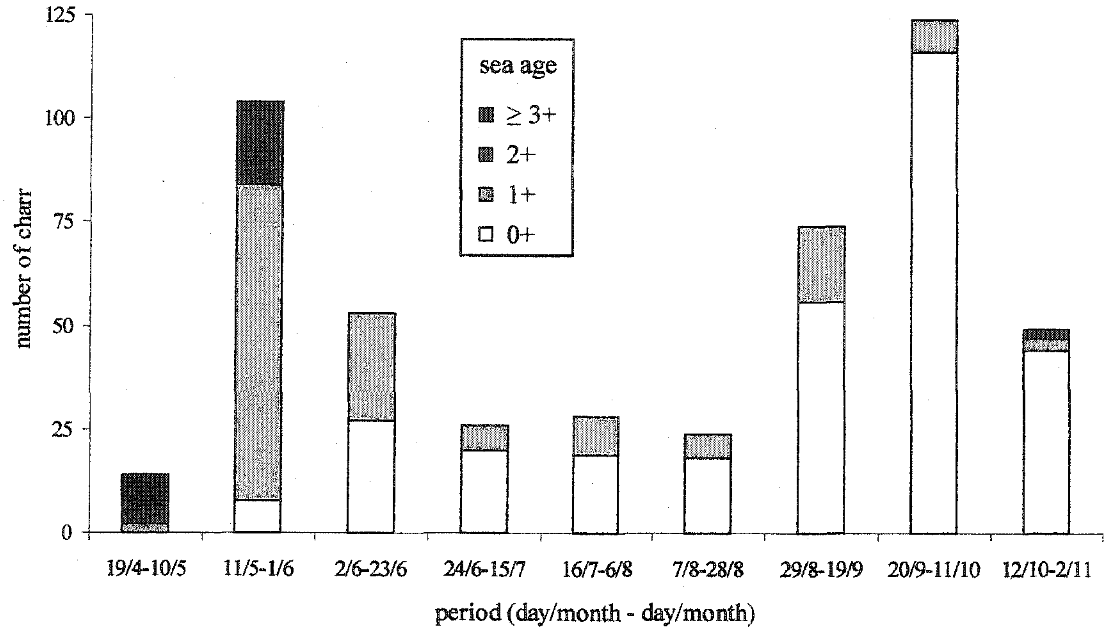

Figure 2-6. Number of brook charr sub-sampled for laboratory analysis while monitoring sport-fishery in the Sainte-Marguerite Bay, Québec, according to date and sea age (1998-2000, pooled data). Numbers of sampled fish per period were approximately proportional to catches. Percentages of each sea age class for a given period did not differ between years (χ^2 test, $p > 0.2$ in all cases).

Table 2-1. Number and mean length (± S.D) of tagged brook charr from the Sainte-Marguerite River, Québec, reported by anglers, according to date, area and sea age. Data were pooled over the 1999-2001 experiment period. Tags return rates at a given sea age were similar every year. Fish recaptured less than two weeks after tagging were omitted. Proportions of recaptures according to sea age do not represent absolute proportions of sea age classes but comparisons may be made between cells, except those including sea age 0 charr in May-July, due to their small size for the sport-fishery. "S"= spawners, "P-S"= post-spawners.

Date	Sea age	Area					
		Saguenay freshwater	Fjord, upstream SMB	Ste-Marguerite Bay (SMB)	Fjord, downstream SMB	River downstream	River upstream
19 Apr.-10 May	0+	***0***	***0***	***0***	***0***	no angling	no angling
	1+	***4***; 254.3 ± 9.0 (0 P-S)	***4***; 251.0 ± 21.2 (0 P-S)	***1***; 293 (0 P-S)	***1***; 240 (0 P-S)		
	2+	***6***; 363.0 ± 47.8 (3 P-S)	***3***; 328.3 ± 36.2 (3 P-S)	***5***; 370.5 ± 20.8 (2 P-S)	***0***		
	≥ 3+	***6***; 456.0 ± 72.2 (6 P-S)	***1***; 430 (1 P-S)	***16***; 466.7 ± 49.0 (16 P-S)	***0***		
11 May-1 June	0+	***0***	***0***	***3***; 154.7 ± 26.9 (0 P-S)	***0***	no angling	no angling
	1+	***4***; 226.4 (1 meas.) (0 P-S)	***2***; 250 (1 meas.) (0 P-S)	***64***; 230.6 ± 29.6 (2 P-S)	***10***; 216.5 ± 27.2 (0 P-S)		
	2+	***7***; 355.2 ± 45.7 (4 P-S)	***2***; 355.5 ± 50.2 (1 P-S)	***28***; 341.6 ± 37.8 (7 P-S)	***3***; 359.7 ± 48.6 (0 P-S)		
	≥ 3+	***8***; 446.3 ± 46.0 (8 P-S)	***3***; 469.0 ± 32.6 (3 P-S)	***4***; 435.0 ± 24.3 (4 P-S)	***2***; 481.5 ± 0.7 (2 P-S)		
2 June-23 June	0+	***0***	***1***; 153	***34***; 159.4 ± 15.8	***6***; 166.7 ± 14.6	***0***	***0***
	1+	***2***; 266 (1 meas.)	***8***; 265.0 ± 42.4	***41***; 231.4 ± 29.7	***27***; 246.5 ± 23.7	***0***	***0***
	≥ 2+	***2***; 455.5 ± 62.9	***2***; not measured	***0***	***18***; 422.9 ± 48.3	***0***	***0***
24 June-15 July	0+	***0***	***5***; 154.3 ± 27.7	***20***; 159.3 ± 32.0	***12***; 172.7 ± 28.7	***0***	***0***
	1+	***1***; not measured	***4***; 270.5 ± 17.8	***22***; 241.7 ± 24.7	***31***; 273.6 ± 32.4	***0***	***0***
	≥ 2+	***2***; 427.5 ± 50.7	***3***; 382.0 ± 37.0	***1***; 339	***7***; 408.8 ± 48.3	***0***	***1***; 466.6 (1 S)
16 July-6 Aug.	0+	***0***	***1***; not measured (0 S)	***25***; 180.1 ± 26.7 (0 S)	***12***; 188.2 ± 15.2 (0 S)	***0***	***0***
	1+	***0***	***6***; 298 ± 16.1 (3 S)	***21***; 249.7 ± 23.7 (1 S)	***20***; 283.4 ± 19.8 (3 S)	***0***	***9***; 353.1 ± 22.7 (8 S)
	≥ 2+	***0***	***0***	***2***; 320.5 ± 30.4 (2 S)	***2***; 338 (1 meas.) (2 S)	***0***	***9***; 445.0 ± 61.4 (9 S)
7 Aug.-28 Aug.	0+	***0***	***4***; 197.5 ± 22.8 (0 S)	***29***; 189.8 ± 24.7 (0 S)	***17***; 205.8 ± 28.7 (2 S)	***0***	***1***;*209* (1 S)
	1+	***0***	***0***	***7***; 266.5 ± 17.2 (0 S)	***6***; 304.8 ± 22.0 (4 S)	***0***	***11***; 349.0 ± 16.1 (7 S)
	≥ 2+	***0***	***0***	***0***	***0***	***0***	***23***; 434.5 ± 60.8 (23 S)
29 Aug.-19 Sept.	0+	***2***; 234 (1 meas.) (0 S)	***4***; 238.3 ± 23.2 (0 S)	***73***; 213.5 ± 32.5 (2 S)	***12***; 208.0 ± 23.1 (0 S)	***1***; 220 (0 S)	***0***
	1+	***0***	***0***	***14***; 285.4 ± 23.4 (1 S)	***4***; 261.7 ± 12.6 (0 S)	***21***; 302.1 ± 33.9 (4 S)	***13***; 330.4 ± 46.1 (12 S)
	≥ 2+	***0***	***0***	***1***; 340 (0 S)	***0***	***0***	***25***; 426.2 ± 45.3 (25 S)
20 Sept.-11 Oct.	0+	***9***; 229.7 ± 30.6 (0 S)	***3***; 191.0 ± 3.6 (0 S)	***96***; 229.9 ± 26.7 (0 S)	***0***	***38***; 240.6 ± 18.9 (0 S)	no angling
	1+	***0***	***0***	***21***; 294.8 ± 31.7 (0 S)	***0***	***63***; 306.5 ± 31.5 (4 S)	
	≥ 2+	***0***	***0***	***0***	***0***	***0***	
12 Oct.-1 Nov.	0+	***18***; 224.2 ± 35.1 (0 P-S)	***0***	***33***; 224.4 ± 24.1 (0 P-S)	***0***	***48***; 251.5 ± 26.2 (0 P-S)	no angling
	1+	***0***	***0***	***8***; 283.4 ± 33.4 (4 P-S)	***0***	***35***; 321.3 ± 34.3 (10 P-S)	
	≥ 2+	***0***	***0***	***2***; 472.5 ± 60.1 (2 P-S)	***0***	***22***; 434.4 ± 45.9 (22 P-S)	
2 Nov. -18 Apr.	0+	***44***; 246.4 ± 30.6 (0 P-S)	***1***; not measured (0 P-S)	no angling	***0***	no angling	no angling
	1+	***30***; 354.8 ± 27.6 (17 P-S)	***0***		***0***		
	≥ 2+	***10***; 428.8 ± 50.3 (10 P-S)	***0***		***0***		

In June and July, we observed a general dispersal of migrants in the Saguenay River (Table 2-1). However, by mid-July, large charr (FL > 300 mm) started to be caught at Big Pool, in the upstream part of the SMR (Figure 2-1). In July and August, all but one charr sampled from anglers' captures in the river had spent at least two growing seasons in the Saguenay River ($n = 258$, 1998-2001 pooled data). Sea age ≥ 2 migrants were all spawners ($n = 153$), but only 81% ($n = 104$) of sea age 1 migrants were sexually mature. In August, older migrants (sea age ≥ 2) disappeared from recaptures in the Saguenay River, suggesting that most of them had started their upstream migration to spawning areas by that time of the year. From mid-July until the beginning of September, no tagged fish was caught in the freshwater part of the Saguenay River.

2.5.3.3. Fall and winter

In September, recaptures of sea age 0 and sea age 1 migrants decreased in areas downstream from the SMB (Table 2-1). Sea age 1 migrants disappeared totally from recaptures in the Saguenay River and were only observed in the SMB and in the downstream part of the SMR. Captures of sea age 1 charr in these two areas included a few mature individuals (less than 10% every year). These late upstream migrants were significantly smaller than sea age 1 spawners already present in the river during the summer (1998, summer, $n = 14$, length ± S.D. = 326.9 ± 31.0 mm and fall, $n = 12$, length = 303.1 ± 18.6 mm, $t = 2.33$, $p < 0.03$; 1999, summer, $n = 17$, length = 343.6 ± 26.3 mm and fall, $n = 15$, length = 314.5 ± 28.0 mm, $t = 3.04$, $p < 0.005$; 2000, summer, $n = 19$, length = 345.5 ± 28.1 mm and fall, $n = 13$, length = 284.9 ± 28.6 mm, $t = 5.94$, $p < 0.0001$). At the same period, sea age 0 juveniles were also observed in the SMB and the SMR. However, tag returns in the upstream part of the Saguenay River indicated that part of the migrants-of-the-year had moved into this freshwater area (Table 2-1).

The return of some of the juveniles towards the SMR in the fall was accompanied by an increase of the sport-fishery in both the SMB and the SMR. Catches of juveniles were almost only made up of sea age 0 and sea age 1 migrants (only five catches of immature sea age 2 migrants were recorded in four years, out of 1546 juveniles sampled in the fall). There were significant differences in length and sea age structures of captures between the SMR and the

SMB. Every year, and for every sampling period, the length of charr caught in the downstream part of the SMR was significantly greater than the length of charr caught in the SMB (Table 2-2). The greater body size of charr caught in the river was associated with a higher proportion of recaptures of sea age 1 charr (Table 2-1), which were larger than migrants-of-the-year in every sampling area (see mean lengths of recaptures in Table 2-1, $p < 0.01$ in all cases). Sea age 1 charr made up 34% of non-tagged juveniles sampled from anglers in the river in 1998 ($n = 438$), 60% in 1999 ($n = 255$) and 69% in 2000 ($n = 74$). In contrast, they constituted only occasional catches in the SMB (Figure 2-6). The length of charr caught in the SMB and in the SMR tended to decrease from mid-September until the end of October (Table 2-2). The parallel increase of sea age 0 juveniles in recaptures from the SMR (Table 2-1) suggests that part of the migrants-of-the-year were leaving the SMB to enter the river. At the end of October, catches of juveniles in the SMB were dominated by small migrants-of-the-year. Stomachs continued to contain prey in almost all the charr collected in the SMB in October 1998, 1999 and 2000, while, at the same periods, less than 52% of the charr collected in the river had stomach contents (Table 2-3). The end of October was also characterized by a downstream migration of part of the adults after reproduction, as shown by tag returns of post-spawners in the downstream part of the SMR and in the SMB (Table 2-1). Catches of brook charr always decreased in the SMB at the end of October, followed by a usual cessation of the sport-fishery.

Table 2-2. Fork length (mean ± S.D) of juvenile brook charr measured while monitoring sport-fishery in the Sainte-Marguerite Bay and the Sainte-Marguerite River (Québec) in the fall 1998, 1999 and 2000, according to period and area. For a given year, different letters (associated with a given number, if need be) mean significant difference at a p level of 0.05 (t-test).

Year	Period	Area			
		Ste-Marguerite Bay		Ste-Marguerite River	
1998	29 Aug. – 19 Sept.	241.7 ± 48.8 ^{a}	(n=36)	286.3 ± 36.9 ^{b}	(n=188)
	20 Sept. – 11 Oct.	235.3 ± 28.7 ^{a}	(n=109)	270.4 ± 39.8 ^{c}	(n=415)
	12 Oct. – 2 Nov.	228.6 ± 20.3 ^{a}	(n=19)	265.6 ± 33.6 ^{d}	(n=515)
1999	29 Aug. – 19 Sept.	238.3 ± 32.7 ^{a}	(n=39)	295.4 ± 41.8 ^{c1}	(n=139)
	20 Sept. – 11 Oct.	238.6 ± 34.9 ^{a}	(n=220)	299.9 ± 43.8 ^{c2}	(n=441)
	12 Oct. – 2 Nov.	226.3 ± 22.9 ^{b}	(n=59)	292.8 ± 52.7 $^{c1, d2}$	(n=285)
2000	29 Aug. – 19 Sept.	259.1 ± 36.8 ^{a}	(n=28)	301.2 ± 37.4 ^{c}	(n=39)
	20 Sept. – 11 Oct.	272.0 ± 39.8 ^{a}	(n=42)	297.7 ± 46.1 ^{c}	(n=324)
	12 Oct. – 2 Nov.	220.5 ± 27.6 ^{b}	(n=18)	290.6 ± 53.3 ^{c}	(n=55)

Table 2-3. Percentage of stomachs with contents in anadromous brook charr sampled in the fall and winter, according to area : Sainte-Marguerite Bay (SMB), Sainte-Marguerite River (SMR) and upstream part of the Saguenay River (Saguenay), Québec (Geneviève Morinville and Joe Rasmussen, McGill University, Montreal, unpublished data).

Season	Sampling site	Period	N	Percentage of stomachs with contents
Fall	SMB	October 1998	48	93.8
		October 1999	42	92.9
		October 2000	14	100.0
	SMR	October 1998	238	43.3
		October 1999	168	48.8
		October 2000	47	51.1
Winter	Saguenay	Jan./Febr. 2000	11	62.5
	Saguenay	Jan./Febr. 2001	11	100.0
	SMR	February 2000	11	0.9
	SMR (mouth)	February 2001	12	33.3

During winter, we recorded significant tag returns in the freshwater part of the Saguenay River but none in the Saguenay Fjord (Table 2-1). These recaptures included juveniles (sea age 0 and sea age 1 migrants) and post-spawners. Angling was forbidden in the SMR and unusual in the SMB at this time. Direct sampling in the downstream part of the SMR on 20 February 2000 revealed only the presence of sea age 1 and sea age 2 migrants. Sea age 2 migrants ($n = 2$) were post-spawners but sea age 1 migrants included juveniles (7 out of 9). In 2001, we did not catch any charr in the downstream pools of the SMR. These pools contained large amounts of frazil ice and flow was constrained to narrow high velocity channels. Two half-day samplings at the river mouth led to the eventual catch of ten post-spawners and four sea age 1 juveniles. The significant number of adults tagged before reproduction in 1999 ($n = 463$) enabled a comparison between fish which migrated downstream just after reproduction and these which did so in the following spring. Post-spawners recaptured while leaving the SMR in early spring were part of the largest spawners tagged during the previous year and were significantly larger at the time of tagging than post-spawners recaptured in the Saguenay River during winter (Figure 2-7). Survival from reproduction to the following summer was higher in large than in small spawners tagged in 1999 but we did not observe any size-selective mortality in spawners tagged in 2000 (comparison of the length distributions, at tagging, of all fish tagged and of fish tagged and recaptured the following year: 1999, 463 spawners tagged and 67 recaptures, Mann-Whitney U test, $p < 0.03$ and 2000, 171 spawners tagged and 46 recaptures, Mann-Whitney U test, $p = 0.51$).

As anticipated by the differences in abundance and size of prey in winter between the SMR and the Saguenay, most of the stomachs collected in the SMR area were empty, while 84% of the stomachs collected in the Saguenay River during the same period contained prey (Table 2-3).

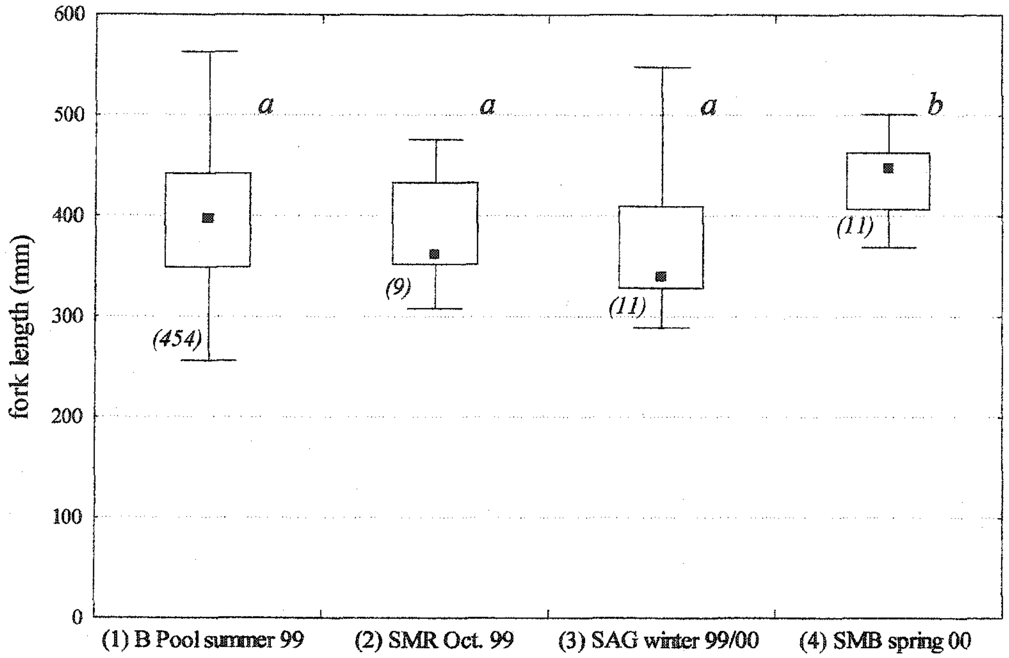

Figure 2-7. Length at tagging (median, 25%-75% range, total range) of (1) all brook charr spawners tagged at the Big Pool, Sainte-Marguerite River, Québec, during summer 1999 and (2), (3), (4), spawners tagged at the Big Pool in 1999 and recaptured migrating downstream the Sainte-Marguerite River in October (2), recaptured while over-wintering in the Saguenay River (3), recaptured in the Sainte-Marguerite Bay in spring 2000 (4). Samples sizes are given in brackets. Different letters mean significant difference at a p level of 0.05 (Mann-Whitney U test).

2.6. Discussion

A model of the migration patterns of anadromous brook charr from the SMR, based on the data reported here, is presented in Figure 2-8. We observed a synchronous emigration of migrants-of-the-year ("smolts") in spring, during a short period of time. The fact that size of descending charr did not differ between 1999 and 2000 samplings, that length distributions were right skewed in both years, that larger charr migrated first and that we did not observe any size-selective mortality following migration all suggest that there has been a strong selection for a threshold size at first migration. As in other salmonids, where a size-dependent salinity tolerance (and associated survival) is observed (McCormick and Naiman 1984), the growth/mortality trade-off associated with migration to estuarine areas may not be profitable before having reached a critical body size. Part of the migrants-of-the-year stayed in the SMB at least until the beginning of August. Others left the bay as soon as early June and dispersed in the Saguenay Fjord. In July, sea age 0 migrants caught in the fjord were significantly larger than sea age 0 migrants caught in the SMB. Thus, larger migrants left the SMB earlier and/or growth is enhanced when fish leave the SMB. The study of Montgomery et al. (1990) suggested that larger sea age 0 brook charr moved to deeper and more saline water more readily than did smaller ones. A regular departure of largest migrants-of-the-year from the SMB would explain why we did not observe any significant increase in the length of fish present in that area in July (see Figure 2-7). Laboratory studies on brook charr have shown that exposure to intermediate salinities prior to exposure to sea water had a positive effect on survival (McCormick and Naiman 1982) and that salinity tolerance of juveniles increased with body size (Sutterlin et al. 1976, McCormick and Naiman 1984). The prolonged residence of smaller migrants-of-the-year in the SMB (where salinity does not exceed 14 PSU) may constitute a necessary period of acclimation and growth before entering salt water, as suggested by McCormick et al. (1985). The major decrease of seine catches in August indicated that the majority of fish had left for the fjord by this time of the summer.

During the fall, migrants-of-the-year moved back towards fresh water. This observation is in accordance with many studies on charr and trout (see Randall et al. 1987), showing a return to the natal river at the end of the summer. However, in our population, migrants-of-the-year had access to fresh water either in the natal river or in the upstream part of the Saguenay and used both areas. Thus, juveniles' return to fresh water in the fall does not appear to involve homing behaviour. As suggested by Dutil and Power (1980), it is more likely that they "sheltered" from the decrease of salt water temperature, which can create a severe osmotic stress in this species (Saunders et al. 1975). This hypothesis is particularly relevant in the Saguenay Fjord, where the decrease of temperature in the fall induces a major increase of surface water salinity (up to 22 PSU). During winter, migrants-of-the-year were still observed in the upstream part of the Saguenay River. As angling stopped in the SMR at the end of October, we only have indirect information about the fate of migrants which moved back to their natal river in the fall. We did not observe any sea age 0 juveniles while sampling in the river or at the river mouth during winter, nor did we observe any significant emigration of sea age 1 charr from the SMR the following spring. Knowing that during the ice-covered period of the Saguenay Fjord, surface temperature stays around 0°C and surface salinity stabilizes at low

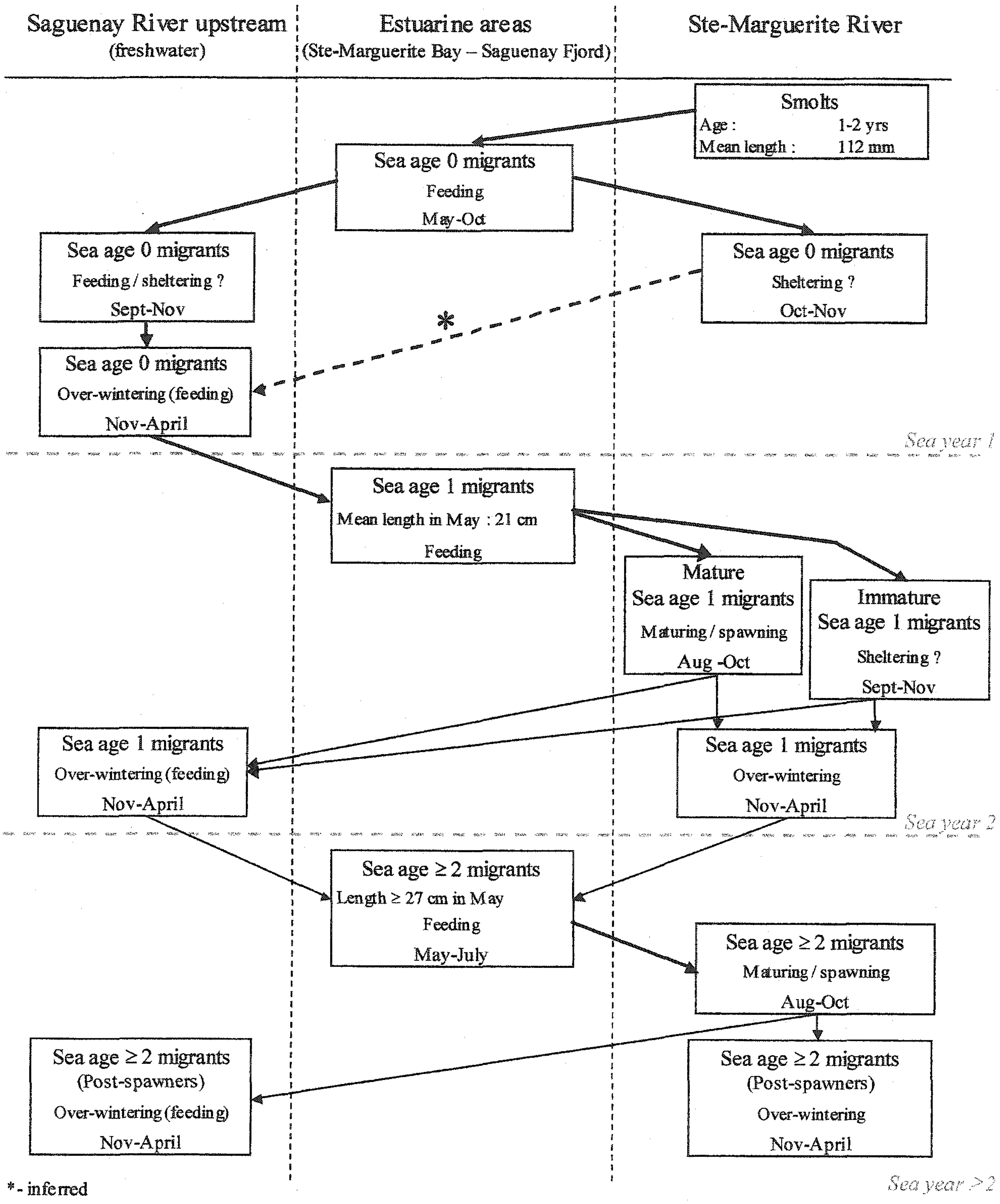

Figure 2-8. Schematic model for the migratory patterns of anadromous brook charr from the Sainte-Marguerite River, Saguenay, Québec, Canada, according to sea age and maturity stage.

values (< 7 PSU), it is possible that, after the unfavourable fall period, juveniles descended the river a second time to reach the freshwater part of the Saguenay River. We know that such movements occurred as four juveniles tagged in the SMR in October were caught during the following winter in the upstream part of the Saguenay River. Downstream movements of anadromous brook charr at the end of fall have been observed in other studies (e.g. Smith and Saunders 1958, Castonguay et al. 1982).

Sea age 1 migrants reappeared in the SMB in the following spring, during a 15-day period, starting around May 15. Their good condition and their dark orange flesh suggested that they were already feeding intensively on crustaceans in the fjord when they arrived, in accordance with their probable arrival from upstream areas of the Saguenay River. Sea age 1 migrants left the bay more readily than migrants-of-the-year and occupied all areas of the Saguenay Fjord (including the more saline areas downstream of the SMB) by the beginning of June. Part of the sea age 1 charr were mature and migrated to spawning areas from mid-July to September, larger ones returning to the river earlier in the summer. However, even immature sea age 1 migrants moved back to the river at the end of the summer. They dominated captures of juveniles in the SMR in the fall of 1999 and 2000 and were never observed in the upstream part of the Saguenay River during that period, unlike migrants-of-the-year. We also had evidence that part of them actually over-wintered in the SMR and waited until the following spring to move back to the Saguenay Fjord. These observations agree with those of Castonguay et al. (1982), who suggested that migration patterns of sea age 0 and sea age 1 juvenile brook charr are different in some populations.

The analysis of stomach contents confirmed that food was still abundant in the Saguenay River in winter and that fish present in the Saguenay during that period fed more than fish present in the SMR. Whether or not smaller migrants may face starvation if staying in the SMR in winter is not known. Starvation risk may have a significant influence on the decision to over-winter in the Saguenay, where the increased costs associated with variable abiotic conditions and higher predation risk would be compensated by greater growth opportunities. The decision to over-winter in the Saguenay may also reflect a more risky behaviour of sea age 0 charr, maximizing growth during their first year in salt water to increase the probability of reproducing the next fall. It could be the case in an environment selecting for early maturation (for instance, where adult survival is low relative to juvenile survival (see Stearns 1992)). Sea age 1 juveniles adopted a more conservative behaviour: they returned to the SMR earlier in the fall and a significant portion of them stayed there until the following spring. This observation is in accordance with our prediction, coming from Clark's (1994) asset-protection principle: at the end of their second growing season in estuarine areas, charr give priority to increasing survival by sheltering instead of increasing growth in a riskier environment. In the fall, sea age 1 charr are larger than migrants-of-the-year. Size is intimately connected with reproductive success in salmonids as fecundity of fish generally increases with body size and because a larger size may constitute an advantage in territorial competitions at the time of reproduction (Dodson 1997). Thus, without considering age at maturity, sea age 1 migrants have greater reproductive assets to protect than migrants-of-the-year. In addition, sea age 1 charr (having reached size at maturity) will reproduce the following fall, which is not the case of many migrants-of-the-year. Therefore, in terms of time to reproduction, sea age 1 charr have greater reproductive prospects to protect than migrants-of-the-year. The more conservative behaviour of older juveniles may be limited by energy constraints, as suggested by the arrival of some sea age 1 juveniles in the Saguenay River during winter. A portion of sea age 1 juveniles may not have had sufficient energy reserves to spend winter without feeding and/or to reproduce the following year.

Charr having spent more than two growing seasons in the Saguenay River showed migration patterns very similar to sea age 1 charr, except that they were almost all mature and undertook their upstream migration to spawning areas early in the summer. After reproduction, some moved back to the estuary to over-winter in the upstream part of the Saguenay River while the rest over-wintered in the SMR. The mark/recapture experiment carried out on adults present on spawning grounds (including part of sea age 1 migrants) showed that post-spawners leaving the SMR in early spring were part of the largest spawners tagged during the previous year and were significantly larger, at the time of tagging, than post-spawners recaptured in the Saguenay River during winter. This observation was associated with a higher mortality in smaller adults. Therefore, the larger size of fish leaving the SMR in early spring may be the result of two phenomena that are not mutually exclusive: smaller post-spawners have a greater probability of mortality if they remain within the SMR and smaller post-spawners exhibit a greater probability of out-migration from the SMR to exploit the richer feeding areas of the Saguenay River in winter. Both scenarios suggest that smaller adults face higher energy constraints following reproduction. As such, the larger size of post-spawners leaving the SMR in early spring is indicative of a conservative behaviour in larger adults.

Finally, we had evidence that abiotic factors may affect the seasonal behaviours of anadromous brook charr. The presence of large amounts of frazil ice during winter 2001 seemed to have driven fish towards the river mouth. A telemetry study on winter movements of cutthroat trout showed that fish moved downstream when their habitat was affected by frazil and anchor ice (Brown 1999). In Ellerslie Brook (Prince Edward Island), major outward movements of brook charr at 0°C may be associated with the formation of frazil ice (Smith and Saunders 1958). Frazil ice represents a major danger for fish (which may be affected by ice crystals in their mouth and gills), limits available habitat and constrains flow to channels where velocity may be too high for fish to maintain position (see references in Brown 1999).

Growth rate and mortality risk in fresh water and estuarine areas will change according to specific environmental settings. Migratory behaviour of brook charr populations should reflect local opportunities and constraints. For instance, age at first downstream migration tends to increase with latitude (Castonguay et al. 1982), which could result from a slower growth in northern rivers (e.g. Dutil and Power 1980) where charr need a longer stay in fresh water to reach the size at first migration observed in southern rivers (e.g. White 1940). However, brook charr from the SMR migrate earlier and at smaller size than those from either the Moser River, Nova Scotia (age 2 and 3, modal sizes 170-200 mm, White 1940), located south of the SMR, or from the Saint-Jean River, Québec (age 2 to 4, 100-200 mm, Castonguay et al. 1982), located at a similar latitude. If the existence of a threshold size at first migration is associated with the size-dependent salinity tolerance of brook charr, a lower size at downstream migration in the SMR may be explained by the low salinity of the SMB (< 5.5 PSU in spring). Comparable sizes of smolts, associated with low salinity conditions, were also observed in the Moisie River estuary (Montgomery et al. 1990). Similarly, the thermo-haline stratification of the Saguenay River may promote the long distance movements (as far as 100 km) of juveniles and adults, that are rarely observed in other populations (see Power 1980). It could be especially true in winter as, in populations where brook charr were observed over-wintering outside their natal river, those fish were caught at short distances from the river mouth (e.g. Smith and Saunders 1958, Castonguay et al. 1982). A low age at downstream migration and an intense exploitation of estuarine areas in brook charr from the SMR is associated with fast growth and a low age at maturity (3+) relative to other populations from Québec and the maritimes (see Power 1980, Castonguay et al. 1982), emphasizing the link between migratory behaviour and life-history.

In summary, our results showed that, if anadromous behaviour depends on a growth/mortality trade-off, it is dynamic in nature. Migratory patterns of brook charr from the Sainte-Marguerite River imply that fitness payoffs in river and estuary may vary according to time of year, growth, maturity stage and condition of individuals. As predicted by behavioural models, migratory patterns of charr changed throughout their ontogeny and, as fish grew and accumulated fitness assets, they tended to adopt a more conservative behaviour. Factors affecting migration may have an effect on life-history and vice versa. Environmental differences related to geographical location can be responsible for the variation of migration patterns and life-histories that we commonly observe within salmonid species or between closely related ones. An accurate knowledge of the influence of environmental factors on growth and mortality of salmonids is necessary to fully understand the link between migratory behaviour and the life-history of anadromous species.

2.7. Acknowledgements

We acknowledge S. Bilodeau-Gauthier, A. Boivin, F. Charlebois, M. Desgagnés, J.-M. Fréchette, S. Gaouette, C. Garneau, M.-C. Landry-Pelchat, C. Langlois, R. Lavoie, J.-G. Marquis, G. Morinville, P.-A. Paradis, C. Poirier, J.-F. Rigalbuteau, J. Savard, V. Thériault and S. Trépanier for field and laboratory assistance. We are also very grateful to the Association de la Rivière Sainte-Marguerite, the Club de Pêche de la Rivière Sainte-Marguerite and the Saguenay anglers, for their collaboration to the study. Funding of this project was provided to J.J.D. by the Natural Sciences and Engineering Research Council of Canada (Strategic Grant and Collaborative Special Projects), the Fondation de la Faune du Québec, the Government of Québec (Faune et Parc Québec), the Government of Canada

(Economic Development, Saguenay – Saint-Lawrence Marine Park) and the financial partners of CIRSA Inc. (Corporation de soutien aux Initiatives de Recherche sur le Saumon Atlantique). This study is a contribution to the research programs of CIRSA (Centre Interuniversitaire de Recherche sur le Saumon Atlantique) and GIROQ (Groupe Interuniversitaire de Recherches Océanographiques du Québec. S.L. was financially supported by funding from CIRSA and GIROQ.

3. Life-history consequences of age at downstream migration in anadromous brook charr (*Salvelinus fontinalis*).

Sophie Lenormand and Julian J. Dodson

3.1. Résumé

La variabilité de l'âge à la première dévalaison au sein des populations de salmonidés implique qu'il n'y a pas un patron de migration optimal mais une gamme de tactiques migratoires possibles, maximisant le fitness des individus de différentes façons. Étant donné que les poissons à croissance lente ont tendance à dévaler plus tard que les poissons à croissance rapide, les bénéfices en terme de fitness d'une dévalaison à un âge donné semblent dépendre de la croissance des individus (et de leur perspectives de croissance) en eau douce. En migrant à un âge inférieur, les poissons à croissance rapide maximiseraient leur fitness en maximisant leur taux de croissance. Les migrants les plus gros bénéficiant généralement d'une meilleure survie durant ou suivant la migration, les poissons à croissance lente, qui migrent à un âge et une taille supérieure, maximiseraient leur fitness en maximisant leur survie. Nous avons testé cette hypothèse dans une population d'ombles de fontaine anadromes. Les ombles dévalaient à 1 ou 2 ans, les poissons migrant à 2 ans étant significativement plus grands que ceux migrant à 1 an. La croissance était plus rapide en estuaire qu'en rivière. Dans une même cohorte, les ombles ayant migré à 1 an obtenaient et maintenaient un avantage en taille sur les ombles ayant migré à 2 ans et se reproduisaient plus tôt dans la vie et à une taille à l'âge plus élevée. Une taille à l'âge supérieure était associée à une fécondité à l'âge supérieure. Cependant, pour une année de migration donnée, les ombles ayant migré à 2 ans gardaient un avantage en taille sur ceux ayant migré à 1 an, au moins jusqu'à la fin de la deuxième saison de croissance en estuaire. Ils se reproduisaient pour la première fois à un âge en mer inférieur. Ils ne bénéficiaient pas d'une meilleure survie à la dévalaison mais ils bénéficiaient d'une meilleure survie globale jusqu'à la première reproduction, parce qu'ils passaient plus de temps dans l'habitat caractérisé par des taux survie supérieurs (la rivière) et moins de temps dans l'habitat le plus risqué (l'estuaire) avant cette première reproduction. Une meilleure survie globale jusqu'à la première reproduction chez les migrants les plus âgés pourrait compenser, en terme de fitness, leur taille inférieure à un âge donné. Avec ou sans égalité des fitness associés aux deux tactiques, la variabilité environnementale, une sélection dépendante des fréquences d'expression des tactiques et des contraintes spécifiques au sexe des individus pourraient être impliquées dans le maintien de différents âges à la première dévalaison.

3.2. Abstract

Variability in age at smolting within salmonid populations implies that there is not one optimal migratory pattern but an array of possible migratory tactics, maximizing individuals' fitness in different ways. As slow growing parr tend to smolt later than fast growing ones, the fitness payoff of migrating at a given age seems to be conditional on individuals' growth (and scope of growth) in fresh water. By smolting at a younger age, faster growers would maximize their fitness by maximizing growth rate. By smolting at an older age and a larger size, slower growers would maximize their fitness by maximizing survival, as larger smolts usually benefit from a better migratory or post-migratory survival. In the present study, we tested this hypothesis in a population of anadromous brook charr. Charr left the river at age 1 or at age 2, fish migrating at age 2 being significantly larger than fish migrating at age 1. Growth was enhanced in the estuary relative to the river. In a given cohort, charr migrating at age 1 achieved and maintained a significant size advantage over charr migrating at age 2. They reproduced earlier in life and at a larger size at a given age. A larger size-at-age resulted in a higher age-specific fecundity. However, for a given downstream migration year, migrants at age 2 kept a size advantage over migrants at age 1, at least until the end of the second growing season in the estuary. They first reproduced at a lower sea age, relative to migrants at age 1. They did not benefit from improved size-related estuarine survival, relative to migrants at age 1, but they benefited from a higher overall survival to first reproduction because they spent more time in a safer habitat (fresh water) and less time in a more risky habitat (the estuary) before first reproduction. A higher survival to first reproduction in older smolts could compensate, in terms of life-time reproductive success, for their lower size-at-age. With or without equal fitness for the two migratory tactics, environmental variability, frequency-dependent selection and sex-specific constraints could act as stabilizing factors in the maintenance of alternative ages at downstream migration.

3.3. Introduction

The life cycle of anadromous salmonids is marked by a niche-shift from fresh water nursery habitats to salt water feeding habitats. From that time on, growth is usually enhanced but mortality may be much higher than in fresh water (Jonsson and Jonsson 1993). Thus, through its effect on size-at-age and survival to reproduction, the timing of first downstream migration should have major effects on individuals' life-history and life-time reproductive success. Within many salmonid populations, juveniles migrate at different ages (Randall et al. 1987). Variability in age at smolting implies that there is not one optimal migratory pattern but an array of possible migratory tactics, maximizing fitness in different ways. If growth rates are enhanced in salt water areas, the younger smolts could exhibit a greater size at age than the older smolts and may reproduce earlier in life and/or at larger size. On the other hand, osmotic stress is lower for larger smolts (Hoar 1976, McCormick and Saunders 1987) and, in Atlantic salmon (*Salmo salar*), large smolts seem to be less vulnerable to predators and disease (Marschall et al. 1998). A size-selective mortality at downstream migration has been observed in several salmonid species (Bohlin et al. 1996). The older smolts (providing they are larger) may then suffer lower mortality rates.

Age at downstream migration seems to be controlled by both genetic and environmental influences (Randall et al. 1987). Within the same population, the existence of alternative migratory tactics may be condidered in the theoretical context of a conditional reproductive strategy (summarized in Gross and Repka 1998). All individuals can express the different tactics observed in the population. The expression of a given tactic depends on the individual's state at a specific period of its life and results in higher fitness for the individual. This theory underlines the existence of a switch point at threshold state (simple case of only two alternative tactics), below which individuals will express one tactic and above which they will express another. Though a conditional strategy is a form of adaptive phenotypic plasticity (*sensu* Houston and McNamara 1992), it does not exclude inheritance of the state (see Roff 1996). Furthermore, theoretical studies have shown that inheritance (of the tactic or of the underlying trait) does not prevent alternative tactics associated with unequal fitness to be maintained in a stable equilibrium (Hazel et al. 1990, Gross and Repka 1998).

As far as anadromy is concerned, there is a minimum size below which fish from a given population do not migrate (Randall et al. 1987, Økland et al. 1993, Hutchings and Jones 1998), suggesting that the growth/mortality trade-off associated with migration is not profitable before reaching a critical body size. However, all individuals do not smolt as quickly as possible after having passed this threshold size (Randall et al. 1987 and, e.g., Økland et al. 1993, Thériault and Dodson, submitted), showing that size alone does not determine age at smolting. Age at first downstream migration seems to be regulated by individuals' growth (and scope of growth) in the years prior to migration. In arctic charr (*Salvelinus alpinus*), brook charr (*S. fontinalis*), brown trout (*Salmo trutta*) and Atlantic salmon (*S. salar*), there is a general trend for slow growing parr to smolt later and at a larger size than fast growing parr (e.g. Jonsson 1985, Svenning et al. 1992, Økland et al. 1993, Metcalfe 1998, Forseth et al. 1999, Rikardsen and Elliott 2000, Thériault and Dodson, submitted). Jonsson and Jonsson (1993) and Økland et al. (1993) suggest that fast growers may be constrained earlier than slow growers by the limited food resources in rivers and may then maximize their growth rate by migrating at a younger age. Slow growers would delay the niche-shift without reducing their growth rate in freshwater, due to lower energy requirements. They would benefit from smolting at a larger size because of higher survival when migrating to sea.

Proximate mechanisms regulating alternative migratory tactics in salmonids (freshwater residence or migration, age at first downstream migration) have received considerable attention in the last decade. At the same time, theoretical models, based on ultimate considerations (expected reproductive success), have been developed to explain the existence of alternative migratory tactics in salmonid populations (e.g. Bohlin et al. 1990, Økland et al. 1993, Hutchings and Myers 1994). However, there are few studies looking at the actual consequences, in terms of life-history and life-time reproductive success, of alternative migratory tactics in wild populations, although such studies could provide interesting insights into the evolution of anadromy and test the predictions (or the assumptions) of theoretical models (Dodson, 1997). As such, they are also an essential step in the development of management plans for anadromous populations.

The brook charr is native to eastern North America where it is one of the most popular game fishes. Like many salmonids, it may exist as migratory and freshwater resident forms that differ in life-history patterns (Power 1980). Marine movements of anadromous brook charr are of short duration (usually 2-4 months) and seem to be limited to estuarine and coastal regions nearby their natal river (Power 1980 and references therein, Castonguay et al. 1982, Montgomery et al. 1990). Reproduction takes place in the fall but adults start their upstream migration during the summer. Anadromous brook charr usually mature during their second or third growing season in salt water and multiple spawning is common (Power 1980). The brook charr population of the Sainte-Marguerite River, Québec, Canada, is partially anadromous (presence of migrants and freshwater residents). First downstream migration occurs essentially at 1+ or 2+; charr migrating at age 2 being significantly larger than charr migrating at age 1 (Chapter 2). As observed in other salmonid species, charr migrating at a younger age are recruited from the fastest growers in fresh water (Thériault and Dodson, submitted). Therefore, this population constitutes an excellent model to assess the life-history consequences of age at first downstream migration and test the hypothesis of Jonsson and Jonsson (1993) and Økland et al. (1993): 1) by smolting at a younger age, faster growers maximize their fitness (relative to slower growers) by maximizing growth rate and 2) by smolting at an older age and a larger size, slower growers maximize their fitness by maximizing survival to reproduction (relative to faster growers), as larger smolts benefit from a better migratory or post-migratory survival.

In the present study, we first tested the hypothesis that anadromous brook charr from the Sainte-Marguerite River migrating at an older age benefit from better migratory or post-migratory survival. We then assessed the life-history consequences of age at downstream migration: growth (size-at-age), age-specific fecundity, age at maturity and survival to reproduction. These parameters were evaluated by combining a monitoring of first downstream migration, direct samplings in estuarine areas, creel census and a mark-recapture experiment, in collaboration with anglers. We predicted that younger smolt would exhibit a greater size at age (and, hence, a lower age at maturity and/or a larger size at maturity) and older smolt a higher survival in the estuary. Finally, we explored the consequences of varying the critical life-history parameters identified in the study on the life-time reproductive success associated with the two tactics.

3.4. Materials and methods

3.4.1. Study Area

The Sainte-Marguerite River (48°27' N, 69°95' W; Figure 3-1 and Chapter 2) empties into the Saguenay Fjord, 25 km upstream from its confluence with the Saint-Lawrence maritime estuary (Québec, Canada).

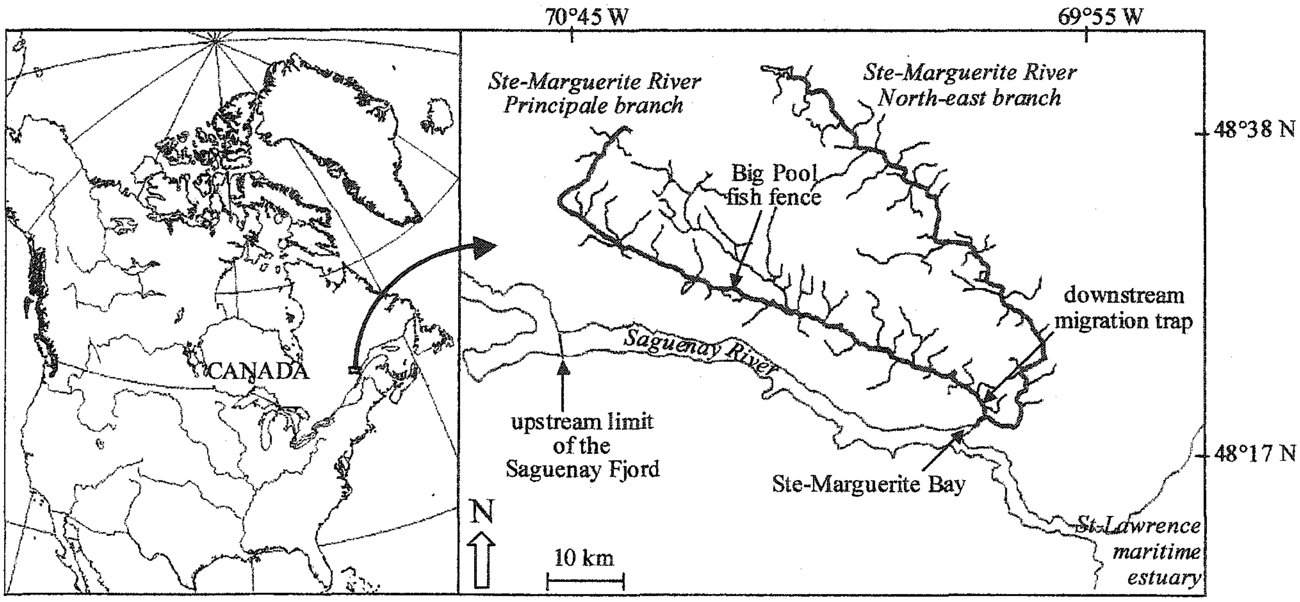

Figure 3-1. Location of the Sainte-Marguerite/Saguenay river system and of sampling sites.

Anadromous charr from the Sainte-Marguerite River migrate to its estuary, which forms a large shallow bay named the Sainte-Marguerite Bay. From there, they have access to the Saguenay River (Figure 3-1). The 100 km downstream part of the Saguenay River (the Saguenay Fjord), under tidal influence, is a mixing zone between fresh water from upstream and salt water from the Saint-Lawrence maritime estuary (see Chapter 2).

3.4.2. Sampling and mark-recapture experiment

Anadromous brook trout were sampled and tagged at different life-stages during four years (1998-2001). In 1998, 1999, and 2000, first time migrants were caught by an Alaskan trap (1 cm mesh) set on the Principal branch of the Sainte-Marguerite River, at 7 km from the river's mouth (Figure 3-1). Monitoring started just after the ice break-up period, when discharge was beginning to decrease and ended when catches had been minor (less than 20 fish per day) for 10 consecutive days. Fish were measured (fork length (FL), to the nearest mm). Twelve percent of total catches in 1998 and 1999 and 10% in 2000 were sacrificed for laboratory analyses (see below). In 1998, we missed part of the downstream migration due to late trap setting and only size at age data were used for this study. In 1999 and 2000, the trap was set on time and fish were marked with clear, individually labelled T-bar anchor tags (Floy FF-94), providing that their fork length was greater than 75 mm. Tag retention was tested in aquarium on 20 fish ranging from 75 mm and 132 mm FL. No tag loss, mortality or serious injury was observed after 3 months.

In the Sainte-Marguerite Bay, sampling and tagging of anadromous charr was carried out by weekly hauls of a 40-m beach seine. Every year, anadromous spawners were sampled and tagged during their upstream migration in the Sainte-Marguerite River (see Chapter 2 for details).

Fishing for anadromous charr is permitted in the Saguenay (including the Sainte-Marguerite Bay) all year long and in the Sainte-Marguerite River, from June 15 to October 31. Until September 16, fishing essentially targets adults, in the upstream part of the river. From September 16, fishing is only allowed downstream of spawning grounds and targets juveniles. Tag returns from the sport-fishery were encouraged with a 5 $ cash reward and the opportunity to participate in an annual draw for prizes. In 1998, 1999 and 2000, we completed the mark-recapture experiment by a general monitoring of sport-fishing in the Sainte-Marguerite River and the Sainte-Marguerite Bay (see Chapter 2).

Charr that had been sacrificed or sampled from anglers (tagged fish and sub-samples of untagged fish) were measured, weighed and classified with respect to sex and maturity stage (Nikolskii 1963). Age and age at downstream migration were determined on sagittal otoliths (see Chapter 2). Absolute fecundity (total number of eggs) was evaluated on females at maturity stage 4 (Nikolskii 1963): total gonads were weighed to the nearest 0,1 mg and a sub-sample (representing 25-30% of total egg mass and weighed to the nearest 0,1 mg) was taken for counting.

3.4.3. Data analysis

3.4.3.1. Downstream migration and subsequent growth

First downstream migration was characterized according to body size, age and sex. Growth of migrants was first analysed by cohort (all fish born in the same year), age at downstream migration and sex. We tested the effect of year of downstream migration on size-at-age in males and in females having migrated at age 1 and at age 2 by analyses of variance and the effect of sex on size-at-age in the two tactics by multivariate analyses of variance (crossed design, year of downstream migration × sex). We also compared size at given sea age in males and in females having migrated in the same year but at a different ages by analyses of variance (crossed design, year of downstream migration × age at migration). Finally, pooling the data obtained during the 1998-2001 sampling period, we modelled size at a given sea age, according to age at downstream migration and sex (user specified regression, quasi-Newton estimation method in Statistica 5.5).

3.4.3.2. Age at maturity

Juveniles and adults had different migratory patterns (Chapter 2). Larger spawners undertook their upstream migration to spawning grounds, in the upstream part of the river, from mid-July to the end of August. Smaller spawners returned to the river in August and September, with larger juveniles. Whereas most juveniles stayed in the downstream part of the river, spawners migrated to spawning grounds. Thus, direct sampling in a given area could not provide a good estimate of the percentage of mature charr in sea age classes made up of juveniles and adults. In such a case, we used an indirect method to evaluate the incidence of maturity in charr that migrated at age 1 (migrants at age 1) and in charr that migrated at age 2 (migrants at age 2). For a given sea age class, if M_1(%) is the incidence of maturity in migrants at age 1 and M_2 (%) the incidence of maturity in migrants at age 2, the ratio M_1/M_2 (α) can be evaluated from the relative proportions of migrants at age 1 and migrants at age 2 in catches of sexually mature fish. Similarly, for a given sea age class, I_1 being the percentage of immature fish in migrants at age 1 ($I_1 = 100 - M_1$) and I_2 the percentage of immature fish in migrants at age 2 ($I_2 = 100 - M_2$), the ratio I_1/I_2 (β) can be evaluated from the relative proportions of migrants at age 1 and migrants at age 2 in catches of immature fish. M_1 and M_2 are the solutions of :

(1) $M_1 = \alpha M_2$,

and

(2) $M_1 = 100 - I_1 = 100 - \beta I_2 = 100 - \beta(100-M_2)$.

3.4.3.3. Survival

Survival during the first two years in the estuary and survival of adults from one upstream migration to the next were estimated following Brownie et al. (1985) multi-year tagging model 1 (year-specific survival, year-specific recovery rate). Computation was performed on program MARK 3.0 (White and Burnham 1999). Migrants of year 1998 were tagged in May 1999 and in May 2000. Migrants of year 1999 were tagged at downstream migration (1999), in May 2000 and in May 2001. Migrants of year 2000 were tagged at downstream migration and in May 2001. Annual tag returns were analysed by sea age and year of downstream migration. The probability of recovering in year *n* a fish alive at the beginning of year *n* was estimated from fish both tagged and reported in year *n*. Survival from year *n-1* to year *n* was estimated from recovery probability in year *n* and recoveries in year *n* of fish tagged in year *n-1*. In adults, it was not possible to estimate sea age according to size. Therefore, we made global year-specific estimates of survival of adults from one upstream migration to the next.

3.4.3.4. Life-time reproductive success

To explore the consequences of age at downstream migration on individuals' fitness, we modelled the life-time reproductive success (Ro) of females having migrated at age 1 and females having migrated at age 2 ($Ro = \sum l_x m_x$ where l_x is the probability of surviving from birth to age *x* and m_x is the mean number of female eggs produced by a female aged *x*, see Stearns 1992). In fresh water, minimum survival at age 1 was estimated by the disappearance of fish between age 1 and age 2 (including both mortality and emigration at age 2, Chapter 4). As disappearance between age 1 and age 2 ranges between 48% and 69%, depending on the incidence of out-migration, survival at age 1 is likely to be much higher than 31%. Survival at age 1 should have a major effect on the life-time reproductive success of migrants at age 2. We thus modelled Ro for different values of this parameter. We set survival in fresh water from birth to the beginning of the second year of life (age 1) at 0.025. This value was chosen because it ensures a life-time reproductive success of 1 in resident females from the Sainte-Marguerite River (see Chapter 4). An under or over-estimate of survival from birth to age 1 in anadromous charr would not affect the comparison between the life-time reproductive success of fish having migrated at age 1 and fish having migrated at age 2.

3.5. Results

3.5.1. Size, age and sex at first downstream migration

In 1999 and 2000, downstream movements of first-time migrants were concentrated within a month, starting around mid-May (Chapter 2). The Principale branch trap caught 1483 and 1019 migrants-of-the-year in 1999 and 2000, respectively. Sub-samples of 178 fish in 1999 and 92 in 2000 were used for sex and age determination. There was no significant difference in length, age and length at age of migrants between 1999 and 2000 samplings (Chapter 2). Charr left the river at a mean length ± SD of 112 ± 17 mm but belonged to three age classes: 1+ (29% of migrating charr in 1999 and 26% in 2000), 2+ (68% of migrating charr in 1999 and 69% in 2000) and exceptionally 3+ (for detailed data, see Chapter 2). Fish migrating at age 2 were significantly larger than fish migrating at age 1 (t-test, 1999, 2+ length ± S.D. = 118,4 ± 14,7 mm and 1+ length = 89.0 ± 9.8 mm, $p < 0.001$; 2000, 2+ length 114.5 ± 16.2 mm and 1+ length = 91.0 ± 10.8 mm, $p < 0.0001$). Males outnumbered females in 1-year-old fish and females outnumbered males in 2-year-old fish (χ^2-test, 1999, 1+, F:M=1:1.91, $p < 0.01$ and 2+, F:M=1:0.67, $p < 0.06$; 2000, 1+, F:M=1:2.33, $p < 0.05$ and 2+, F:M=1:0.49, $p < 0.02$) but global sex-ratio at downstream migration was not different from 1:1 in both years. Length at age did not differ between males and females (t-test, 1999, 1+, $p = 0.60$ and 2+, $p = 0.99$; 2000, 1+, $p = 0.20$ and 2+, $p = 0.22$). None of the sampled fish showed any signs of a previous reproduction.

3.5.2. The tagging program

A total of 8412 charr were marked with T-bar tags from September 1998 until August 2001. We recaptured 1262 (15.0%) of these fish during subsequent samplings. Anglers from the Sainte-Marguerite River (SMR) or the Saguenay River reported 1402 catches of tagged fish (16.7%) while sport-fishing before December 2001. We did not observe any effect of tagging on growth (Chapter 2). In addition, no size-specific mortality due to tagging was detected: length distributions at the time of downstream migration of fish recaptured one year after migration did not differ significantly from length distributions revealed by downstream migration monitoring (Figure 3-3).

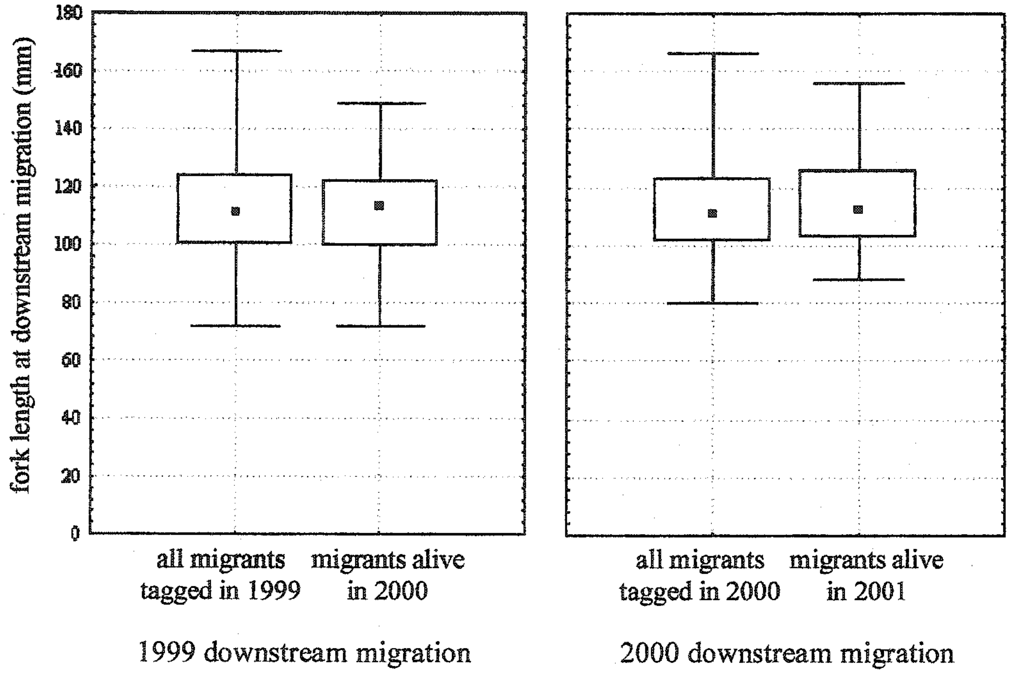

Figure 3-3. Length distribution (median, 25-75% range, total range) of anadromous brook charr tagged in the trap set on the Sainte-Marguerite River, Québec, and length ditribution, at downstream migration, of charr tagged in the trap and recaptured the following year, for 1999 and 2000 downstream migrations. There was no significant difference between the two distributions in both years (Mann-Whitney U test, 1999, n migrants = 1214, n recaptures = 54, z = -0.17, p = 0.87 and 2000, n migrants = 899, n recaptures = 34, z = -0.61, p = 0.54).

3.5.3. Effect of size and age at downstream migration on survival following downstream migration

In 1999 and 2000, only three fish caught in the downstream migration trap were not tagged because of their small size or poor condition. Therefore, the fact that we did not observe any size-selective mortality on tagged fish (Figure 3-3) shows the complete absence of size-specific mortality following downstream migration. In addition, the relative proportions of charr having migrated at age 1 and charr having migrated at age 2 in fish recaptured one year after downstream migration did not differ from the relative proportions of age 1 charr and age 2 charr at first downstream migration (recaptures of 1999 migrants in 2000, age 1 = 28% and age 2 = 72%, $\chi^2 = 0.119$, $p = 0.73$; recaptures of 2000 migrants in 2001, age 1 = 33% and age 2 = 67%, $\chi^2 = 0.70$, $p = 0.67$). Thus, charr that migrated at age 2 did not benefit from improved size-related estuarine survival relative to charr that migrated at age 1.

3.5.4. Growth and fecundity

A total of 3412 fish from 8 cohorts, sacrificed or sampled from anglers, were used for the determination of migrants' size in a given season (spring, summer, fall), according to sex, age at downstream migration and sea age. At least three cohorts were represented in every sex × age at migration × sea age groups until sea age 3. For any given cohort, charr having migrated at age 1 achieved and maintained a size advantage over charr having migrated at age 2 (see Figure 3-4 for 1996 and 1997 cohorts). Year of downstream migration had a significant effect on size at age in the fall following downstream migration, in males and in females having migrated at age 1 and at age 2 (ANOVA, $p < 0.05$ in the four groups) but in mature charr, this effect disappeared from the end of the second growing season in the estuary (ANOVA, $p > 0.07$ at sea age 1 and $p > 0.2$ at sea ages ≥ 2). In charr that migrated at age 1, males were significantly larger than females from the fall following downstream migration until sea age 2 (MANOVA, sex and year of downstream migration, $p(\text{sex}) < 0.04$ at sea ages ≤ 2). In charr that migrated at age 2, length of males did not differ from length of females at sea ages 0 and 1 (MANOVA, sea age 0, $p(\text{sex}) = 0.44$ and sea age 1, $p(\text{sex}) = 0.23$) but males were significantly larger than females at sea age 2 (MANOVA, $p(\text{sex}) < 0.003$).

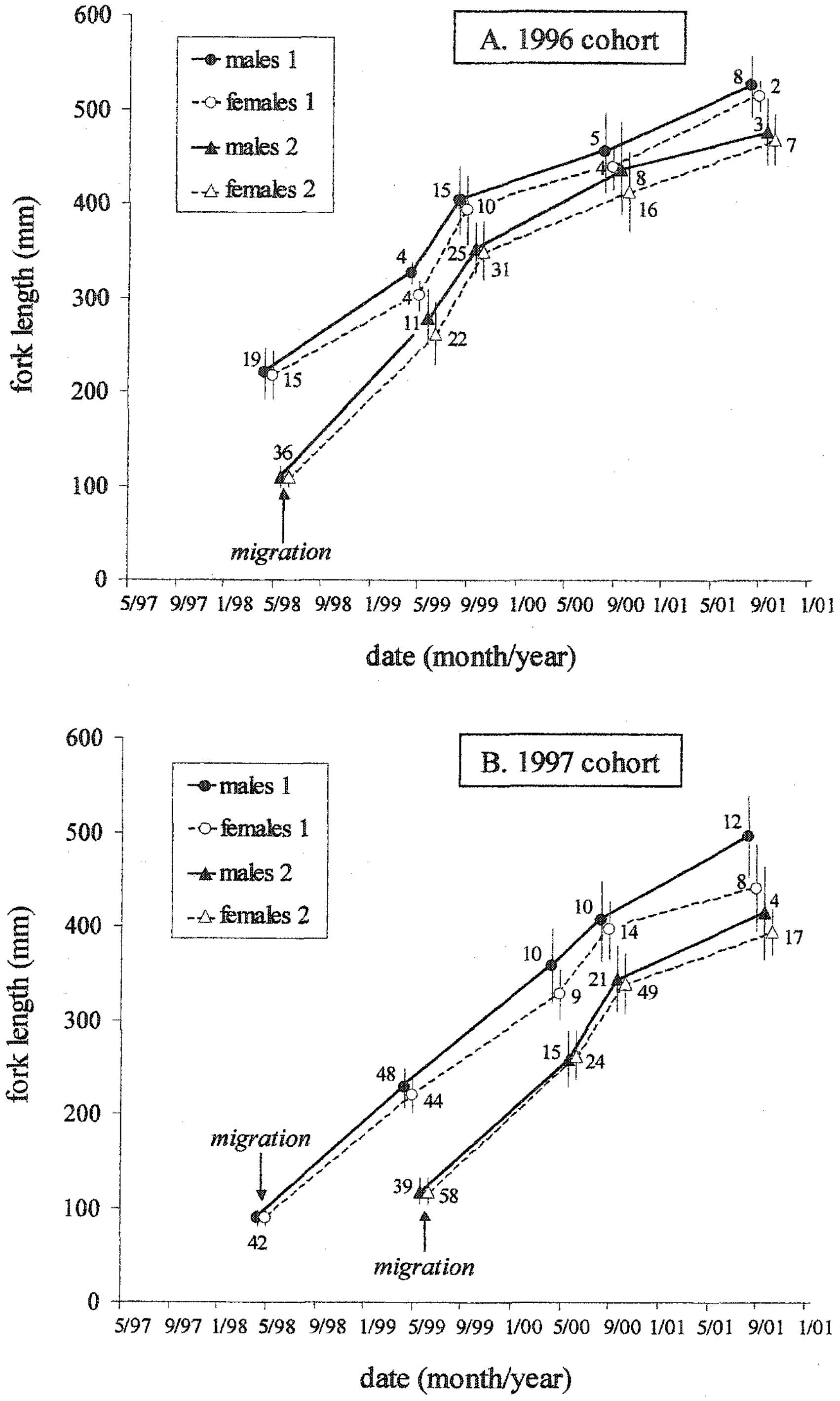

Figure 3-4. Evolution of the length (mean ± S. D.) of anadromous charr sampled in the Sainte-Marguerite River, Québec, from 1998 to 2001, according to year of birth (A, 1996 and B, 1997), age at downstream migration (circles, migrants at age 1 and triangles, migrants at age 2) and sex. Sample sizes are given next to data points. Sexes were not determined while sampling 1998 migrants-of-the-year. At the same sampling period, migrants at age 1 were significantly larger than migrants at age 2 at a p level of 0.05 (t-test), in males and in females from both cohorts, expected in the case of 1996 cohort / age 4 (September 2000).

In charr having migrated in the same year, fish that migrated at age 2 kept their size advantage over fish that migrated at age 1, until the end of the second growing season in the estuary in females (MANOVA, age at downstream migration and year of downstream migration, p(age at migration) < 0.0001 at sea age 0 and sea age 1, and $p > 0.1$ at sea ages ≥ 2) and until the end of the third growing season in the estuary in males (MANOVA, p(age at migration) < 0.002 at sea ages ≤ 2 and $p > 0.5$ at sea ages ≥ 3).

As growth was suddenly enhanced at the time of downstream migration (relative to growth in fresh water), we could not obtain a growth model fitting length data from birth to maximal observed age in the estuary. In order to achieve better estimates of size at age at reproduction in males and in females expressing one migratory tactic or the other, we modelled growth from age at first downstream migration to maximal observed age. The best models we obtained in the four groups were von Bertalanffy-like growth functions (Figure 3-5). Models obtained in females were subsequently used to estimate fecundity at age and to model the life-time reproductive success associated with the two migratory tactics. We observed a strong relationship between body size and fecundity and this relationship did not differ between the two tactics (Figure 3-6). Females having migrated at age 1, which grew faster, exhibited a higher fecundity-at-age (Figure 3-7).

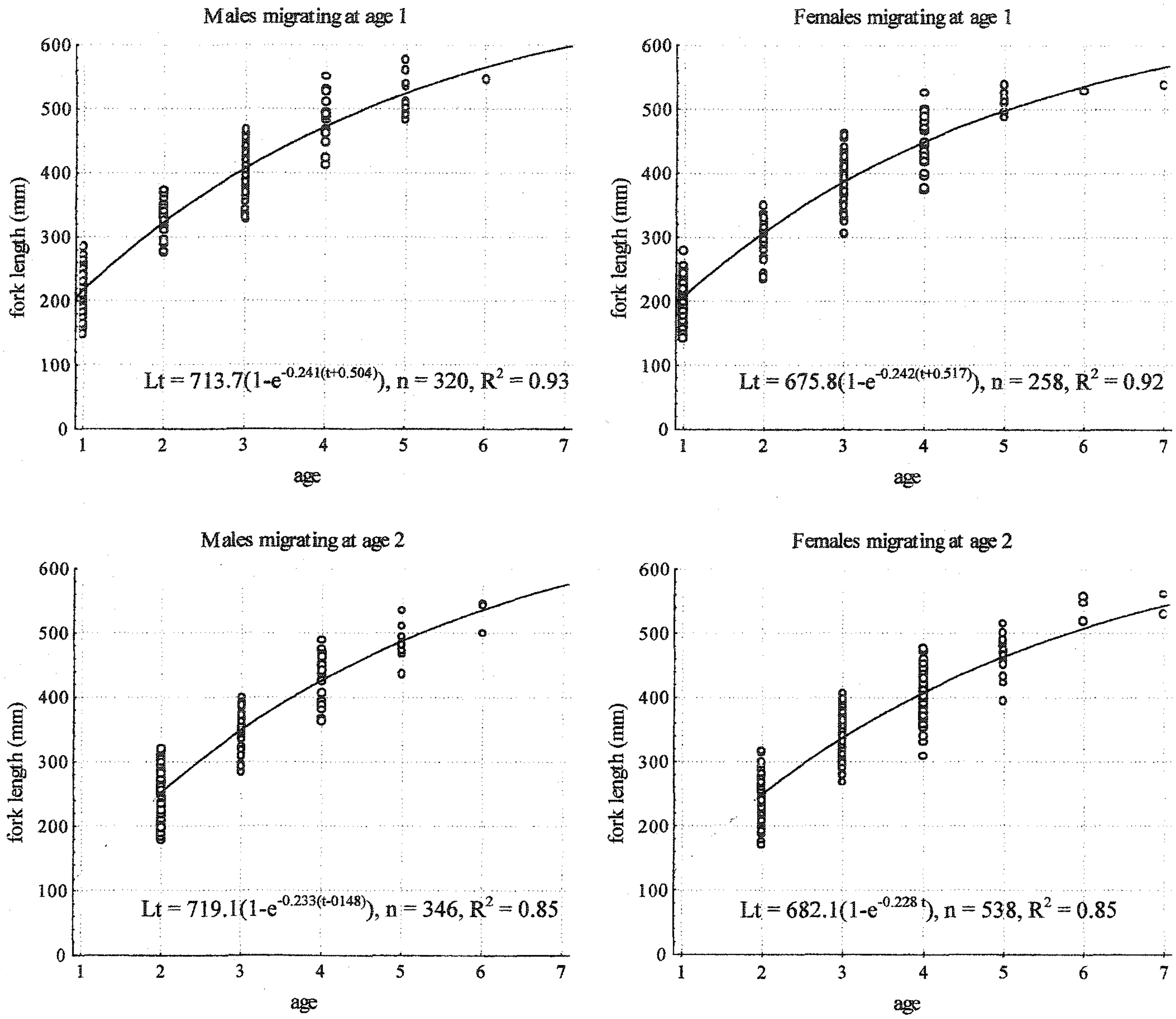

Figure 3-5. Modelled growth curves (fork length, in the fall, at a given age) of male and female anadromous brook charr from the Sainte-Marguerite River, Québec, having migrated at age 1 or at age 2, from age at first downstream migration (1998-2001, pooled data). Corresponding functions are in the form of $Lt = L\infty(1-e^{-K(t-to)})$ were Lt is fork length at year t, $L\infty$ is the asymptotic length, K is the rate at which $L\infty$ is achieved and to is a constant inserted to improve the fit; n is the number of fish in each group. In age classes including mature and immature fish, only sizes of mature fish were retained for the model.

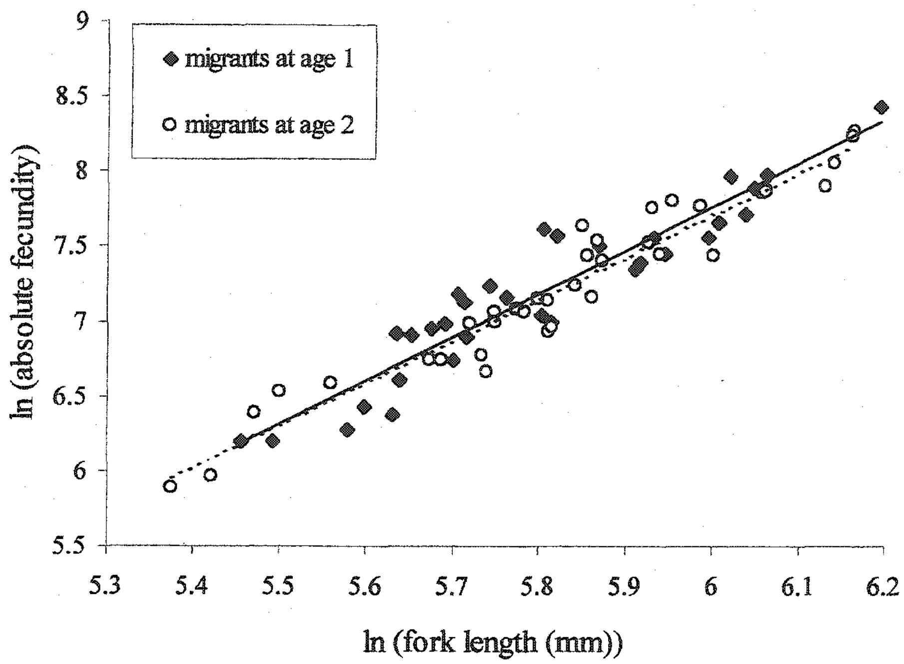

Figure 3-6. Relationship between absolute fecundity (total number of eggs) and fork length in anadromous brook charr sampled in the Sainte-Marguerite River, Québec, from 1998 to 2001, for females having migrated at age 1 (filled diamonds and solid regression line, n = 32) and females having migrated at age 2 (open circles and dashed regression line, n = 37). Age at downstream migration did not have any significant effect on size-specific fecundity (ANCOVA, $p > 0.3$ for slope and intercept). Estimated relationship on pooled data was ln(fecundity) = 2.8338 ln (fork length) – 9.2723, $R^2 = 0.91$, $p < 0.001$.

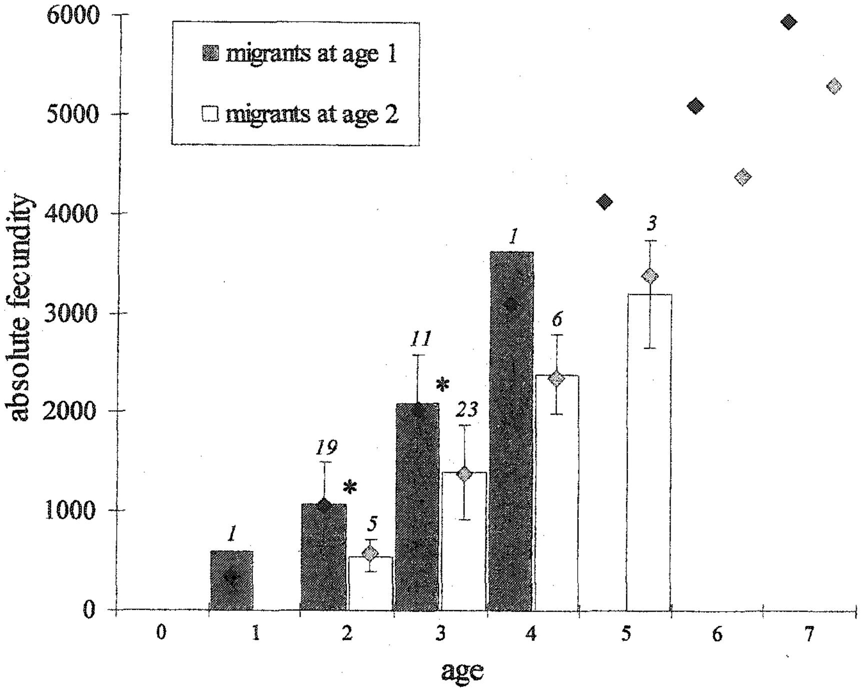

Figure 3-7. Observed fecundity at age (mean ± S.D., bars) and estimated fecundity at age (using estimated length at age and estimated relationship between length and fecundity, diamonds) in anadromous brook charr from the Sainte-Marguerite River, Québec, having migrated at age 1 and age 2. Sample sizes are above corresponding bar; asterisks indicate a significant difference in observed values at a p value of 0.05 (Student t-test).

3.5.5. Age at maturity

Almost all migrants were still immature in the fall following downstream migration. From 1998 to 2001, only one sea age 0 charr caught on spawning grounds was recorded and more than 98% of sea age 0 charr caught in the fall were immature (migrants at age 1, 350/351, migrants at age 2, 670/682). In sea age 2 charr, fish having migrated at age 1 (1/2+ migrants) were almost exclusively caught as adults (all the 105 fish collected in the upstream part of the river were mature and only 5 catches of immature fish were recorded in four years, out of 1546 juveniles sampled in the fall). All the migrants at age 2 having spent three growing seasons in the estuary (2/2+ migrants) which were sampled were mature ($n = 70$). Significant numbers of sea age 1 charr were caught as adults but significant numbers of sea age 1 charr were also caught as juveniles in the fall sport-fishery. In this sea age group, the ratio of immature charr having migrated at age 1 (1/1+) to immature charr having migrated at age 2 (2/1+) was significantly higher than the ratio of age 1 to age 2 charr observed at downstream migration, in males and in females (Table 3-1, χ^2 –test, $p< 0.004$ in all cases). We observed a least four times more immature 1/1+ migrants relative to immature 2/1+ migrants than expected if maturity incidences had been equal for the two groups. We observed only a few mature 1/1+ migrants relative to 2/1+ migrants in catches of adults. Analysis by sex did not reveal a significant difference between observed and expected frequencies. However, overall observations of mature 1/1+ migrants relative to observations of mature 2/1+ were significantly lower than expected ($p < 0.05$ in both years), confirming a higher percentage of mature fish in migrants at age 2. Subsequent estimates of maturity incidence in 2/1+ migrants (M_2) were approximately two times higher than estimates of maturity incidence in 1/1+ migrants (M_1) (Table 3-1).

Thus, overall, charr having migrated at age 1 reproduced earlier in life (33-45% of mature fish at age 2 and more than 95% of mature fish at age 3) than charr having migrated at age 2 (less than 2% of mature fish at age 2 and 86-89% of mature fish at age 3). However, charr having migrated at age 2 reproduced at a lower sea age (i.e. spent less time in the estuary before first reproduction).

Table 3-1. Numbers of males and females that migrated at age 1 and of males and females that migrated at age 2 in mature and immature sea age 1 brook charr sampled in the Sainte-Marguerite River, Québec, in 2000 (A) and 2001 (B), and expected values assuming equal maturity incidences at sea age 1 for the two tactics. The comparison of observed and expected value gives an estimate of $\alpha = M_1/M_2$ (M_1, maturity incidence in fish that migrated at age 1 and M_2, maturity incidence in fish that migrated at age 2) and $\beta = I_1/I_2$ (I_1 percentage of immature individuals in fish that migrated at age 1 and I_2 percentage of immature individuals in fish that migrated at age 2). α and β give subsequent estimates of M_1 and M_2.

A. 2000 sampling : 1999 migrants

Age at first migration	Proportions at first migration (= expected)		Sampling of immature sea age 1 charr				Sampling of mature sea age 1 charr			
			Observed values		Expected values		Observed values		Expected values	
	Males	Females	Males	Females	Males	Females	Males	Females	Males	Females
1^+	0.199 (a)	0.104 (c)	37 (e)	29 (g)	20	11	6 (i)	3 (k)	11	6
2^+	0.280 (b)	0.417 (d)	12 (f)	24 (h)	29	43	17 (j)	31 (l)	16	24
Total	1		102		102		57		57	

Males : $\beta = I_1/I_2 = (e/f)/(a/b) = 4.340$ and $\alpha = M_1/M_2 = (i/j)/(a/b) = 0.497$ → $M_1 = 43.2\%$ and $M_2 = 86.9\%$

Females : $\beta = I_1/I_2 = (g/h)/(c/d) = 4.839$ and $\alpha = M_1/M_2 = (k/l)/(c/d) = 0.388$ → $M_1 = 33.4\%$ and $M_2 = 86.2\%$

B. 2001 sampling : 2000 migrants

Age at first migration	Proportions at first migration (= expected)		Sampling of immature sea age 1 charr				Sampling of mature sea age 1 charr			
			Observed values		Expected values		Observed values		Expected values	
	Males	Females	Males	Females	Males	Females	Males	Females	Males	Females
1^+	0.195 (a)	0.083 (c)	16 (e)	13 (g)	10	4	5 (i)	2 (k)	9	4
2^+	0.236 (b)	0.486 (d)	4 (f)	16 (h)	12	24	12 (j)	27 (l)	11	22
Total	1		49		49		46		46	

Males : $\beta = I_1/I_2 = (e/f)/(a/b) = 4.854$ and $\alpha = M_1/M_2 = (i/j)/(a/b) = 0.506$ → $M_1 = 44.8\%$ and $M_2 = 88.6\%$

Females : $\beta = I_1/I_2 = (g/h)/(c/d) = 4.737$ and $\alpha = M_1/M_2 = (k/l)/(c/d) = 0.432$ → $M_1 = 37.5\%$ and $M_2 = 86.8\%$

3.5.6. Survival to and after reproduction

We did not observe any significant difference in survival between migrants-of the-year tagged in the river trap and migrants-of the year tagged in the SMB during the downstream migration period (z-test, 1999, n trap = 1284 and n SMB = 1214, $p = 0.40$ and 2000, n trap = 899 and n SMB = 536, $p = 0.42$). Therefore, we pooled all the migrants-of-the-year tagged from mid-May to mid-June to estimate survival from downstream migration to the following spring (Table 3-2). Anadromous charr suffered a large mortality during their first and second year in the estuary. However, exploitation may have had a larger effect at sea age 1 than at sea age 0.

Sacrifices at the time of tagging sea age 1 charr and the analysis of sea age 1 fish recovered soon after tagging suggested that we marked 1/1+ charr and 2/1+ charr in equal proportions. As fish having migrated at age 2 were more numerous than fish having migrated at age 1 at any sea age, seine hauls caught 2/1+ charr in lower proportions than expected i.e. missed part of 2/1+ charr. We could not estimate sea age 1 survival in charr having migrated at age 1 and in charr having migrated at age 2 separately as the number of complete recaptures (tag with fish) in the following year was not large enough to do so. However, in anglers' catches, the ratio of charr having migrated at age 2 to charr having migrated at age 1 decreased, on average, from 2.3:1 at sea age 1 to 1.4:1 at sea age 2, suggesting a lower survival in 2/1+ migrants (approximately 33% lower than in 1/1+ migrants). A lower survival from sea age 1 to sea age 2 in charr having migrated at age 2 may be explained by a reproductive cost, which would have affected charr having migrated at age 2 in greater proportions as 86-89% of them reproduced at sea age 1 *vs* 33-45% of charr having migrated at age 1.

Overall survival of spawners was more variable than survival at sea age 0 and sea age 1 (Table 3-2). Survival of 1999 spawners was significantly lower than survival of 2000 spawners (z-test, $p < 0.03$) and marginally significantly lower than survival of 1998 spawners (z-test, $p < 0.08$). The summer 1999 - summer 2000 period was characterized by a higher incidence of tag recovery (Table 3-2), suggesting a higher exploitation of adults during that year, relative to 1998-1999 and 2000-2001. However, this difference in recovery incidence was not sufficient to explain the difference in survival between adults tagged in 1999 and adults tagged in 1998 and 2000. Survival of 2000 spawners was significantly greater than the survival of sea age 0 fish in 1999-2000 and 2000-2001 (z-test, $p < 0.05$ for both years) and marginally significantly larger than the survival of sea age 1 charr in 1999-2000 and 2000-2001 (z-test $p < 0.06$ for both years).

In subsequent modelling, survival estimates were corrected for exploitation during summer to generate a better estimate of survival to reproduction at a given sea age.

Table 3-2. Annual survival (June to June) of sea age 0 and sea age 1 anadromous brook charr from the Sainte-Marguerite River, Québec, and annual recovery incidence (percentage of tagged fish that were caught and reported) in fish tagged at the beginning of each period. As fish were marked with the same tags, differences in recovery incidence are assumed to reflect differences in exploitation.

Sea age	First period of tagging	Number of tagged charr	Survival from tagging to the following spring (%)	Standard error (%)	Recovery incidence (%)
0 (1999 migrants)	spring 1999	2498	10.22	1.62	9.29
0 (2000 migrants)	spring 2000	1435	12.83	2.80	9.82
1 (1998 migrants)	spring 1999	330	12.27	6.75	30.07
1 (1999 migrants)	spring 2000	194	9.57	3.12	30.93

Table 3-3. Survival of anadromous brook charr spawners from the Sainte-Marguerite River, Québec, from one upstream migration to the next in 1998, 1999 and 2000, and annual recovery incidence (percentage of tagged fish that were caught and reported) in fish tagged at the beginning of each period. Smaller adults (sea age 1) were under-represented in tagged fish as some migrated upstream in September, after the sampling. As fish were marked with the same tags, differences in recovery incidence are assumed to reflect differences in exploitation.

First period of tagging	Number of tagged charr	Survival from tagging to the following summer (%)	Standard error (%)	Recovery incidence (%)
summer 1998	64	28.94	14.24	17.64
summer 1999	463	8.14	3.30	25.32
summer 2000	172	36.00	13.59	15.43

3.5.7. Life-time reproductive success (Ro)

Neither migrants at age 1 nor migrants at age 2 matured during their first growing season in the estuary and they all suffered the same mortality during that period. Therefore, sea age 0 survival is not a key factor increasing or decreasing the life-time reproductive success of individuals expressing one tactic relative to individuals expressing the other. As most migrants at age 2 first reproduce at sea age 1 and most migrants at age 1 first reproduce at sea age 2, survival from sea age 1 to sea age 2 appears to have a much greater effect on the life-time reproductive success of migrants at age 1 (Figure 3-8). For the parameters set in Figure 3-8, an increase of survival during the second year in the estuary from 0.1 to 0.2 increases Ro by 46% in migrants at age 1 but only by 23% in migrants at age 2. In females having migrated at age 2, survival in fresh water from age 1 to age 2 has a small effect on the slope of the Ro line modelled in Figure 3-8, but a large effect on its intercept. For any given survival from sea age 1 to sea age 2, an increase of survival from age 1 to age 2 by 10% would increase Ro by at least 20%. For a survival from sea age 1 to sea age 2 of 0.123 in the two tactics (higher estimated value, in 2000-2001), a survival of 0.45 from age 1 to age 2, in migrants at age 2, would ensure an equal life-time reproductive success of the two tactics. In the case of a reproductive cost in mature sea age 1 charr (and hence a lower survival in migrants at age 2 where more fish are mature at sea age 1), a higher survival in fresh water is needed for migrants at age 2 to compensate for their lower size at age (see points B and C). Survival at sea ages ≥ 2 has a greater impact on Ro of migrants at age 1 than on Ro of migrants at age 2. For instance, at point A, a decrease of survival at sea ages ≥ 2 to 0.081 (value observed in 1999-2000 spawners) decreases Ro by 14% in migrants at age 1 but only by 7% in migrants at age 2.

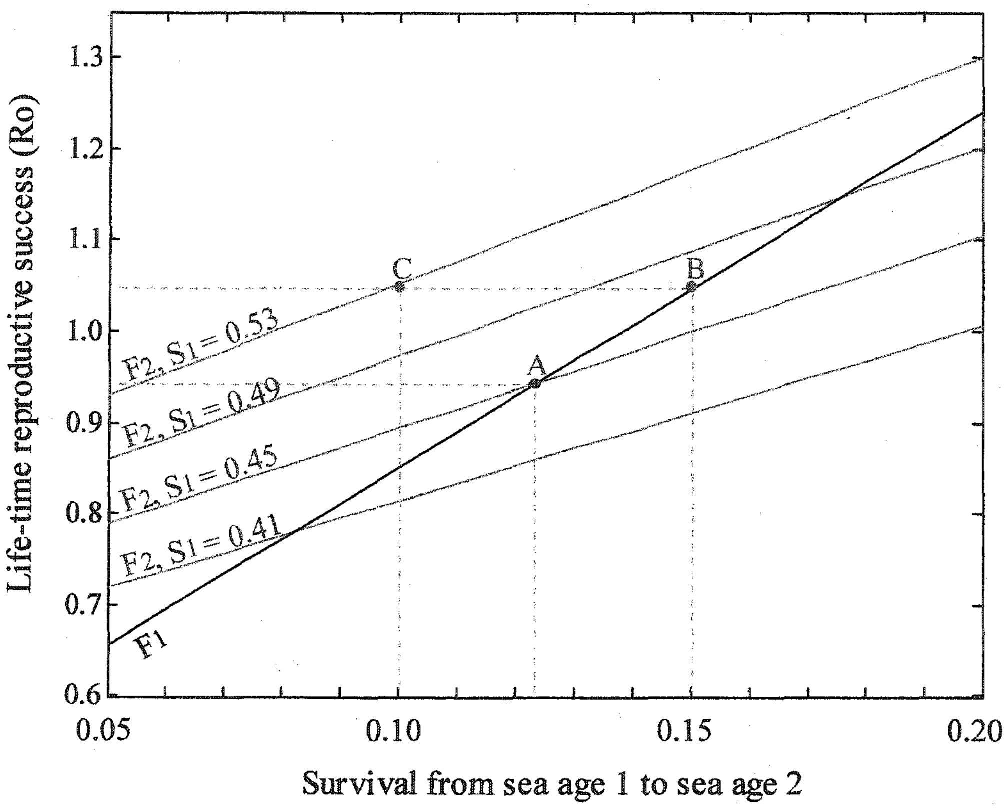

Figure 3-8. Life-time reproductive success (Ro) of female anadromous brook charr from the Sainte-Marguerite River, Québec, having migrated at age 1 (F_1) or having migrated at age 2 (F_2), according to survival during second year in the estuary. In migrants at age 2, Ro was modelled for different values of survival during second year in fresh water i.e. from age 1 to age 2 (S_1). Survival in the year following downstream migration (sea age 0) was set at 0.115 and survival at sea ages ≥ 2 (sea age at which almost all individuals are mature) was set at 0.244, for the two tactics. Incidence of maturity at sea age 1 was set at 0.355 in migrants at age 1 and 0.865 in migrants at age 2. These values correspond to the mean values observed during the study. For a survival from sea age 1 to sea age 2 of 0.123 in the two tactics, a S_1 of 0.45 would ensure an equal life-time reproductive success in the two tactics (point A). For a survival from sea age 1 to sea age 2 of 0.15 in migrants at age 1 (point B) and 0.10 in migrants at age 2 (case of a reproductive cost in migrants at age 2), a S_1 of 0.53 (point C) is needed to ensure an equal life-time reproductive success for the two tactics.

3.6. Discussion

In the present study, we explored the life-history consequences of migrating at age 1 (and at a smaller size) or at age 2 (and at a larger size) in anadromous brook charr from the Sainte-Marguerite River, Québec, Canada. Contrary to our hypothesis and to other studies on anadromous salmonids (references in Bohlin et al. 1996), we did not detect any size-selective mortality following downstream migration. Observing that length distributions of first time migrants did not differ between 1999 and 2000 samplings (and were right skewed in both years) and that smaller charr migrated last (Chapter 2), we suggested that brook charr from the Sainte-Marguerite River do not migrate before having reached a critical body size (under which mortality following migration may be more costly and size-selective). In addition, new migrants did not enter the more saline areas of the Saguenay Fjord directly (Chapter 1). They stayed up to two months in the Sainte-Marguerite Bay, a shallow area under the freshwater influence of the Sainte-Marguerite River, where salinity does not exceed 5.5 PSU in May and 14 PSU in June. Growth and progressive acclimation to salt water in the SMB may prevent size-dependent osmotic stress and, hence, associated size-dependent mortality (see McCormick et al. 1985). This might explain why, though larger, charr migrating at age 2 did not benefit from improved marine survival relative to charr migrating at age 1.

Growth was enhanced in the estuary relative to the river. This observation is in accordance with many studies on anadromous salmonids (see Jonsson and Jonsson 1993). In a given cohort, charr migrating at age 1 obtained and maintained a significant size advantage over charr migrating at age 2. They reproduced earlier in life and at a larger size at a given age. In females having migrated at age 1, a larger size-at-age resulted in a higher age-specific fecundity. However, for a given downstream migration year, migrants at age 2 kept a size advantage over migrants at age 1, at least until the end of the second growing season in the estuary. A long term size advantage in larger smolts has also been observed in Atlantic salmon (e.g. Nicieza and Braña 1993). In addition, larger Atlantic salmon smolts tend to mature after fewer winters at sea and at smaller sizes than individuals that were smaller at downstream migration (Marschall et al. 1998). Similarly, in the Sainte-Marguerite River, brook charr having migrated at age 2 (i.e. larger smolts) first reproduce at a lower sea age and at a smaller size, relative to charr having migrated at age 1 (i.e. smaller smolts). The fact that migrants at age 2 reproduce at a lower sea age has two possible explanations: 1) the size advantage of migrants at age 2 at sea age 1 is large enough for them to reach size at maturity in a significantly greater proportion than migrants at age 1, or 2) optimal size at maturity differs between individuals expressing one tactic or the other. By staying one more year in a safer habitat (fresh water) and spending less time in a more risky habitat (the estuary) before first reproduction, migrants at age 2 increase their overall survival to reproduction, relative to migrants at age 1 (even in the absence of size-dependent mortality at downstream migration). Thus, a trade-off between fast growth and survival to maturity may play a major role in the maintenance of alternative ages at downstream migration and of variation in growth rates of anadromous charr (see Mangel and Stamps 2001).

The conditional strategy theory accounts for the existence of alternative tactics associated with unequal fitnesses. In most cases, the average fitnesses of individuals expressing one tactic and of individuals expressing another would actually be unequal (Dominey 1984). In the present study we had no evidence that a given age at downstream migration is associated with a higher average life-time reproductive success in females. A survival from age 1 to age 2 of about 0.5 in migrants at age 2 can ensure an equal life-time reproductive success for the two tactics. Based on the observation of 48-69% loss between age 1 and age 2 classes in fresh water, depending on out-migration incidence (Chapter 4), a survival from age 1 to age 2 of 0.5 can reasonably be expected in the Sainte-Marguerite River. In addition, an annual survival of 0.5 in juvenile resident brook charr has been observed in other Canadian rivers (e.g. Hutchings 1993). Moreover, two factors having a major influence on the difference between the life-time reproductive successes of migrants at age 1 and migrants at age 2 - survival in fresh water from age 1 to age 2 and survival from sea age 1 to sea age 2 - may vary from one year to another. In a given cohort, migrants at age 1 and migrants at age 2 will not necessarily experience the same conditions at downstream migration and may not suffer the same mortality at sea age 0. Therefore, it is possible that environmental variability regulates the relative costs and benefits of having migrated at age 1 or at age 2. In Atlantic salmon, grilse may offset their lower reproductive success relative to multi-sea winter fish by returning earlier to reproduce, depending on the relative return probabilities associated with the two tactics (Garant et al. 2003). Variability in survival at sea can give a fitness advantage to grilse in some years and to multi-sea winter fish in other years. Similarly, in brook charr from the Sainte-Marguerite River, we can expect that variability of survival from age 1 to age 2 in freshwater and variability of survival in the estuary may give a fitness advantage to migrants at age 1 in some cohorts and to migrants at age 2 in others.

However, the two migratory tactics are characterized by unequal ages at maturity. In such a case, a comparison of average life-time reproductive successes as a comparison of fitnesses is incomplete (Giske et al. 1993). Migration at age 1 (and earlier maturity) may result in a higher fitness expectancy, even if the average life-time reproductive successes associated with the two tactics are equal. A more precise estimate of survival in fresh water would be needed to assess if, by delaying migration, slower growers may maximize their fitness up to a point where it would equal (at least in some years) the fitness of faster growers migrating at a younger age.

Our results suggest that exploitation could have a larger impact on the life-time reproductive success of migrants at age 1, relative to migrants at age 2. Brook charr from the Sainte-Marguerite River are not exploited before first downstream migration and exploitation is maximal at sea age 1. If exploitation and natural mortality are additive, an increase of fishing pressure at sea age 1 could induce a selective pressure for migration at age 2, while a decrease could favour migration at age 1. However, the conditional strategy theory does not exclude frequency-dependent selection, which could act as a stabilizing selection of the proportions of migrants at age 1 and migrants at age 2 (see Gross 1996). For instance, a decrease of the fitness of migrants at age 1 (the faster growers in fresh water) should induce an increase of the size or growth threshold for migration at age 1 and, hence, a decrease of the proportion of migrants at 1. On the other hand, delaying average age at migration in the population would increase freshwater densities of age 1 fish. An increase of freshwater densities could decrease growth and/or survival from age 1 to age 2, decreasing the fitness of fish delaying migration, what would tend to move the threshold in the opposite direction (towards a smaller size or a lower growth at first downstream migration).

Many partially anadromous populations exhibit a sex-biased migratory strategy, with more females than males migrating to salt water (Jonsson and Jonsson 1993). The evolutionary explanation of this observation is that reproductive success is more dependent on size in females than in males. In females, production of offspring is highly correlated with production of eggs, which increases with body size. In males, a large size is an advantage in competition for mates at the time of reproduction but small resident males may fertilize eggs of large anadromous females, using sneaking tactics (Jonsson and Jonsson 1993). In the present study, we did not observe a bias in the overall sex-ratio at downstream migration. However, there were more males in age 1 charr and more females in age 2 charr, suggesting that the migratory strategy of the population is actually sex-biased. A similar kind of sex-biased strategy is suggested in the Rikardsen et al. (1997) study on Artic charr from Storvatn Lake, Norway and in the Montgomery et al. (1990) study on brook charr from the Moisie River, Canada, with more males migrating at a younger age and more females at an older age. However, in the first case, samples size were small and the bias did not prove to be significant and, in the second case, the relationship between sex and age is only indirect. Interestingly, in anadromous brook charr from the Sainte-Marguerite River migrating at age 1, males exhibited a faster growth than females, even at the immature stage. If faster growers migrate earlier than slower growers and if the fastest growers of the population are primarily males, we should observe more males than females migrating at a younger age. In rainbow trout (*Oncorhynchus mykiss*) juvenile males are more aggressive than juvenile females (Johnsson and Åkerman 1998). Johnsson and Åkerman (1998) suggest that aggression in juvenile males is linked to competition ability on spawning grounds. In salmonids, aggression and dominance have shown to be positively correlated with metabolic rate (e.g. Metcalfe et al. 1995, Cutts et al. 1998). Therefore, one possible explanation for males migrating at a younger age would be a higher average metabolic rate in males, relative to females. The bias towards females in migrants at age 2 could result from the deficit in males following migration at age 1 and/or a greater tendency in remaining females to migrate than to stay as freshwater residents, relative to remaining males.

In summary, our results show that, as suggested by Jonsson and Jonsson (1993) and Økland et al. (1993), younger smolts maximize their life-time reproductive success by maximising growth rate and older smolts by maximizing overall survival to first reproduction. However, in the Sainte-Marguerite River, older (and larger) smolts do not improve their survival to first reproduction (relative to younger smolts) because they escape a size-selective mortality at downstream migration but because they spend more time in a safer habitat (fresh water) and less time in a more risky habitat (the estuary) before first reproduction. A higher survival to first reproduction in older smolts could compensate, in terms of life-time reproductive success, for their lower size-at-age. With or without equal fitness for the two tactics, environmental variability, frequency-dependent selection and sex-specific constraints could act as stabilizing factors in the maintenance of alternative ages at downstream migration.

3.7. Acknowledgements

We acknowledge S. Bilodeau-Gauthier, A. Boivin, F. Charlebois, M. Desgagnés, J.-M. Fréchette, S. Gaouette, C. Garneau, M.-C. Landry-Pelchat, C. Langlois, R. Lavoie, J.-G. Marquis, A. Ménard, G. Morinville, P.-A. Paradis, C. Poirier, J.-F. Rigalbuteau, J. Savard, V. Thériault and S. Trépanier for field and laboratory assistance. We also thank K. McCann who taught S.L. basic modelling and programming with MatLab and F. Bérubé for precious help in programming. We are very grateful to the Association de la Rivière Sainte-Marguerite, the Club de Pêche de la Rivière Sainte-Marguerite, the Saguenay and the Sainte-Marguerite River anglers, for their collaboration to the study. Funding of this project was provided to J.J.D. by the Natural Sciences and Engineering Research Council of Canada (Strategic Grant and Collaborative Special Projects), the Fondation de la Faune du Québec, the Government of Québec (Faune et Parc Québec), the Government of Canada (Economic Development, Saguenay – Saint-Lawrence Marine Park) and the financial partners of CIRSA Inc. (Corporation de soutien aux Initiatives de Recherche sur le Saumon Atlantique). This study is a contribution to the research programs of CIRSA (Centre Interuniversitaire de Recherche sur le Saumon Atlantique) and GIROQ (Groupe Interuniversitaire de Recherches Océanographiques du Québec. S.L. was financially supported by funding from CIRSA and GIROQ.

4. Role of environment-gene interactions in the evolution of the residency-anadromy dichotomy in brook charr (*Salvelinus fontinalis*).

Sophie Lenormand and Julian J. Dodson

4.1. Résumé

Les facteurs qui régulent l'expression de la résidence en eau douce, ou sinon de l'anadromie, devraient être principalement ceux qui affectent la façon dont certains individus peuvent maximiser leur fitness en restant en eau douce. Nous nous sommes intéressés à l'effet de l'isolation géographique, de la compétition intra- et inter-spécifique et des fluctuations environnementales sur le cycle de vie d'ombles de fontaine résidants, parmi des communautés différant par leur tendance à la migration. Nous avons comparé le cycle vital des ombles de trois tributaires de la rivière Sainte-Marguerite, Québec, en deux années différentes. Un des tributaires était isolé du reste de la rivière depuis 35 ans. Bien que les ombles de ce tributaire avaient les moins bonnes perspectives de croissance, ils ne migraient pas mais se reproduisaient à un âge et une taille inférieurs à ceux des ombles des deux autres tributaires, suggérant un effet de la sélection « de bord d'abîme » sur leur comportement migratoire et/ou sur leur norme de réaction aux opportunités de croissance. Les deux tributaires non isolés différaient par leur densités relatives de saumons atlantique juvéniles et d'ombles, ainsi que par l'ampleur des montaisons d'ombles anadromes. Les perspectives de croissance diminuaient avec le niveau potentiel de compétition inter-spécifique mais l'âge à maturité et la fécondité à l'âge ne différaient pas entre les deux tributaires. La communauté caractérisée par les plus faibles perspectives de croissance présentait une dévalaison d'ombles juvéniles plus importante. Cependant, elle était aussi caractérisée par une survie inférieure jusqu'à la reproduction chez les femelles résidantes et par une montaison d'ombles anadromes supérieure. Ainsi, une dévalaison plus importante d'ombles juvéniles dans ce ruisseau peut être expliquée à la fois par des opportunités de croissance inférieures et par l'héritabilité de la tactique exprimée. Globalement, les ombles résidants avaient une croissance beaucoup plus faible que les ombles anadromes de la rivière Sainte-Marguerite mais une meilleure survie jusqu'à la reproduction. Un compromis entre croissance - et donc, fécondité - et survie pourrait avoir un rôle majeur dans le maintien de tactiques migratoires alternatives dans cette population. Les mâles présentaient une tendance à la résidence supérieure à celle des femelles, suggérant qu'ils ont de meilleures chances de maximiser leur fitness en rivière que ces dernières. La variabilité environnementale temporelle avait un effet sur le cycle vital et le

succès reproducteur des ombles résidants, et pourrait aussi favoriser le maintien simultané de la résidence et de l'anadromie.

4.2. Abstract

Factors regulating the expression of freshwater residency, and hence otherwise anadromy, should be primarily those affecting the way in which some individuals can maximise their fitness by staying as freshwater resident. We focused on the effect of geographical isolation, intra- and inter-specific competition and environmental fluctuations on the life-history of freshwater resident brook charr, among communities differing in migratory tendency. We compared major life-history traits of resident charr among three tributaries of the Sainte-Marguerite River, Québec, in two different sampling years. One of these tributaries had been isolated from the rest of the river for 35 years. Although fish from this tributary had the poorest growth prospects, they did not migrate but reproduced at a lower age and at a smaller size than fish from the two other tributaries, suggesting an effect of knife-edge selection on their migratory tendency and/or their reaction norm to growth opportunities. The non-isolated tributaries differed in relative densities of Atlantic salmon parr and brook charr and in the extent of upstream migration of anadromous charr. Growth prospects decreased with the potential for inter-specific competition but age at maturity and age-specific fecundity of resident charr did not differ between the two tributaries. The community characterized by the poorer growth prospects showed a greater downstream migration run of juvenile charr. However, it was also characterized by a lower survival to reproduction in resident females and by a greater upstream migration of anadromous charr. Thus, both poorer growth opportunities and inheritance of the tactic may explain a greater migration run of juvenile charr in this creek. Overall, resident fish had a much poorer growth than anadromous fish from the Sainte-Marguerite River but greater chances to survive to reproduction. A trade-off between growth, and hence fecundity, and survival to reproduction may significantly contribute to the maintenance of alternative migratory tactics in this population. Males showed a greater tendency towards residency, relative to female, suggesting that they have greater chances to maximize their fitness in the river than females. Temporal environmental variability had an effect on the life-history and the life-time reproductive success of resident charr and could also favour the maintenance of both anadromy and residency.

4.3. Introduction

Anadromy is a key feature of salmonid life-history. However, in several species, migration to salt water is not obligatory. Firstly, in some populations where anadromy is observed, there are individuals that reproduce without migrating to sea (McDowall 2001). In such partially anadromous populations, freshwater residency may be observed in males only (e.g. in *Salmo salar* (Fleming 1996), *S. trutta* (L'Abée-Lund et al. 1990)) or in both sexes (e.g. in *Salvelinus* spp., *S. trutta* and several *Oncorhynchus* species, Jonsson and Jonsson 1993). Secondly, there are entire breeding populations which have evolved towards a resident life-history and where all individuals spend their whole lives in fresh water (McDowall 2001). Anadromous individuals usually benefit from enhanced growth in salt water and, hence, a greater size at age. A greater size at age results in a higher age-specific fecundity in females (Gross 1987 and e.g. Jonsson 1985, Morita and Takashima 1998). In both sexes, a large size constitutes an advantage in territorial competitions at the time of reproduction (Dodson 1997). However, migrants may suffer much higher mortality than freshwater residents. The fitness benefit of residency, relative to anadromy, would thus be a greater survival to first reproduction which, in addition, may occur earlier in life (Jonsson and Jonsson 1993).

In partially anadromous populations, migratory behaviour may be partly heritable (e.g. Nordeng 1983) but the expression of a resident or of an anadromous life-history seems to be conditional on individuals' growth in fresh water (Northcote 1992, Jonsson and Jonsson 1993). Anadromy and residency may thus be seen as two alternative tactics in the theoretical context of a conditional reproductive strategy (summarized in Gross and Repka 1998), in which the expression of a given tactic depends on the individual's state and the expressed tactic results in higher fitness for the individual. If several studies have shown the importance of freshwater growth in the expression of anadromy or residency, different trends have been observed among salmonid populations. Fast growth may promote early maturation without any niche-shift (e.g. Nordeng 1983, Thorpe 1987, L'Abée-Lund et al. 1990, Hutchings and Myers 1994). In such a context, migration would occur when local growth opportunities are not sufficient to reproduce in fresh water. On the other hand, within a given population, fast growth may be associated with early migration (e.g. Jonsson 1985, Svenning et al. 1992, Rikardsen and Elliott 2000). However, achieved growth rate in a given niche is not necessarily correlated with scope of growth and energy availability for maturation in that niche. Size at a given age results from both food consumption and growth efficiency (the ratio of growth to energy intake). Fish with high metabolic rates and low growth efficiency can maintain a fast growth early in life through high energy intake, relative to more efficient fish consuming less (Forseth et al. 1999, Morinville and Rasmussen 2003). However, they may be soon constrained by the limited food resources in rivers, relative to their high energy demands (Jonsson and Jonsson 1993, Økland et al. 1993 and e.g. Forseth et al. 1999). Thus, in both cases (fast growth associated with maturation or fast growth associated with migration), the expression of residency or anadromy could depend more on individuals' reproductive prospects in fresh water than on their absolute growth.

When parts of anadromous populations become geographically isolated from the central population, they may eventually fail to express migratory behaviour. Two mechanisms may explain why anadromy is not expressed in these situations. In reaches where fish have been isolated a long time by natural impassable barriers such as waterfalls, a long term "knife-edge" selection (individuals migrating downstream were never able to come back and contribute to the next generation) may have resulted in the loss of anadromous behaviour (Northcote 1992). When geographical isolation is recent (e.g. originating from dam construction), the expression of the resident tactic in all individuals could result solely from phenotypic plasticity. Lower densities and better growth in reaches where anadromous fish can no longer reproduce may be sufficient to explain differences in migratory tendency and life-history between individuals from above-dam areas and individuals from below-dam areas (e.g. Morita et al. 2000). From a theoretical point of view, this implies that individuals from above-dam areas have a much greater chance of exceeding the threshold level of growth for the expression of the resident tactic.

However, geographical isolation may not inevitably result in decreased densities. In salmonids, mortality in early life-stages can be strongly density-dependent (e.g. Elliot 1994). Therefore, a greater survival in early life-stages in areas where anadromous fish can no longer reproduce may maintain high densities at older life-stages. In addition, if the heritable basis of anadromy lies partly in heritance of metabolic rates and growth efficiency, a barrier to return migration may select against both migratory behaviour and high metabolic rate. By progressively eliminating individuals with higher metabolic rates, a "knife-edge" selection may result in a decrease of the average metabolic rate of remaining individuals. A decrease of metabolic requirements may increase survival and hence densities. In such a scenario, the maintenance of high densities in above reaches could still promote migration for a certain time. On the other hand, the effect of density on growth and migratory behaviour may be counteracted by the reduction of metabolic requirements of remaining fish and migratory tendency could rapidly decrease.

The relative influences of genes and environment on anadromy is an old issue (e.g. Ricker 1938). Many studies have explored it focusing on proximate mechanisms regulating the expression of migratory behaviour (e.g. Jonsson 1982, Nordeng 1983, Svenning et al. 1992, Hindar and Jonsson 1993, Forseth et al. 1994, 1999, Rikardsen and Elliott 2000, Morinville and Rasmussen 2003, Thériault and Dodson, submitted). However, direct insights into the evolution of salmonid life-history may be provided by the study of intra-specific phenotypes. Factors regulating the expression of residency (and hence otherwise anadromy) should be primarily those affecting the way in which some individuals can maximise their fitness by staying as freshwater resident i.e. their size and age at maturity and their survival to reproduction. In this regard, variation in individuals' growth efficiency and environmental factors influencing growth opportunities may be key factors in the evolution of salmonid life-history and migratory behaviour. Among factors affecting growth opportunities, absolute feeding resources, densities of conspecifics (e.g. Bohlin et al. 1994, Jenkins et al. 1999) and of heterospecific competitors (e.g. Rodriguez 1995 and references therein) could be of major importance at the community level. Life-history variability among fish expressing residency in different environmental conditions, including geographical isolation, should reflect environmental opportunities and constraints for the evolution of freshwater residency in anadromous species and may highlight some of the factors involved in the evolution of salmonids life-history and migratory behaviour.

We studied the life-history of resident brook charr originating from three tributaries of the Sainte-Marguerite River, Québec, which supports a large partially anadromous population of brook charr (Chapter 2, Chapter 3). One of these tributaries has been geographically isolated from the main branch of the river for 35 years and is characterized by a dense population of charr that do not show any migratory behaviour. The two other tributaries are characterized by an upstream migration of anadromous brook charr and by the presence of Atlantic salmon juveniles. Downstream migration of juvenile brook charr is greater in the tributary showing the higher ratio of salmon parr to brook charr. We compared major life-history traits of resident charr (size-at-age, size and age at maturity, size and age-specific fecundity, sex-ratio) among the three tributaries, in two different sampling years, and estimated survival expectancy in the three tributaries from age classes densities. Our first objective was to assess if fish from the isolated creek do not migrate because of better growth prospects or because their reaction norm to growth opportunities has changed since isolation i.e. they have a different growth threshold for maturation in fresh water than fish from the two other creeks. Our second objective was to test the hypothesis that fish from the creek showing the greater extent of downstream migration have lower growth opportunities and lower reproductive prospects as freshwater residents. Our last objective was to assess the effect of inter-annual environmental variability on resident charr life-history. The results are discussed with special emphasis on the existence and the maintenance of alternative migratory tactics in salmonid populations.

4.4. Materials and methods

4.4.1. Study Area

The Sainte-Marguerite River (48°27' N, 69°95' W; Figure 4-1 and Chapter 2) empties into the Saguenay Fjord, 25 km upstream from its confluence with the Saint-Lawrence maritime estuary (Québec, Canada). Anadromous brook charr from the Sainte-Marguerite River migrate back and forth between their natal river and Saguenay Fjord (Figure 4-1 and Chapter 2, Chapter 3).

Brook charr were sampled in three secondary-order tributaries, Allaire, Épinette and Morin (Figure 4-1). The three creeks are characterized by the presence of a high (> 10 m) impassable waterfall, located respectively at approximately 2 km, 3.5 km and 5.5 km from their confluence with the Sainte-Marguerite River. This study focused on areas below these waterfalls. Average widths measured in sampling sections (see below) in August 1999 and June 2000 were, respectively, 5.9 m and 6.3 and in Allaire, 4.8 m and 5.2 in Épinette, 6.2 m and 6.5 m in Morin. Average depths were 0.29 and 0.25 m in Allaire, 0.19 m and 0.18 m in Épinette, 0.26 m for both years in Morin. Maximum depths at the same periods were 0.98 m and 0.97 m in Allaire, 0.71 m and 0.75 m in Épinette, 1.02 m and 1.12 m in Morin. However, contrary to the two other creeks, Allaire is characterized by a dominance of step-pool systems, resulting in a more frequent occurrence of deep pools (> 0.4 m).

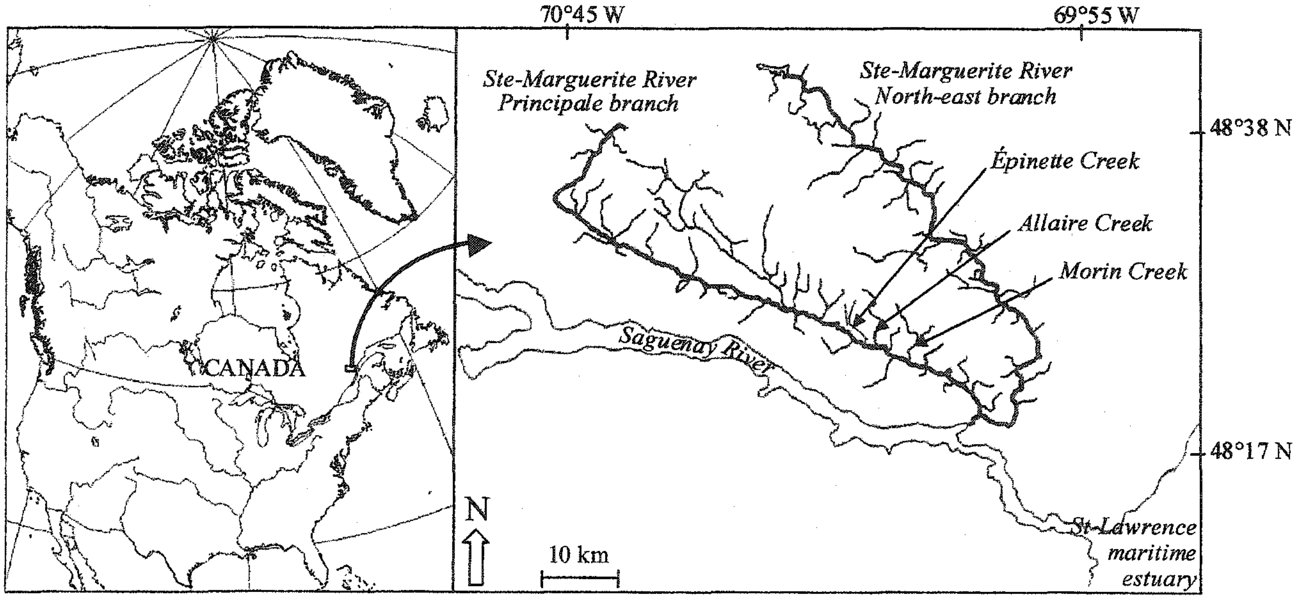

Figure 4-1. Location of the Sainte-Marguerite River, Québec, Canada and of sampling sites: Allaire Creek, Épinette Creek and Morin Creek.

Anadromous brook charr reproduce in Allaire and Morin. However, upstream migration on Morin (at least 20 spawners per year, Véronique Thériault and Julian J. Dodson, Laval University, Quebec, unpublished data) is likely to be more important than on Allaire (1 to 4 spawners per year observed during extensive electro-fishing in September 1999, 2000 and 2002). These two tributaries are also characterized by an upstream migration of Atlantic salmon juveniles and, occasionally, Atlantic salmon adults. Brook charr and Atlantic salmon have not been able to enter Épinette from the Sainte-Marguerite River since 1964, due the deviation of the creek outflow (related to road construction) into a long (15 m) sloping pipe, ending in a 1.5 m waterfall and located at 20 m from Épinette's confluence with the main branch of the river. Thus, at the time of the study, there had not been any gene flow between Épinette charr and anadromous charr from the Sainte-Marguerite River for 35 years, and fish that left Épinette during that period had no chances to reproduce on this creek thereafter.

4.4.2. Sampling and laboratory analysis

Downstream migration of anadromous charr was monitored by setting Alaska traps on the three creeks in spring 1999 and 2000. Fish that were not sacrificed for laboratory analysis were marked with T-bar tags and released 30 m upstream from the traps (see Thériault and Dodson, submitted). Subsequent recaptures gave an estimate of trapping efficiency and of total run (following Bailey 1951).

Age-specific densities (number of fish per 100 m^2) of brook charr and Atlantic salmon juveniles in the three creeks were estimated by electro-fishing in closed sections of approximately 100 m^2. In August 1998, we sampled 3 adjacent but physically heterogeneous sections on Allaire (325 m^2), 4 adjacent sections on Épinette (420 m^2) and Morin (584 m^2). In August 1999, we extended sampling areas to 1507 m^2 on Allaire (13 sections), 1162 m^2 on Épinette (11 sections) and 2057 m^2 on Morin (15 sections). The same sections were fished again in June 2000, just after the end of downstream migration. To estimate densities in each section, we carried out a removal procedure (see Bohlin et al. 1989). Sections were electro-fished on at least three consecutive occasions (waiting 30 min between passes). Fish were removed after each pass, measured and returned to their section at the end of the day. Age classes were discriminated by length-frequency analysis and from age readings on charr sampled in the same creeks (see below). Age 0 fish (born in spring of the same year) could not be caught in June 2000 due to their small size. Densities were estimated separately for each age class, using program 2CAPTURE (removal procedure, population estimation with variable probability removal estimator, see Pollock and Otto 1983 and Rexstead and Burnham 1991).

Brook charr from Allaire, Morin and Épinette were regularly sampled by electro-fishing from June to September 2000. All charr sacrificed during that period were used to determine sex-ratios at a given age. All charr sacrificed from July to September were used to determine maturity incidence at a given age, in males and in females. We made the largest sampling at the end of August - beginning of September to complete data for determination of age at maturity and sex-ratios, and to evaluate size at age at the end of the summer season, size at maturity and size-specific fecundity. To evaluate potential effects of temporal environmental variability on the life-history of resident charr, we made another large sampling at the end of August 2002 to determine size at age, sex-ratios, size and age at maturity and size-specific fecundity in the three creeks. Year 2002 was characterized by a late spring and a dry summer, relative to year 2000.

Charr that had been sacrificed were measured, weighed and classified with respect to sex and maturity stage (Nikolskii 1963). Sagittal otoliths were removed, cleaned and fastened to glass slides with a clear mounting adhesive at its melting point (50°C). Age was read under a binocular microscope, using reflected light. Absolute fecundity (total number of eggs) was evaluated on females at maturity stage 4 (Nikolskii 1963). Opaque (atresic) eggs were not included in the determination of absolute fecundity.

4.4.3. Data analysis

As areas sampled for densities were representative of overall available habitat in the three creeks, we assumed that the ratios of age $n+1$ to age n fish in these areas provided reliable estimates of the disappearance of fish between age n and age $n+1$. As between-sampling periods included spring downstream migration period, disappearance from age n to age $n+1$ reflected both mortality from age n to age $n+1$ and potential emigration at age n. Estimates of disappearance from age n to age $n+1$ were thus estimates of maximum mortality from age n to age $n+1$. We assumed that pooling data from three different years would significantly reduce bias associated with variability in egg deposition and cohort-specific survival. Lower and upper limits of the 95% confidence interval for the ratio of age $n+1$ fish to age n fish were obtained from the 95% confidence interval associated with densities estimate as follows: lower limit = min C.I._{n+1} / max C.I._{n} and upper limit = max C.I._{n+1} / min C.I._{n}.

Effect of origin (creek) on size at age, in a given year, was tested by an analysis of variance. When needed, post-hoc Tukey's HSD tests were performed. Effects of sampling year on size at age was determined separately for each creek by Student t-tests. Overall effect of origin on size at age was tested by multivariate analyses of variance (crossed design, sampling year × creek). Effect of sex on size at age was tested separately for each creek by multivariate analysis of variance (crossed design, sampling year × sex).

For each sex, maturity incidence at a given age was compared among the three creeks by χ^2 tests when samples were large and by Fisher's exact tests and Yates' corrected χ^2 tests when some expected frequencies became less than ten. Results were qualitatively the same in all cases. As Yates' corrected χ^2 test is more conservative, p values given with significant results are Yates' corrected χ^2 test p values and p values given with non significant results are Fisher's exact test p values. We also compared age-specific maturity incidence between 2000 and 2002 in both sexes (for each creek) and age-specific maturity incidence in males and in females in 2000 and in 2002 (for each creek).

Effect of sampling year on size-specific fecundity in each creek was evaluated by an analysis of covariance. The functions best estimating the increase of fecundity with size were of linear form in Allaire and Épinette and of power form in Morin. As correlation coefficients differed only slightly (less than 0.02) between linear regression and power regression for the three creeks, we chose to present linear relationships for the three creeks, to facilitate visual comparisons. Effect of origin (creek) on the increase of fecundity with size was evaluated by analyses of covariance. Effect of sampling year on age-specific fecundity in a given creek was evaluated by Student t-test and effect of origin (creek) on age-specific fecundity was evaluated by multivariate analysis of variance (crossed design, sampling year × creek).

Finally, in each creek, sex-ratio at a given age was compared to parity in 2000 and 2002, by χ^2 test when samples were large and by Fisher's exact test and Yates' corrected χ^2 test when some expected frequencies were less than ten.

4.5. Results

4.5.1. Downstream migration

In Morin, total run of juvenile anadromous brook charr (± S.E.) was estimated at 1755 ± 157 individuals in 1999 and 2617 ± 97 individuals in 2000. Fish were one-year-old (1999, length = 86.9 ± 9.9 mm, and 2000, length = 81.9 ± 14.6 mm) or two-years-old (1999, length = 101.3 ± 16.2 mm and 2000, length = 107.6 ± 16.8 mm) (Thériault and Dodson, submitted). In Allaire, total downstream migration was estimated at 160 ± 13 individuals in 1999 and 241 ± 39 individuals in 2000. Fish were one-year-old (1999, length = 85.2 ± 11.9 mm, and 2000, length = 85.8 ± 8.5 mm), two-years-old (1999, length = 115.1 ± 12.9 mm and 2000, length = 113.7 ± 8.9 mm) and exceptionally three-years-old (Véronique Thériault and Julian Dodson, Laval University, Québec, unpublished data). The Alaskan trap set on Épinette caught four charr in 1999 and five in 2000. Three of these fish were later recaptured as freshwater residents. None of the fish sampled at downstream migration (in any of the creeks) showed any signs of a previous reproduction.

4.5.2. Densities and mortality

Sections sampled in Épinette were characterized by higher densities of age 1 and age 2 brook charr, relative to sections sampled in Allaire and Morin, in all years (Table 4-1, z-test, $p < 0.05$ in all cases). Age 1 charr were more abundant in Allaire than in Morin in 1999 ($p < 0.0004$) but not in 1998 nor in 2000 ($p > 0.6$). Age 2 charr were more abundant in Allaire than in Morin in all years ($p < 0.04$ in all cases). Overall, age 1 to 4 charr were more abundant in Épinette than in Allaire and Morin in all years ($p < 0.0001$ in all cases). Age 1 to 4 charr were more abundant in Allaire than in Morin in 1998 and 1999 ($p < 0.05$ in both cases) but not in 2000 ($p > 0.6$).

No Atlantic salmon juveniles were observed in Épinette in any year. Age 0 salmon were very abundant in Allaire in 1998 (suggesting that one or several Atlantic salmon female(s) reproduced in Allaire in 1997 or that salmon fry escaped from an in-situ incubator situated next to Allaire, for stocking the main stem). No salmon fry were observed in 1999. Age 0 salmon were not observed in Morin in 1998 or in 1999. In 1999, as expected from the presence of Atlantic salmon fry in Allaire the previous year, sections sampled in Allaire contained much more age 1 (and older) salmon juveniles than sections sampled in Morin ($p < 0.0001$). However, the opposite tendency was observed in 1998 and 2000 with more salmon juveniles in Morin ($p < 0.02$ in both cases). Overall, the ratio of salmon parr to brook charr tended to be higher in Morin (average 3.0:1 in Morin *vs* 1.8:1 in Allaire).

In 1998, overall densities of age 1 to 4 salmonids were higher in Épinette and Morin than in Allaire ($p < 0.0001$ in both cases) but not different between Épinette and Morin ($p > 0.1$). In 1999, due to high densities of Atlantic salmon in Allaire, overall densities of salmonids were higher in Allaire than in Épinette and Morin ($p < 0.0001$). In 2000, overall densities of salmonids did not differ among the three creeks ($p > 0.1$ in all cases).

The ratios of age $n+1$ to age n fish in each creek provided estimates of disappearance from age n to age $n+1$ (Table 4-2). The disappearance of fish between age 1 and age 2 included both mortality and emigration in Allaire and Morin but was only associated with mortality in Épinette. From age 2 , the ratio of age $n+1$ to age n fish reflected only natural mortality of freshwater resident fish in the three creeks. Disappearance from age 1 to age 2 tended to be greater in Morin than in Allaire and Épinette for every sampling year (Table 4-2). The overall ratio of age 2 fish to age 1 fish (pooled data) was significantly lower in Morin than in Allaire (z-test, $p < 0.04$) and Épinette ($p < 0.05$). The overall ratio of age 3 to age 2 fish was significantly greater in Allaire than in Épinette ($p < 0.0002$) and Morin ($p < 0.003$) but not different between Épinette and Morin ($p > 0.1$), suggesting a higher survival at age 2 in Allaire.

Table 4-1. Average densities (number of fish per 100 m^2) of brook charr (juveniles and freshwater resident adults) and Atlantic salmon juveniles in the sections sampled by electro-fishing (closed captures with removal) in August 1998, August 1999 and June 2000, in Allaire, Épinette and Morin. The 95% confidence interval is given into brackets. Age 0 fish could not be caught in 2000 as in June they are too small in June to be caught by electro-fishing.

Year	Creek	Species								Total	
		Brook charr						Atlantic salmon			
		Age					Total age 1 to 4	Age		Age	
		0	1	2	3	4		0	≥ 1	0	≥ 1
1998	Allaire	9 (7-13)	5 (4 - 6)	3 (2 - 4)	2 (2 – 2)	≤ 1	9 (9 – 12)	30 (26 - 33)	≤ 1	38 (33 – 56)	10 (9 – 12)
	Épinette	34 (30 - 48)	15 (13 - 25)	6 (5 -10)	1 (1 - 1)	≤ 1	23 (20 – 32)	0 (0 - 0)	0 (0 - 0)	34 (30 – 48)	23 (20 – 32)
	Morin	6 (4 - 11)	4 (4 - 7)	1 (1 - 2)	≤ 1	0 (0 - 0)	6 (5 – 9)	0 (0 - 0)	10 (9 – 17)	6 (4 – 11)	16 (14 – 26)
1999	Allaire	6 (6 - 10)	4 (4 - 6)	2 (2 - 2)	1 (1 - 1)	≤ 1	7 (6 – 9)	0 (0 - 0)	37 (33 – 50)	6 (6 – 10)	44 (39 – 60)
	Épinette	7 (7 - 13)	10 (9 - 15)	6 (6 – 8)	1 (1 - 1)	0 (0 - 0)	18 (17 – 25)	0 (0 - 0)	0 (0 - 0)	7 (7 – 13)	18 (17 – 25)
	Morin	5 (4 - 10)	2 (2 - 3)	1 (1 – 1)	≤ 1	0 (0 - 0)	3 (3 – 4)	0 (0 - 0)	18 (16 – 26)	5 (4 - 10)	21 (18 - 30)
2000	Allaire	N.D.	4 (4 - 6)	2 (2 – 3)	1 (1 - 1)	≤ 1	7 (6 – 10)	N.D.	9 (9 – 13)	N.D.	17 (15 – 23)
	Épinette	N.D.	8 (7 - 13)	6 (5 – 6)	1 (1 - 2)	≤ 1	15 (14 – 21)	N.D.	0 (0 - 0)	N.D.	15 (14 – 21)
	Morin	N.D.	5 (4 - 7)	1 (1 - 1)	1 (1 - 1)	≤ 1	7 (6 - 9)	N.D.	14 (12 - 20)	N.D.	20 (19 – 29)

Table 4-2. Ratio of age $n+1$ to age n brook charr in sections sampled in Allaire, Épinette and Morin in 1998, 1999, 2000 and ratio of age $n+1$ fish to age n fish in pooled data obtained from 1998 to 2000. The confidence interval given in brackets is: (min C.I.$_{n+1}$ / max C.I.$_n$ – max C.I.$_{n+1}$ / min C.I.$_n$).

Creek	Sampling period	age $n+1$ / age n		
		age 2 / age 1	age 3 / age 2	age 4 / age 3
Allaire	August 1998	0.60 (0.38 – 0.86)	0.56 (0.42 – 0.63)	0.20 (0.20 – 0.20)
	August 1999	0.50 (0.31 – 0.70)	0.52 (0.35 – 0.54)	0.07 (0.05 – 0.08)
	June 2000	0.45 (0.31 – 0.70)	0.33 (0.24 – 0.45)	0.09 (0.07 – 0.10)
	1998 – 2000	0.52 (0.34 – 0.74)	0.48 (0.35 – 0.61)	0.14 (0.12 – 0.14)
Épinette	August 1998	0.41 (0.26 – 0.78)	0.19 (0.12 – 0.23)	0.20 (0.20 – 0.20)
	August 1999	0.59 (0.38 – 0.84)	0.24 (0.18 – 0.25)	0 (0 – 0)
	June 2000	0.62 (0.35 – 0.84)	0.25 (0.19 – 0.36)	0.27 (0.21 – 0.29)
	1998 – 2000	0.52 (0.32 – 0.82)	0.23 (0.16 – 0.28)	0.15 (0.14 – 0.15)
Morin	August 1998	0.31 (0.13 - 0.61)	0.25 (0.14 – 0.40)	0 (0 - 0)
	August 1999	0.33 (0.22 – 0.48)	0.20 (0.16 – 0.21)	0 (0 – 0)
	June 2000	0.31 (0.20 – 0.33)	0.37 (0.37 – 0.37)	0.09 (0.09 – 0.09)
	1998 – 2000	0.31(0.18 – 0.46)	0.30 (0.21 – 0.34)	0.05 (0.05 – 0.05)

4.5.3. Growth

Size at age differed among the three creeks, in 2000 and in 2002 (Table 4-3). At the end of the first summer of life (age 0), charr from Allaire were larger than charr from both Épinette and Morin in both years (Table 4-3). At age 1, charr from Allaire were larger than charr from Épinette in 2000 and 2002, and larger than charr from Morin in 2002. At older ages, charr from Allaire were larger than charr from Épinette but not than charr from Morin (except in age 2 males caught in 2002, Table 4-3). Charr from Morin were larger than charr from Épinette from age 1 in 2000, and from age 2 in 2002 (Table 4-3). Sampling year had no effect on size at age 0, in any given creek (Student t-test, $p > 0.3$ in all cases). Age 1 charr sampled in Morin were smaller in 2002 than in 2000 ($p < .0001$) but sampling year had no effect on size at age 1 in Allaire and Épinette (t-test, $p > 0.2$ in both cases). In age 2 charr, males and females from Morin and females from Épinette were smaller in 2002 than in 2000 ($p < 0.04$ in all cases) but sampling year had no effect on size at age 2 in males from Épinette and in males and females from Allaire ($p > 0.1$ in all cases). At age 3, females from Morin were marginally significantly smaller in 2002 ($p = 0.059$) but there was no difference in the size at a age 3 of Morin males, Allaire and Épinette males and females between 2000 and 2002.

Overall, charr from Allaire and charr from Morin were larger than charr from Épinette at all ages (MANOVA, year and creek, p(creek) < 0.0001 in all cases, Tukey's HSD test, $p < 0.0004$ in all cases). Charr from Allaire were larger than charr from Morin at age 0, at age 1 and at age 2 in males ($p < 0.0003$ in all cases, and $p > 0.6$ for age 2 females, age 3 and age 4 males and females). At age 2, males were larger than females in Allaire (MANOVA, sex and sampling year, p(sex) < 0.0006) but not in Morin and Épinette (p(sex) > 0.4). At age 3, males were larger than females in the three creeks ($p < 0.05$ in all cases).

Table 4-3. Length at age of brook charr sampled by electro-fishing at the end of summer (August 23 – September 10) 2000 and 2002, in Allaire, Morin and Épinette Creeks. Length distributions of age 0 and age 1 charr were estimated from total observed length distributions and from sacrifices. Length distributions in older ages were determined from sacrifices only. There was no overlap between length distributions of age 0 and age 1 charr and less than 9% overlap between length distributions of age 1 charr and age 2 charr, for all creeks and both sampling years. Different letters in a given row means significant difference at a p level of 0.05 (Tukey's HSD test). Sampling sizes are given in brackets.

Sampling Year	Age	Sex	Creek			ANOVA results
			Allaire	Épinette	Morin	
2000	0+		68.1 ± 6.1^{a} (24)	57.2 ± 4.7^{b} (19)	61.5 ± 5.1^{b} (26)	$p < 0.0001$
	1+		109.2 ± 8.6^{a} (107)	90.5 ± 13.5^{b} (20)	107.0 ± 10.4^{a} (65)	$p < 0.0001$
	2+	Female	145.0 ± 15.4^{a} (23)	127.3 ± 21.4^{b} (8)	153.5 ± 16.6^{a} (6)	$p < 0.02$
		Male	154.4 ± 15.9^{a} (45)	126.5 ± 19.9^{b} (14)	148.3 ± 15.3^{a} (12)	$p < 0.0001$
	3+	Female	175.0 ± 15.4^{a} (5)	126.0 ± 21.4^{b} (5)	180.6 ± 20.7^{a} (8)	$p < 0.003$
		Male	183.3 ± 13.6^{a} (7)	138.3 ± 9.0^{b} (3)	202.0 ± 25.9^{a} (4)	$p < 0.007$
	4+	Female			226 (1)	
		Male	214.5 ± 6.5 (2)		238 (1)	
2002	0+		67.8 ± 5.7^{a} (47)	56.4 ± 5.2^{b} (54)	59.8 ± 6.1^{b} (15)	$p < 0.0001$
	1+		110.1 ± 9.0^{a} (57)	93.0 ± 61^{b} (61)	95.3 ± 8.3^{b} (72)	$p < 0.0001$
	2+	Female	138.5 ± 13.0^{a} (26)	111.1 ± 12.9^{b} (14)	129.5 ± 16.0^{a} (13)	$p < 0.0001$
		Male	149.4 ± 16.2^{a} (28)	118.7 ± 10.2^{b} (20)	130.4 ± 12.9^{c} (21)	$p < 0.0001$
	3+	Female	160.9 ± 18.4^{a} (13)	118.7 ± 7.4^{b} (6)	157.3 ± 20.6^{a} (6)	$p < 0.003$
		Male	182.1 ± 19.9^{a} (10)	130.0 ± 11.3^{b} (2)	176.3 ± 26.7^{a} (12)	$p < 0.007$
	4+	Female	203.3 ± 20.3^{a} (3)	141.2 ± 12.7^{b} (6)		$p < 0.0007$
		Male	208.0 ± 20.1^{a} (4)	139.3 ± 9.1^{b} (7)		$p < 0.0001$
	5+	Female	(6)	146.3 ± 13.8 (3)		
		Male		191 (1)		

4.5.4. Age and size at maturity, fecundity

In every creek, less than 15% of males and females were sexually mature at age 1 (Figure 4-2). At age 2, maturity incidence was much higher in males and in females from Épinette (males, 94-100% and females, 79-100%) than in males and in females from Morin (males, 13-32% and females 35-50%), in both sampling years (Figure 4-2). Maturity incidence at age 2 was higher in males from Épinette than in males from Allaire (37-39%) in 2000 and 2002, and higher in females from Épinette than in females from Allaire (44-50%) in 2000 (Figure 4-2) but not in 2002 ($p > 0.1$). Maturity incidence at age 2 did not differ between females from Allaire and females from Morin in any year (two-tailed Fisher's exact test, $p > 0.3$ in all cases). Maturity incidence in age 2 males was higher in Allaire than in Morin in 2002 (Morin, 13% and Allaire 39%, Yates' corrected χ^2 test, $p = 0.05$ and Fisher's exact test, $p < 0.04$) but not in 2000 (Morin, 32% and Allaire, 37%, Fisher's exact test, $p = 0.45$). In a given creek, maturity incidence at a given age did not differ significantly between 2000 and 2002, in males and in females (Fisher's exact test, $p > 0.1$ in all cases). In 2000 and 2002, maturity incidence at a given age did not differ significantly between males and females from any creek (Fisher's exact test, $p > 0.1$ in all cases).

In females, minimum observed lengths at sexual maturity were 99 mm in Épinette, 114 mm in Morin and 125 mm in Allaire. In males, minimum observed lengths at maturity were 93 mm in Épinette, 114 mm in Morin and 124 mm in Allaire.

In a given creek, size-specific fecundity did not differ between sampling years (ANCOVA, $p > 0.1$ for slope and intercept, for each of the three creeks). Data from 2000 and 2002 were thus pooled to estimate the relationship between length and fecundity in each creek. Slopes and intercepts obtained did not differ between Allaire and Morin (Figure 4-3). The slopes obtained for Allaire and Morin females were significantly greater than the slope obtained for Épinette females (Figure 4-3). However, when restricting the analysis to size ranges common to the three creeks, slopes and intercepts did not differ among the three creeks (ANCOVA, $p > 0.2$ in all cases).

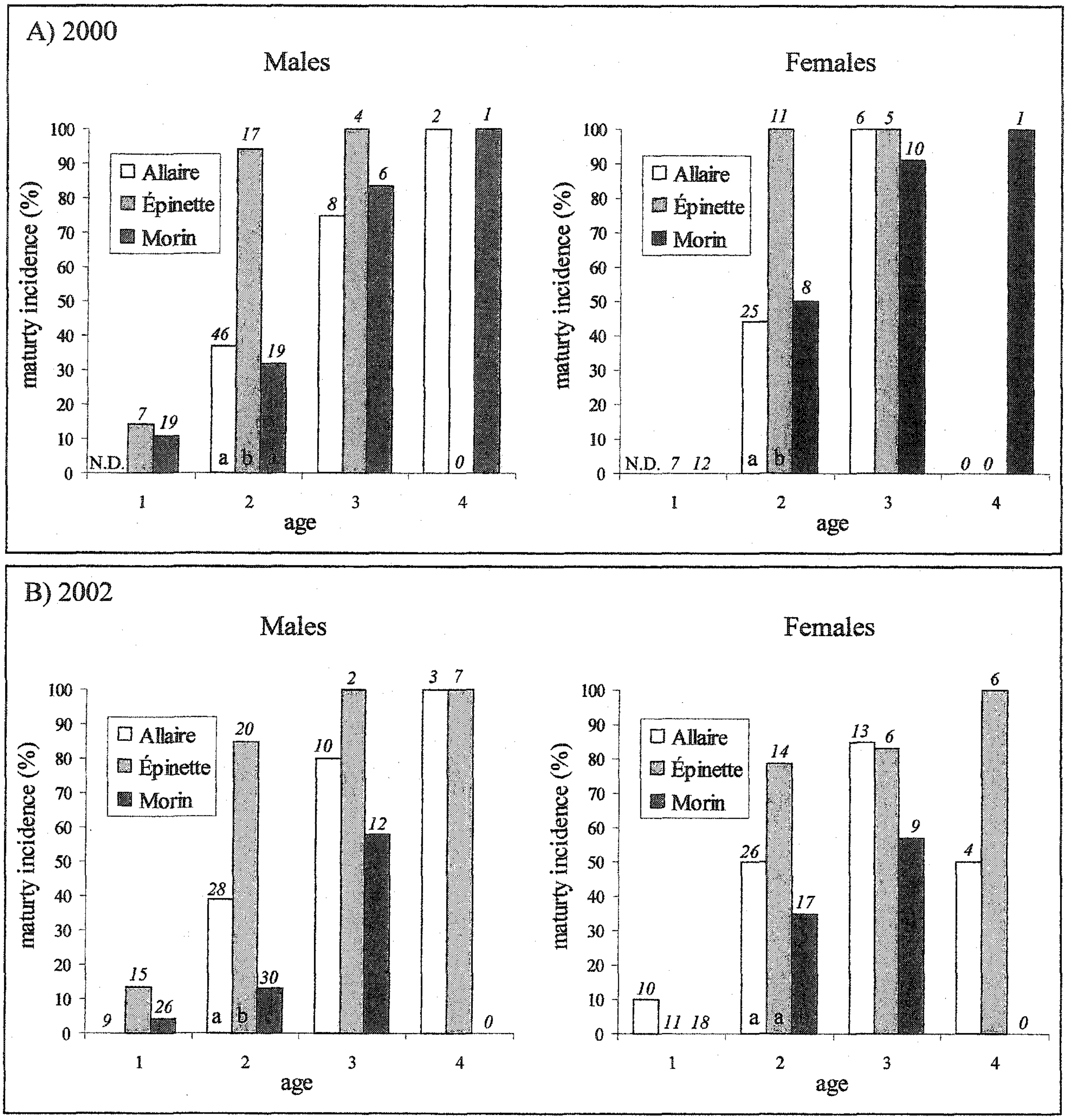

Figure 4-2. Maturity incidence at a given age in male and female resident brook charr sampled by electro-fishing in 2000 (A) and 2002 (B) in Allaire, Morin and Épinette. Sampling sizes are given in italics, above corresponding bars. Different letters in a given group of three bars indicate a significant difference at a p value of 0.05 (Yates' corrected χ^2 test and Fisher's exact test). Maturity incidence in age 1 charr from Allaire was not determined in 2000 due to a bias in size classes sub-sampled for laboratory analysis.

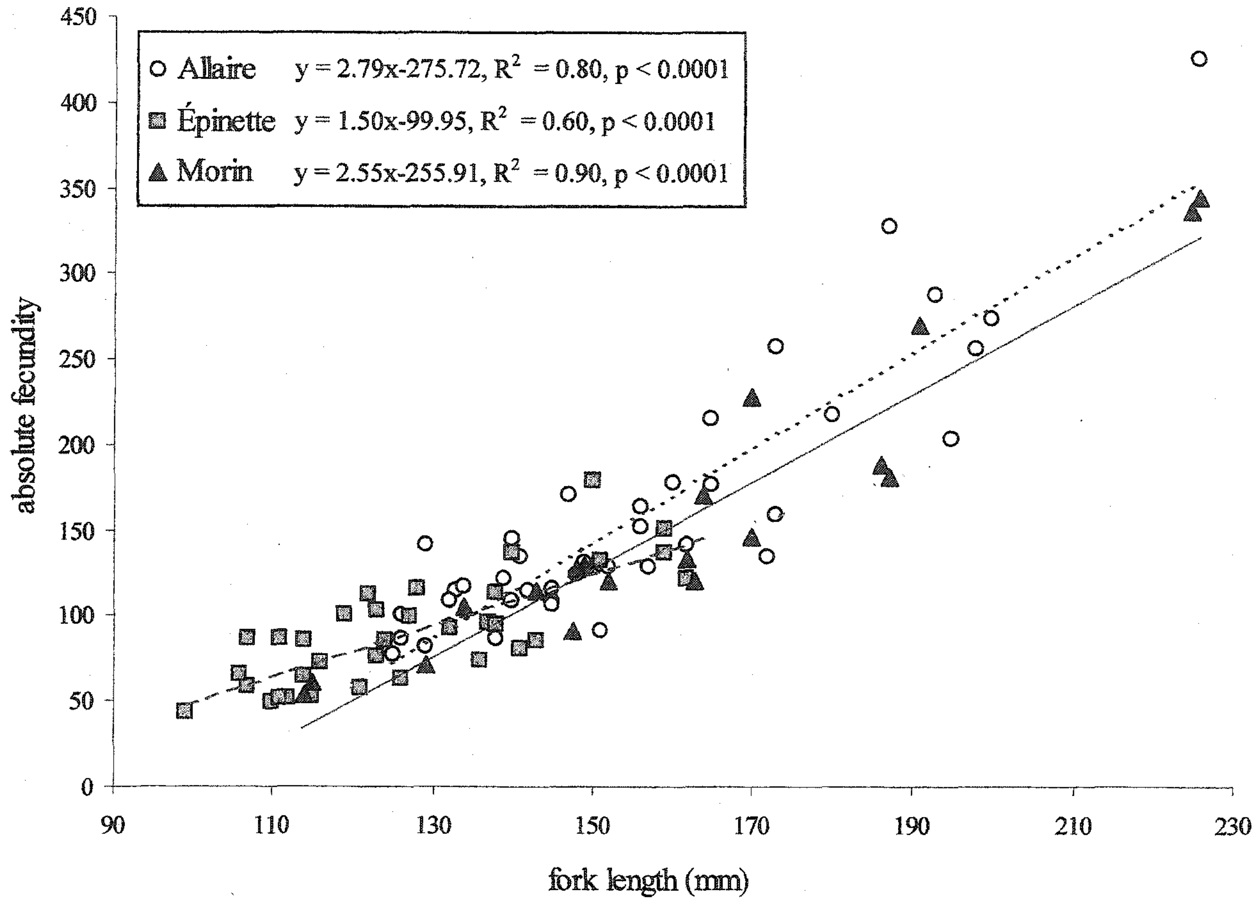

Figure 4-3. Estimated relationships between absolute fecundity (total number of eggs) and fork length in resident brook charr sampled in Allaire (dotted line, n = 42), Morin (solid line, n = 19) and Épinette (dashed line, n = 34) in 2000 and 2002 (pooled data). Slopes and intercepts did not differ between Allaire and Morin (slope, p = 0.99 and intercept, p = 0.75). The slopes obtained for Allaire and Morin females were significantly than the slope obtained for Épinette females (ANCOVA, p < 0.0001 in both cases). However, when restricting the analysis to size ranges common to the three creeks, slopes and intercept did not differ among the three creeks (p > 0.2 in all cases).

Fecundity at a given age did not differ between years in Allaire and Épinette (Student t-test, $p > 0.2$ in all cases). In Morin, fecundity at age 2 in 2002 was marginally significantly lower than in 2000 ($p = 0.059$) but fecundity at age 3 did not differ between and 2000 and 2002. Overall, fecundity at age 2 was higher in Allaire than in Épinette (Figure 4-4, MANOVA, sampling year and creek, p(creek) < 0.003, Tukey's HSD test on creek, $p < 0.0017$) but not different between Allaire and Morin nor between Morin and Épinette ($p > 0.2$ in both cases). At age 3, fecundity was not different between Allaire and Morin females (MANOVA, sampling year and creek, p(creek) < 0.004, Tukey's HDS test on creek, $p = 0.89$) and fecundity in Allaire and Morin females was higher than fecundity in Épinette females ($p < 0.008$ in both cases).

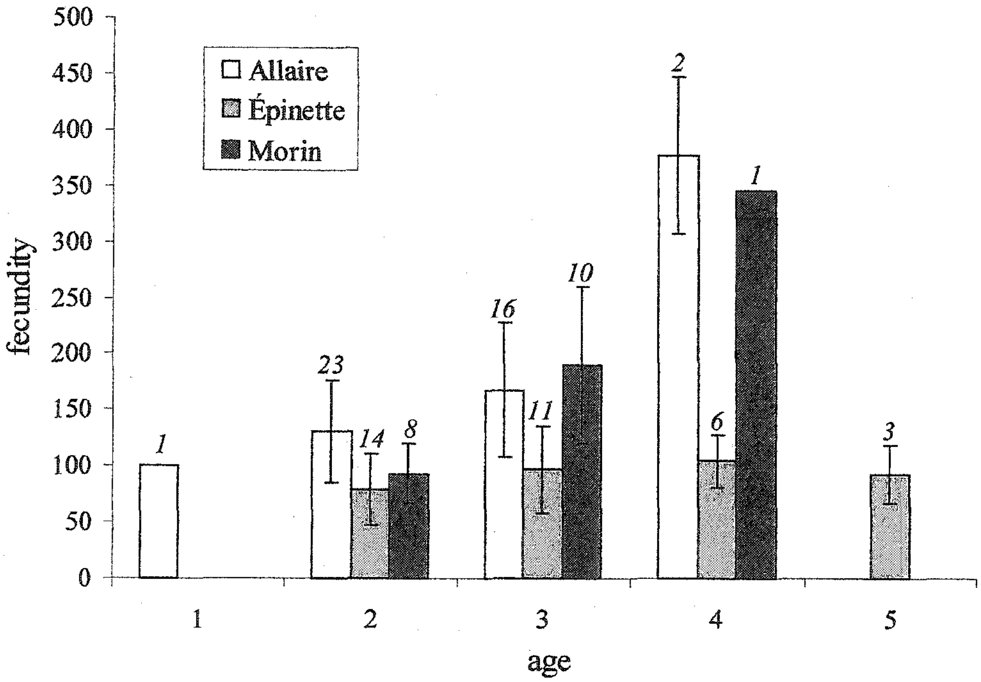

Figure 4-4. Fecundity at age (mean ± S.D.) in brook charr females sampled by electro-fishing in Allaire, Épinette and Morin (2000 and 2002, pooled data). Sample sizes are given in italics, above corresponding bars.

4.5.5. Sex-ratio

At any given age and for both sampling years, sex-ratios observed in Épinette were not different from parity (Figure 4-5). In 2000, we observed a significant dominance of males in age 2 resident charr from Morin and Allaire. In 2002, a marginally significant bias towards males was observed in age 2 charr from Morin but age 2 sex-ratio was not different from parity in Allaire. Bias towards males at age 2 disappeared at age 3 and 4. Overall sex-ratios of resident charr (age 2 to 4) were significantly biased towards males in charr from Allaire in 2000 ($p < 0.05$) but not in 2002 ($p = 1$), and marginally significantly biased towards males in charr from Morin in 2000 and in 2002 (2000, $p = 0.080$ and 2002, $p = 0.052$). Overall sex-ratio in sexually mature charr was not different from parity in any year and in any creek (Yates' corrected χ^2 test, $p > 0.1$ in all cases).

4.6. Discussion

In the present study, we compared the life-history of brook charr among three tributaries of the same river system. Épinette has been geographically isolated from the main branch of the river for 35 years (Épinette). Allaire and Morin are characterized by an upstream migration of anadromous charr and by the presence of Atlantic salmon juveniles. We observed a spring downstream migration (at age 1 or at age 2) in the two creeks where anadromous charr reproduce but not in the isolated creek. The absence of downstream migration in parts of anadromous populations which have been isolated above an impassable barrier is commonly observed in salmonids (Northcote 1992). When geographical isolation is recent, the non-expression of anadromous behaviour could reflect solely the adaptive phenotypic plasticity of the population. Lower densities resulting in better growth (and hence greater reproductive prospects) in reaches where anadromous fish can no longer reproduce may be sufficient to explain the difference in migratory tendency between individuals growing in above-barrier areas and individuals growing in below-barrier areas (e.g. Morita et al. 2000). In the present study, brook charr densities were higher in Épinette, the isolated creek. However, Morin and Allaire communities include Atlantic salmon, which is not observed in Épinette. Total densities

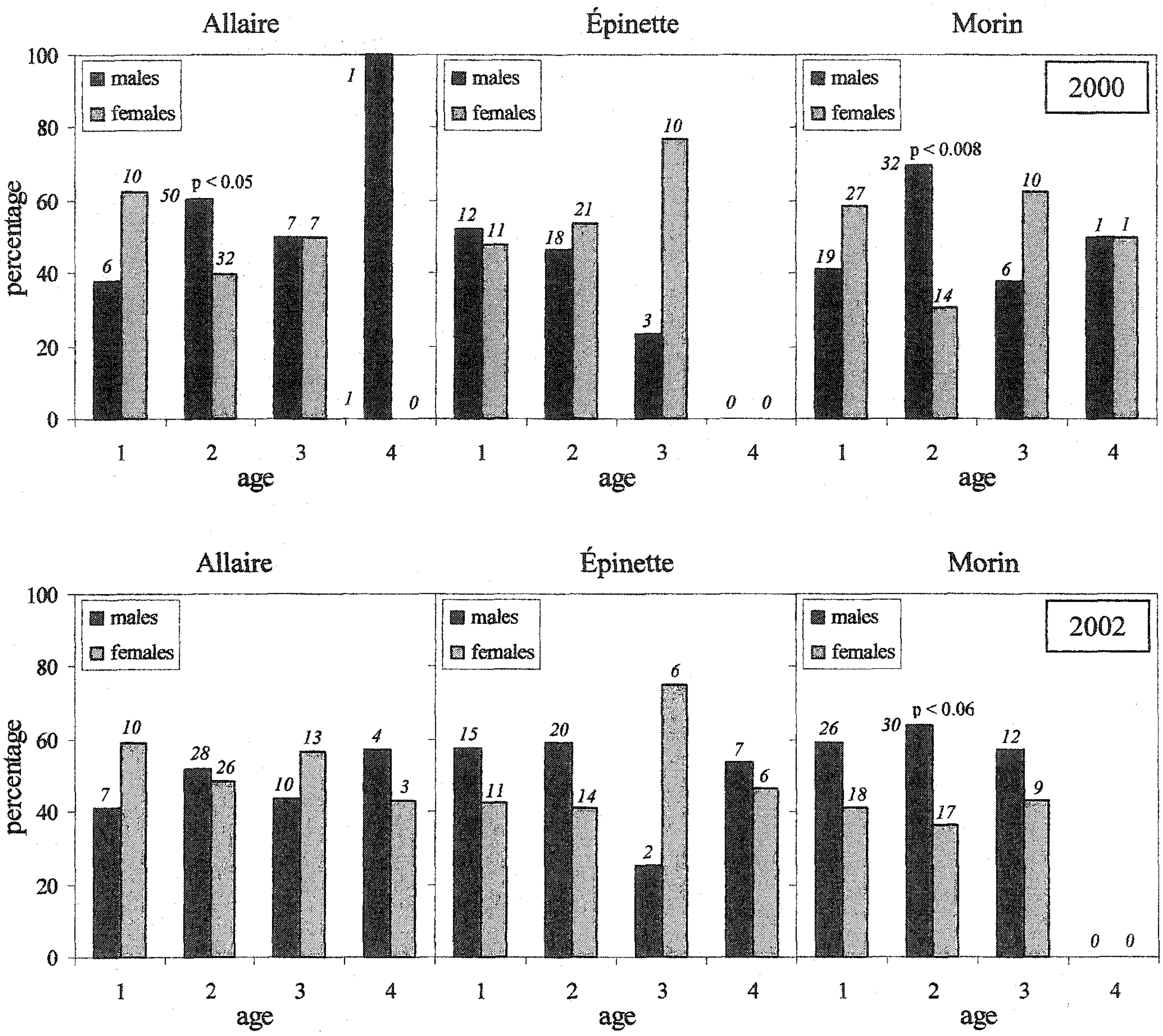

Figure 4-5. Sex frequencies at a given age, in brook charr sampled by electro-fishing in Allaire, Morin and Épinette, in 2000 and in 2002. Samples sizes are given in italics, next to corresponding bars; p values associated with marginally significant or significant differences from a 1:1 sex-ratio (χ^2 test) are given above corresponding ages.

of salmonids (brook charr plus Atlantic salmon) were higher in Épinette in 1998, not different between Épinette and Morin in 1999 and did not differ among the three creeks in 2000. Maintenance rations are approximately two times higher in Atlantic salmon than in brook charr (Tucker and Rasmussen 1999) and, at equivalent densities, communities dominated by salmon depress invertebrate drift densities much more than those dominated by trout (Joe Rasmussen, McGill University, Montreal, unpublished data). Competition with salmon in Allaire and Morin could thus affect the growth prospects of brook charr much more than intra-specific competition in Épinette. However, a negative impact of Atlantic salmon on the growth of brook charr in Allaire and Morin, relative to Épinette, was not evident at the end of the first and second summer of life. Age 0 and age 1 fish from Épinette were smaller than age 0 and age 1 fish from both Allaire and Morin. Thus, the absence of downstream migration in Épinette, relative to Allaire and Morin, is not the result of a better growth in Épinette. Under the hypothesis that charr from Épinette still follow the same conditional strategy as charr from Allaire and Morin, an alternative explanation for the absence of out-migration from Épinette would be that fish can not reach the threshold size for successful migration to salt water (see McCormick et al. 1985) early enough for migration to be worthwhile. However, if age 1 fish from Épinette may actually be too small to migrate in spring, they have reached the size of age 1 migrants from Allaire and Morin by September. They could thus migrate at age 2 (like part of anadromous charr from Allaire and Morin) but remain in fresh water to reproduce instead.

If the absence of anadromous behaviour in Épinette can not be explained solely by adaptive phenotypic plasticity to growth opportunities, it may have a genetic origin. Genetic differences between fish that have been isolated above artificial dams (i.e. relatively recently) and fish from below areas have been observed in other salmonids (e.g. Hansen and Mensberg 1998). Two non-exclusive phenomena may explain a genetically based loss of migratory behaviour in Épinette fish. Firstly, a physical barrier preventing upstream migration selects directly against migratory behaviour because fish that express such behaviour never come back to reproduce. There is a lack of studies having explored the potential for selection of migratory behaviour in fish. However, in birds, response to experimental selection on migratory tendency may be rapid. By a bi-directional selection on migratory restlessness in a partially migratory population of European blackcap warbler (*Sylvia atricapilla*), Berthold (1988) obtained a decrease of the proportion of migrants from 75% to 10% within four generations. An almost complete loss of migratory behaviour in Épinette within 12 to 17 generations is therefore possible. Secondly, Épinette isolation may also have induced a selection against high metabolic rates and low growth efficiency. In the Sainte-Marguerite River, anadromous brook charr are characterized by higher total metabolic costs in the year(s) prior to migration than future residents (Morinville and Rasmussen 2003). Similarly, in other salmonids, metabolic rates are negatively associated with age at downstream migration (e.g. Metcalfe and Thorpe 1992, Metcalfe et al. 1995, Forseth et al. 1999). The variation in metabolic rates among individuals may arise from maternal and developmental effects but could also have a genetic basis (Forseth et al. 1999). In the latter case, a "knife-edge" selection could select against both migratory behaviour and high metabolic rates, and hence be accelerated by a positive feed back with density-dependent mortality due to competition for food in early life-stages (e.g. Elliot 1994). A decrease of average metabolic rates in the community may increase survival and hence densities at older life-stages, tending to push out fish with higher metabolic requirements. If charr from Épinette have lower metabolic requirements than charr from Allaire and Morin, they may have lower feeding requirements to survive in fresh water and to acquire sufficient energy for reproduction (see Wotton 1998). Viewed in the theoretical context of the conditional strategy (see Gross and Repka 1998), their threshold growth for residency may be much lower than in charr from Morin and Allaire, and passed by almost all individuals. The existence of genetically based differences in migratory behaviour and/or energy requirements in Épinette fish could be tested by rearing experiments, comparing growth efficiency and migratory tendency between fish from Épinette and fish from non-isolated tributaries of the Sainte-Marguerite River, in similar environments.

Major life-histories differences between charr from Épinette and charr from Allaire and Morin support the hypothesis of a different reaction norm to growth opportunities in charr from Épinette (and hence of genetic differences between charr from Épinette and charr from the two other tributaries). Though smaller at the juvenile stage, charr from Épinette reproduce earlier in life (at age 2) and at a lower size than charr from Allaire and Morin (less than 50% of which are mature at age 2 and 50-100% at age 3). Considering proximate constraints on maturation, if Épinette charr are characterized by lower metabolic requirements, relative to Allaire and Morin charr, they may be able to reproduce (see Wootton 1998) and survive reproduction (see Hutchings 1994, Hutchings et al. 1999) with lower energy reserves i.e. at a smaller size. From an evolutionary point of view, the poor growth prospects of Épinette fish may actually have favoured a decrease of their age at maturity (see Schaffer 1979). Age at maturity is a trade-off between size at first reproduction (and hence fecundity in females) and survival to first reproduction. For Épinette charr, survival cost associated with delaying reproduction from age 2 to age 3 may not be compensated by size (and hence fecundity) increase from age 2 to age 3. In Allaire and Morin, emigration of anadromous charr give greater growth opportunities to freshwater resident fish, relative to Épinette fish. In the latter creeks, fish may increase their life-time reproductive success by reproducing at an older age, as they can significantly increase their size at reproduction (and their fecundity, see Figure 4-4) by delaying maturity. A juvenile survival at least as high in Allaire as in Épinette and greater growth in Allaire support the hypothesis of a selective advantage of delaying reproduction in Allaire, relative to Épinette.

Although anadromous charr are likely to maintain some gene flow between the communities of Allaire and Morin (see Castric 2002), we observed a much greater downstream migration in Morin than in Allaire. As more anadromous females reproduce in Morin and available habitat for juvenile brook charr in the latter creek is approximately twice that available in Allaire, a higher absolute number of migrants in Morin may be partly explained by a higher absolute number of juveniles in this creek. However, several other factors could be involved, among which growth and growth prospects may be of major importance. In spite of similar densities of conspecifics until age 2 in the two creeks, Allaire charr were larger than Morin charr at age 0 and age 1. In the Sainte-Marguerite River, migratory brook charr show a lower growth efficiency than their resident counterparts in the year(s) prior to migration (Morinville and Rasmussen, 2003). Therefore, there are two, non exclusive, possible explanations for a lower size at age 0 and 1 in Morin charr: 1) extrinsic growth opportunities are greater in Allaire than in Morin and 2) age 0 and age 1 charr from Morin are characterized by a lower average growth efficiency than age 0 and age 1 charr from Allaire.

As a possible initial difference in growth efficiency between Allaire charr and Morin charr should be significantly reduced by the out-migration of fish with higher metabolic costs (see Morinville and Rasmussen 2003), the first hypothesis may be tested by comparing growth in the two creeks from age 2. At age 2 and older ages, densities of remaining freshwater resident charr were higher in Allaire than in Morin. Despite greater chances of intra-specific competition, resident charr from Allaire were as large or larger than resident charr from Morin. Though we can not exclude the possibility that Allaire may be characterized by higher absolute food resources than Morin, another factor that may explain the better growth of Allaire charr is differential potentials for competition with Atlantic salmon in the two creeks. In spite of the presence of salmon fry in Allaire in 1998 (and subsequent significant presence of age 1 salmon in 1999), the ratio of salmon parr to brook charr tended to be higher in Morin (average 3.0:1 in Morin *vs* 1.8:1 in Allaire). Moreover, Allaire is characterized by a frequent occurrence of deep pools, habitats in which brook charr compete more successfully with salmon (Gibson 1981, Rodriguez 1995). Thus, better growth in Allaire relative to Morin supports the idea that heterospecific competitors and habitat characteristics with regard to competition can affect the growth of freshwater resident fish and should be considered as potential factors involved in the expression of residency at the community level, and in the evolution of anadromy at the population level. However, this hypothesis has to be further tested by comparing feeding resources between the two creeks, in emptied sections and in sections carrying observed densities of charr and salmon and by checking whether other environmental factors, such as water temperature, may affect the growth of fish differentially in the two creeks.

Allaire charr were characterized by a better survival from age 2, an overall greater growth in age 2 males and a higher maturity incidence in age 2 males in 2002, relative to Morin. However, we did not observe any differences between the two communities in the age at maturity of males in 2000 and the age at maturity of females in both years, nor in age-specific fecundity. Although our power to detect differences in age-specific maturity incidences and age-specific fecundity between the two creeks was reduced by small sample sizes, this suggest that Morin and Allaire resident charr maximize their individual life-time fitness through similar life-histories. With similar ages at maturity and age-specific fecundities in the two creeks, a better survival to reproduction in Allaire would result in a higher average life-time reproductive success in resident charr from the latter creek. For instance, a survival from birth to age 1 of 0.025 in the two creeks would ensure a life-time reproductive success of 1 in females from Allaire but only of 0.5 in females from Morin. However, the maintenance of a conditional strategy requires the maximization of fitness at the individual level but not relative to other individuals (see Repka and Gross 1995, Gross and Repka 1998). Resident charr from Morin may not do as well as resident charr from Allaire but better than if they had expressed the migratory tactic in their situation.

Overall, the better potential of Allaire for brook charr residency was reflected by higher densities of resident charr and by an apparently higher absolute number of residents in the latter creek (personal observation, reflected in age 2 to 4 sample sizes for 2002, in Table 4-2, obtained by fishing approximately 50% of Allaire length and 70% of Morin length). If more resident charr successfully reproduce in Allaire than in Morin, and given that more anadromous charr reproduce in Morin than in Allaire, the percentage of fry originating from anadromous parents may be much higher in Morin. As migratory behaviour is partly heritable (Jonsson and Jonsson 1993 and e.g. Nordeng 1983), a greater tendency to anadromy in Morin charr may also significantly contribute to the greater migration runs observed in Morin. A greater migratory tendency in Morin charr would explain the much higher disappearance from age 1 to age 2 (which includes both mortality and emigration) observed in this creek, relative to Allaire and Épinette.

Although the conditional strategy theory accounts for the existence of alternative tactics associated with unequal fitnesses (Gross 1996), trade-offs may play a major role in the maintenance of alternative reproductive tactics (Moran 1992, Roff 1996). A comparison between the life-history of anadromous charr from the Sainte-Marguerite River (Chapter 3) and the life-history of resident charr from Allaire and Morin shows that age-specific fecundity is, on average, 9 times higher in fish that migrated at age 1 than in resident fish and 6 times higher in fish that migrated at age 2 than in resident fish. However, survival to reproduction (age 3, where more than 50% of individuals are mature in migrants at age 1, in migrants at age 2 and in residents) is much lower in migrants than in residents. Assuming a survival from age 1 to age 2 of 0.52 in future resident charr and in migrants at age 2 (value observed in resident charr from Allaire and Épinette), survival to reproduction in Allaire resident charr would be 16 times higher than in migrants at age 1 and 5 times higher than in migrants at age 2. Survival to reproduction in Morin resident charr would be 10 times higher than in migrants at age 1 and 3 times higher than in migrants at age 2. Overall, assuming the same survival in the year(s) prior to migration in anadromous charr and resident charr, there is no clear advantage, in terms of life-time reproductive success, for anadromous females from the Sainte-Marguerite or resident females from Allaire. With the same assumption, the average life-time reproductive success of anadromous females from the Sainte-Marguerite River would be greater than the average life-time reproductive of resident females from Morin. However, the small age-specific size at migration of Morin charr (see ¶ 4.5.1), relative to the average age-specific size of migrants from the Sainte-Marguerite River (see Chapter 3), limits the relevance of such a comparison. If anadromous charr from Morin are part of the smallest migrants from the Sainte-Marguerite River, they may not obtain the average life-time reproductive success of migrants from the Sainte-Marguerite River.

We observed more males than females in age 2 resident charr from Morin and Allaire in 2000 and a marginally significant bias towards males in the sex-ratio of age 2 charr from Morin in 2002. Many partially anadromous populations exhibit a sex-biased migratory strategy, with more females than males migrating to salt water (Jonsson and Jonsson 1993). The evolutionary explanation of this observation is that reproductive success is more dependent on size in females than in males. In females, production of offspring is highly correlated with production of eggs, which increases with body size. In males, a large size is an advantage in competition for mates at the time of reproduction but small resident males may fertilize eggs of large anadromous females, using sneaking tactics (Jonsson and Jonsson 1993). In the Sainte-Marguerite River, overall sex-ratio at downstream migration is not different from parity (Chapter 3). However, there are more males in charr migrating at age 1 and more females in charr migrating at age 2, suggesting that the migratory strategy of the population is actually sex-biased (Chapter 3). The present study shows that the bias towards females in migrants at age 2 partly results from a greater tendency in age 2 females to migrate than to stay as freshwater residents, relative to age 2 males. It thus suggests that males have greater opportunities to maximise their life-time reproductive success by staying as freshwater residents, relative to females. The hypothesis that males may increase their reproductive success by fertilizing eggs of anadromous females in addition to eggs of resident females (Jonsson and Jonsson 1993) is particularly relevant in Morin, where a significant number of anadromous charr reproduce, and will be addressed in ongoing studies.

In Allaire and Morin, the majority of fish staying as freshwater residents at age 2 do not mature at age 2. Therefore, temporal environmental variability, in terms of growth opportunities and survival risk, may significantly affect their reproductive prospects once they have expressed the resident tactic. In addition to the variability of Atlantic salmon densities from one year to another (see Table 4-1), we observed direct effects of environmental variability on resident charr life-history. These effects were more visible in Morin where several age classes were smaller in 2002 than in 2000 and where fecundity at age 2 was marginally significantly lower in 2002. Thus, expressing the resident tactic at a given threshold of growth (or related trait) in 2001 or in 2002 may have been associated with a lower life-time reproductive success than expressing the resident tactic in 1999 or 2000, at the same threshold of growth. This suggest that the effect of environmental variability on growth opportunities in the year(s) prior to migration, and hence on the subsequent expression of anadromy or residency (see Jonsson and Jonsson 1993), and the effect of environmental variability on the life-time reproductive success of fish expressing one tactic or another must be considered separately. By affecting the growth of juveniles prior to migration, spatial and temporal environmental variability may decrease heritabilities in the wild (e.g. Garant et al. 2003), which should act against specialization towards a given tactic. By affecting the life-time reproductive success of individuals once they have expressed a given tactic, environmental fluctuations could give a fitness advantage to individuals expressing one tactic in a given year and to individuals expressing the other tactic in another year (e.g. Garant et al. 2003). As such, environmental fluctuations should also favour the maintenance of plasticity (Moran 1992, Roff 1996).

In summary, our results show that recent geographical isolation does not inevitably result in decreased densities and better growth in areas where anadromous fish no longer reproduce. In addition, even when growth opportunities do not increase following isolation, migratory behaviour may quickly disappear. The expression of residency in all individuals from isolated reaches could result from a rapid loss of migratory behaviour and/or from a rapid evolution of reaction norms to growth opportunities. We suggest that a knife-edge selection may select against both migratory behaviour and high metabolic requirements, increasing the average growth efficiency in isolated communities, and hence promoting the expression of the resident tactic in these communities. In non-isolated areas, reproductive prospects of individuals will be influenced by both their growth efficiency and local growth opportunities. By affecting growth opportunities, densities of conspecifics, densities of heterospecific competitors and habitat characteristics, with regard to competition, may play a major role in the expression of residency at the community level, and in the evolution of anadromy at the population level. As in other salmonids, residency in brook charr is a trade-off between survival to reproduction and size at maturity. In at least one tributary of the Sainte-Marguerite River, the average life-time reproductive success of brook charr females having expressed one tactic or another may be similar. Size may be less important in males, which tend stay in greater proportions as freshwater residents, relative to females. In both sexes, environmental fluctuations affect the growth and the subsequent life-history of fish once they have expressed the resident tactic and may favour the maintenance of plasticity.

4.7. Acknowledgements

We acknowledge S. Bilodeau-Gauthier, A. Boivin, V. Castric, M. Desgagnés, S. Gaouette, C. Langlois, K. Lunn, A. Ménard, C. Mimeault, G. Morinville, P.-A. Paradis, V. Thériault and S. Trépanier for field and laboratory assistance. Funding of this project was provided to J.J.D. by the Natural Sciences and Engineering Research Council of Canada (Strategic Grant and Collaborative Special Projects), the Fondation de la Faune du Québec, the Government of Québec (Faune et Parc Québec), the Government of Canada (Economic Development, Saguenay – Saint-Lawrence Marine Park) and the financial partners of CIRSA Inc. (Corporation de soutien aux Initiatives de Recherche sur le Saumon Atlantique). This study is a contribution to the research programs of CIRSA (Centre Interuniversitaire de Recherche sur le Saumon Atlantique) and GIROQ (Groupe Interuniversitaire de Recherches Océanographiques du Québec. S.L. was financially supported by funding from CIRSA and GIROQ.

5. Conclusion

Au cours de cette étude, nous nous sommes attachés à comprendre l'existence et le maintien de tactiques de reproduction alternatives chez l'omble de fontaine, ainsi qu'à mettre en évidence certains des facteurs qui influencent l'évolution de l'anadromie chez les salmonidés. Notre approche reposait sur une comparaison des cycles de vie et des succès reproducteurs sur l'ensemble de la durée de la vie (Ro de Stearns 1992) des individus ayant exprimé l'une ou l'autres des tactiques observées dans la population étudiée. Trois tactiques alternatives majeures, au regard de la migration, ont été mises en évidence : la migration à l'âge de un an, la migration à l'âge de deux ans, ainsi que la résidence en eau douce pour l'ensemble de la durée de la vie.

Tout d'abord, cette étude a clairement démontré que, dans la population considérée, l'utilisation de l'habitat d'eau douce ou de l'habitat estuarien est caractérisé par un compromis entre croissance et survie. L'estuaire offre des possibilités de croissance supérieures mais les risques de mortalité y sont très élevés. En rivière, les opportunités de croissance sont limitées mais les taux de mortalités sont beaucoup plus faibles.

Ce compromis a tout d'abord une influence sur les patrons de migration des populations. Le Chapitre 2 a montré que les mouvements des ombles de fontaine entre l'eau douce et l'eau salée et dans les zones estuariennes ne sont pas aléatoires. Ensuite, il a confirmé que le compromis croissance/survie auquel font face les ombles anadromes ne s'exprime pas dans les mêmes termes pour tous les individus. L'idée que, chez les salmonidés, les bénéfices ou les coûts immédiats associés à la migration dépendent de la taille des individus (p.e. qu'il existe une taille seuil en dessous de laquelle les risques de mortalité en eau salée sont très élevés) n'est pas nouvelle (p.e. Økland et al. 1993). Cependant, à ma connaissance, les patrons de migration des salmonidés n'avaient jamais été analysés dans le cadre théorique des modèles dynamiques d'écologie comportementale, qui prédisent que croissance et survie n'ont pas la même valeur à tous les stades de vie. En fait, ironiquement, ces modèles prédisent que les mouvements des individus doivent être optimisés par une stratégie comportementale conditionnelle. « Ironiquement » parce qu'il existe encore à l'heure actuelle un trop grand fossé entre écologie comportementale et théorie du cycle vital. L'utilisation des modèles d'écologie comportementale est souvent restreinte à l'analyse des comportements d'alimentation en présence de prédateurs, alors qu'ils peuvent s'appliquer à des comportements qui sont la caractéristique même d'un cycle vital, comme la migration dans le cas de l'anadromie. Ces modèles peuvent permettre de mieux comprendre l'évolution conjointe des patrons de migration et du cycle vital anadrome, dans un contexte environnemental spécifique, et donc de mettre en évidence les opportunités et contraintes environnementales sur le cycle vital anadrome et l'évolution de l'anadromie.

Les avantages conditionnels de l'utilisation des zones estuariennes s'expriment aussi par le fait que tous les individus ne migrent pas au même âge. Il y a deux façons, non exclusives, de considérer le problème : 1) il existe une taille seuil à la dévalaison en-dessous de laquelle les coûts de la migration, en terme de mortalité, sont trop élevés ; si cette taille n'est pas atteinte, les individus repoussent la migration et 2) le génotype des individus influence leur âge optimal à la migration parce qu'il peut influencer leurs perspectives de croissance en milieu dulçaquicole et en milieu marin. Le contexte théorique de la stratégie conditionnelle prédit que chaque individu doit adopter la tactique qui maximisera son fitness étant donné sa croissance en eau douce et ses perspectives de croissance en eau douce et en milieu estuarien. Il ne prédit pas que, au bout du compte, les individus qui expriment une tactique ou une autre auront, en moyenne, le même fitness (voir Gross et Repka 1998). Cependant, les résultats présentés dans le Chapitre 3 ont montré que les tactiques associées à l'âge à la migration n'ont pas les mêmes bénéfices et les mêmes coûts, en terme de succès reproducteur, pour les individus qui expriment ces tactiques. Ce compromis est étroitement lié au cycle vital des individus. Ceux qui migrent plus tard dans la vie se reproduisent plus tard dans la vie mais après moins de temps passé en estuaire. Leur croissance est inférieure à celle des individus qui migrent à un plus jeune âge mais leur survie jusqu'à la reproduction est supérieure. Une faible variation (de l'ordre de quelques pour-cent) de la survie en eau douce entre l'âge de 1 an et l'âge de 2 ans peut donner une valeur sélective supérieure aux ombles ayant migré à 1 an chez une cohorte donnée et aux ombles ayant migré à 2 ans chez une autre cohorte. Cela devrait favoriser le maintien de tactiques alternatives au regard de l'âge à la migration (voir Roff 1996) ou, en considérant les bases génétiques qui influencent la croissance en eau douce des individus et donc la tactique adoptée, le maintien d'une variabilité dans les traits qui régulent cette croissance, comme les taux métaboliques (voir Forseth et al. 1999).

L'héritabilité des tactiques migratrices adoptées semblent en effet partiellement basée sur une héritabilité de certains traits liés à l'efficacité d'utilisation des ressources alimentaires et à la capacité de croissance des individus. Outre les études qui ont mis en évidence l'influence des taux métaboliques et de l'efficacité de croissance sur l'expression d'une tactique donnée (p.e. Forseth et al. 1999, Morinville et Rasumussen 2003), le cas du ruisseau Épinette (Chapitre 4) supporte l'idée qu'il faut considérer l'importance potentielle des bases génétiques régulant l'efficacité alimentaire des individus sur l'expression de l'anadromie ou de la résidence. Une pure plasticité phénotype adaptative face aux opportunités de croissance ne peut expliquer l'absence de migration sur ce ruisseau. La croissance et les perspectives de croissance des ombles d'Épinette sont moins bonnes que celles des ombles d'autres tributaires qui expriment l'anadromie. Si l'expression du comportement anadrome n'était basée que sur la croissance en tant que telle, les ombles d'Épinette auraient du continuer à exprimer un comportement migrateur. Cela suggère qu'une sélection de « bord d'abîme » a entraîné une perte du comportement anadrome et/ou fait évoluer la norme de réaction aux opportunités de croissance chez les ombles d'Épinette. Cette dernière hypothèse est supportée par le fait que les ombles d'Épinette présentent un cycle de vie différent de celui des ombles résidants des autres ruisseaux. Bien que l'héritabilité du comportement migratoire en milieu artificiel puisse être élevée (Dingle 1991), la variabilité environnementale devrait ralentir l'évolution de ce comportement en nature. La perte rapide (une quinzaine de générations) du comportement anadrome des ombles d'Épinette pourrait être expliquée par un rétro-contrôle positif sur la sélection de « bord d'abîme », basé sur une mortalité densité-dépendante dans les jeunes stades de vie (voir Elliot 1994). La dévalaison des individus à coûts métaboliques plus élevés, et leur non-retour, pourrait être associée à une augmentation de l'efficacité alimentaire des individus de génération en génération. Une réduction des besoins énergétiques des individus pourrait alors augmenter la survie dans les jeunes stades de vie et donc les densités à des stades de vie ultérieurs, limitant l'énergie disponible par individu et poussant les individus à moins bonne efficacité alimentaire hors du ruisseau.

Le Chapitre 4 a également montré comment les bases génétiques de l'anadromie et les facteurs environnementaux peuvent interagir pour favoriser ou non l'expression de la résidence dans une communauté donnée. Les facteurs environnementaux, tels que la compétition inter-spécifique et les modalités de cette compétition (déterminées par l'habitat), vont agir sur opportunités de croissance en eau douce et donc sur la possibilité de maximiser son fitness par la résidence. L'héritabilité des traits qui influencent l'expression d'une tactique ou d'une autre va agir sur la tendance à la migration des descendants d'individus résidants et des descendants d'individus anadromes, dans des conditions environnementales données. L'environnement peut donc favoriser l'expression de la résidence de deux façons : en favorisant la croissance et les perspectives de croissance, il agit par l'intermédiaire de la norme de réaction des individus à leurs opportunités de croissance. En favorisant le succès reproducteur des individus résidants, il agit sur la proportion d'individus ayant un ou deux parents résidants et donc directement sur la norme de réaction de la communauté aux opportunités de croissance. Différents facteurs peuvent limiter une évolution vers la résidence dans des environnements particulièrement favorables à cette tactique. Un des facteurs impliqués pourrait être une sélection dépendante de la fréquence, notamment chez les mâles. En effet, le succès reproducteur des mâles résidants est susceptible de dépendre des opportunités de fécondation furtive d'œufs de femelles anadromes. La fréquence des mâles « satellites » diminuent ces opportunités (c.f. Hutchings et Myers 1994). Un autre facteur qui pourrait empêcher l'évolution d'une communauté entière vers la résidence est la stochasticité environnementale (Thompson 1991, Moran 1992, Roff 1996). Une variabilité du succès reproducteur des individus résidants (Chapitre 4) et des montaisons d'individus anadromes peut prévenir une spécialisation vers la résidence.

D'une façon générale, cette étude suggère que, si une stratégie conditionnelle peut être une condition suffisante au maintien de tactiques alternatives, plusieurs facteurs peuvent également promouvoir le maintien de la résidence et de l'anadromie dans une même population. Ce sont les mêmes facteurs qui peuvent favoriser, en général, l'existence de différents phénotypes dans une population (Roff 1996) : l'expression d'un phénotype donné est un compromis, la variabilité environnementale est susceptible d'affecter les gains en fitness subséquents à l'expression d'une tactique ou d'une autre, la fréquence d'un phénotype peut influencer le succès reproducteur des individus qui ont exprimé ce phénotype. Bien que, dans les stratégies conditionnelles, le fitness moyen des individus qui expriment une tactique donnée serait généralement supérieur à celui des individus qui en expriment une autre (Gross 1996), les résultats de cette étude sont loin de mettre en évidence un avantage en fitness pour les individus qui expriment la résidence ou pour les individus qui expriment l'anadromie. La question de l'égalité ou non des fitness associés à des tactiques alternatives pose d'ailleurs certains problèmes. Premièrement, évaluer de façon précise le succès reproducteur moyen des individus qui expriment une tactique donnée est une tâche particulièrement difficile. Cela requière une connaissance parfaite du cycle vital des individus (en particulier leur survie) et du nombre de descendants que leur donnera chaque événement reproducteur. De plus, en considérant les erreurs associées à l'échantillonnage et aux analyses de données (voir Austad 1984) et, surtout, une variabilité temporelle du succès reproducteur des phénotypes considérés, il n'est pas évident de pouvoir conclure avec certitude sur cette question. Deuxièmement, ce n'est pas parce que « l'inégalité des fitness » semble caractériser de nombreuses populations exprimant une stratégie conditionnelle, que ces populations n'évoluent pas sous la pression d'autres forces sélectives qu'un lien étroit entre condition et maximisation du fitness par une tactique donnée. Une des questions centrales du maintien de tactiques alternatives dans une population est le maintien de la variabilité génétique sous-jacente à l'expression de ces tactiques. Dans le cas de l'anadromie chez l'omble de fontaine, des taux métaboliques faibles semblent favoriser la résidence et des taux métaboliques élevés, l'anadromie (Morinville et Rasmussen 2003). Des individus caractérisés par des coûts métaboliques inférieurs vont pouvoir utiliser plus efficacement l'habitat d'eau douce où les ressources alimentaires sont réduites. Des individus à taux métaboliques plus élevés ont des efficacités de croissance plus faibles mais un potentiel de croissance supérieur dans des zones où les ressources alimentaires ne sont pas limitatives (Forseth et al. 1999, Morinville et Rasmussen 2003). Si, par exemple, la résidence était toujours plus « payante » que l'anadromie, peu importe la fréquence d'expression de cette tactique dans la population, ne devrait-on pas s'attendre à une spécialisation vers la résidence i.e. à une réduction des taux métaboliques de la population, comme cela semble être le cas dans le ruisseau Épinette ? C'est peut-être le cas dans le sud de l'aire de répartition de l'espèce, où certains changements environnementaux ont pu diminuer les bénéfices ou augmenter les coûts de la tactique anadrome. Les résultats de l'étude présente sont plutôt encourageants en ce qui concerne le devenir à court terme des ombles anadromes des populations plus nordiques. Bien qu'on ne puisse pas conclure que le succès reproducteur des individus résidants et le succès reproducteur des individus anadromes soit égal, on peut conclure qu'ils ne sont probablement pas très différents.

Il semble donc que la dichotomie actuelle entre les concepts théoriques de stratégie conditionnelle et de stratégie mixte (non conditionnelle et supposant l'égalité des valeurs sélectives des individus exprimant une tactique ou une autre) est inadéquate. Une approche plus globale des polymorphismes phénotypiques devrait être considérée. La démarche à adopter pour mieux comprendre le maintien de tactiques de reproduction alternatives pourrait être la suivante. Premièrement, il est effectivement important d'identifier, le cas échéant, la présence d'un mécanisme conditionnel régulant l'expression des différentes tactiques. Seule l'observation de l'existence d'un seuil critique au-dessus duquel les individus exprimeront une tactique donnée et en-dessous duquel ils en exprimeront une autre peut permettre de qualifier la stratégie observée de « conditionnelle » (et non pas l'observation ponctuelle de l'inégalité des fitness des individus exprimant une tactique ou une autre). La nature de ce seuil doit être clairement définie (est-ce la taille ? la croissance ? une augmentation ou une réduction des réserves énergétiques ?), pour préciser la nature de la variabilité génétique sur laquelle repose l'expression de ces différentes tactiques. Dans le même ordre d'idée, il est nécessaire de vérifier si les tactiques sont héritables et, le cas échéant, sur quoi repose cette héritabilité (une héritabilité du comportement ou une héritabilité de certains traits liés à la croissance). Enfin, dans un second temps, que la stratégie soit de type conditionnel ou non, il faut tâcher d'identifier l'ensemble des facteurs qui peuvent permettre le maintien des tactiques alternatives observées ou de la variabilité génétique sous-jacente à l'expression de ces tactiques i.e. compromis, variabilité environnementale temporelle, sélection dépendante de la fréquence. Héritabilités et estimés du succès reproducteur sur l'ensemble de la durée de la vie, quantification des effets éventuels de la fréquence des différentes tactiques sur ce succès reproducteur, devraient permettre de modéliser les stratégies considérées sur le long terme et d'identifier les facteurs clés et les valeurs critiques de ces facteurs qui vont favoriser le maintien de tactiques alternatives ou une spécialisation vers une tactique donnée. Les facteurs parfois utilisés pour discriminer stratégie conditionnelle et stratégie mixte (voir Gross 1996) agissent probablement de concert pour stabiliser les stratégies de reproduction de nombreuses populations (voir, p.e., Roff 1998)…

Bibliographie

Adriaensen, F., and Dhondt, A.A 1990. Population dynamics and partial migration of the European robin (*Erithacus rubecula*) in different habitats. J. Anim. Ecol. **59**: 1077-1090.

Austad, S.N. 1984. A classification of alternative reproductive behaviors and methods for field-testing ESS models. Am. Zool. **24**: 309-319.

Bagenal, T.B. 1978. Aspects of fish fecundity. *In* Ecology of freshwater fish production. *Edited by* S.D. Gerkins. John Whiley and Sons, New-York pp. 75-101.

Bailey, N.T.J. 1951. On estimating the size of mobile populations from capture-recapture data. Biometrika **38**: 293-306.

Berthold, P. 1988. Evolutionary aspects of migratory behavior in Europeans warblers. J. Evol. Biol. **1**: 195-209.

Bohlin, T., Hamrin, S., Heggbert, T.G., Rasmussen, G., and Saltveit, S.J. 1989. Electro-fishing theory and practise with special emphasis on salmonids. Hydrobiologia **173**: 9-43.

Bohlin, T., Dellefors, C., and Faremo, U. 1990. Large or small at maturity – theories on the choice of alternative male strategies in anadromous salmonids. Ann. Zool. Fenn. **27**: 139-147.

Bohlin, T., Dellefors, C., and Faremo, U., and Johlander, A. 1994. The energetic equivalence hypothesis and the relation between population density and body size in stream-living salmonids. Am. Nat. **143**: 478-493.

Bohlin, T., Dellefors, C., and Faremo, U. 1996. Date of smolt migration depends on body-size but not on age in wild sea-run brown trout. J. Fish. Biol: **49**: 157-164.

Brockmann, H. J. 1994. Sperm competition in horseshoe crabs (*Limulus polyphemus*). Behav. Ecol. Sociobiol. **35**: 153-160.

Brown, R.S. 1999. Fall and early winter movements of cutthroat trout, *Oncorhynchus clarki*, in relation to water temperature and ice conditions in Dutch Creek, Alberta. Environ. Biol. Fishes **55**: 359-368.

Brownie, C., Anderson, D.R., Burnhnam, K.P., and Robson, D.S. 1985. Statistical interference from band recovery data: a handbook. 2nd ed. U.S. Fish Wildl. Serv. Resour. Publ. No. 156.

Caro, T.M., and Bateson, P. 1986. Organization and ontogeny of alternative tactics. Anim. Behav. **34**: 1483-1499.

Castonguay, M., FitzGerald, G.J., and Côté, Y. 1982. Life history and movements of anadromous brook charr, *Salvelinus fontinalis*, in the St-Jean River, Gaspé, Québec. Can. J. Zool. **60**: 3084-3091.

Castric, V. 2002. Dynamique de l'organisation géographique de la diversité génétique chez l'omble de fontaine *Salvelinus fontinalis* Mitchill. Ph.D. Thesis, Laval University, Québec, Can.

Chassé, R., and Côté, R. 1991. Aspect of winter primary production in the upstream section of the Saguenay Fjord. Hydrobiologia **215**: 251-260.

Clark, C.W. 1994. Antipredator behaviour and the asset-protection principle. Behav. Ecol. **5**: 159-170.

Clobert, J., Danchin, E., Dhondt, A.A., and Nichols, J.D. 2001. Dispersal. Oxford University Press, Oxford, U.K.

Cutts, C.J., Metcalfe, N.B., and Taylor, A.C. 1998. Aggression and growth depression in juvenile Atlantic salmon: the consequences of individual variation in standard metabolic rate. J. Fish. Biol. **52**: 1026-1037.

Dempson, J.B., and Green, J.M. 1985. Life history of anadromous Artic charr, *Salvelinus alpinus*, in the Fraser River, northern Labrador. Can. J. Zool. **63**: 315-324.

Dieperink, C., Bak, B.D., Pedersen, L.-F., Pedersen, M.I., and Pedersen S. 2002. Predation on Atlantic salmon and sea trout during their first days as postsmolts. J. Fish. Biol. **61**: 848-852.

Dingle, H. 1980. Ecology and evolution of migration. *In* Animal migration, orientation and navigation. *Edited by* S.A. Gauthreaux . Academic Press, New-York. pp. 1-101.

Dingle, H. 1991. Evolutionary genetics of animal migration. Amer. Zool. **31**: 253-264.

Dodson, J.J. 1997. Fish migration : an evolutionary perspective. *In* Behavioral ecology of teleost fishes. *Edited by* J.-G. Godin. Oxford University Press pp. 10-36.

Dominey, W. J. 1984. Alternative mating tactics and evolutionarily stable strategies. Am. Zool. **24**: 385-396.

Doyon, J.-F., Hudon, C., Morin, R. and Whoriskey, F.G. 1991. Bénéfices à court terme des mouvements anadromes saisonniers pour une population d'omble de fontaine (*Salvelinus fontinalis*) du Nouveau Québec. Can. J. Fish. Aquat. Sci. **48**: 2212-2222.

Drainville, G. 1970. «Le fjord du Saguenay. II. La faune ichtyologique et les conditions écologiques». Le Naturaliste Canadien **97**: 623-656.

Dutil, J.D., and Power, G. 1980. Coastal populations of brook trout, *Salvelinus fontinalis*, in Lac Guillaume-Delisle (Richmond Gulf), Québec. Can. J. Zool. **58**: 1828-1835.

Elliot, J.M., 1994. Quantitative ecology and the brown trout. Oxford University Press, Oxford, U.K.

Emlen, D.J. Alternative reproductive tactics and male-dimorphism in the horned beetle *Onthophagus acuminatus* (Coleoptera: Scarabaeidae). Behav. Ecol. Sociobiol. **41**: 335-341.

Fleming, I.A. 1996. Reproductive strategies of Atlantic salmon: ecology and evolution. Rev. Fish. Biol. Fish. **6**: 379-416.

Foote, C.J., Brown, G.S., and Wood, C.C. 1997. Spawning success of males using alternative mating tactics in sockeye salmon, *Oncorhynchus nerka*. Can. J. Fish. Aquat. Sci. **54**: 1785-1795.

Forseth, T., Ugedal, O., and Jonsson, B. 1994. The energy budget, niche shift, reproduction and growth in a population of Arctic charr, *Salvelinus alpinus*. J. Anim. Ecol. **63**: 116-126.

Forseth, T., Næsje, T. F., Jonsson, B., and Hårsaker, K. 1999. Juvenile migration in brown trout: a consequence of energetic state. J. Anim. Ecol. **68**:783-793.

Garant D., Dodson, J.J., and Bernatchez, L. 2003. Differential reproductive success and heritability of alternative reproductive tactics in wild Atlantic salmon (*Salmo Salar* L.). Evolution **57**. (In press.)

Garant, D., Fontaine, P.-M., Good, S.P., Dodson, J.J., and Bernatchez, L. 2002. Influence of male parental identity on growth and survival of offspring in Atlantic salmon (*Salmo salar*). Evol. Ecol. Res. **4**: 537-549.

Gaudreault, A., Castonguay, M., and FitzGerald, G.J. 1982. Répartition des ressources et changements saisonniers de l'alimentation d'ombles de fontaine anadromes, *Salvelinus fontinalis*. Can. J. Zool. **60**: 3068-3070.

Gibson, R.J. 1981. Behavioral interactions between coho salmon (*Oncorhynchus kisutch*), Atlantic salmon (*Salmo salar*), brook trout (*Salvelinus fontinalis*) and steelhead trout (*Salmo gairdneri*), at the juvenile fluviatile stages. Tech. Rep. Fish. Aquat. Sci. (Can.) No.1029.

Giske, J., Aksnes, D.L., and Førland, B. 1993. Variable generation time and Darwininan fitness measures. Evol. Ecol. **7**: 233-239.

Gross, M.R. 1987. Evolution of diadromy in fishes. Am. Fish. Soc. Symp. **1**: 14-25.

Gross, M.R. 1991. Salmon breeding behavior and life history evolution in changing environments. Ecology **72**: 1180-1186.

Gross, M.R. 1996. Alternative reproductive strategies and tactics: diversity between sexes. TREE **11**: 92-98.

Gross, M.R., Coleman, R.M. and McDowall, R.M. 1988. Aquatic productivity and the evolution of diadromous fish migration. Science **239**: 1291-1293.

Gross, M.R., and Repka, J. 1998. Stability with inheritance in the conditional strategy. J. theor. Biol. **192**: 445-453.

Gulseth, O.A., and Nilssen, K.J. 2000. The brief period of spring migration, short marine residence and high return rate of a northern Svalbard population of Artic charr. Trans. Am. Fish. Soc. **129**: 782-796.

Hansen, M.M., and Mensberg, K.-L.D. 1998. Genetic differentiation and relationship between genetic and geographical distance in Danish sea trout (*Salmo trutta* L.) populations. Heredity **81**: 493-504.

Hazel, W.N., Smock, R., and Johnson, M.D. 1990. A polygenic model for the evolution and maintenance of conditional strategies. Proc. R. Soc. Lond. B Bio Sci. **242**: 181-187.

Hazel, W.N., and Smock, R. 2000. Inheritance in the conditional strategy revisited. J. theor. Biol. **204**: 307-309.

Henson, S.A., and Warner, R.R. 1997. Male and female alternative reproductive behaviour in fishes: a new approach using intersexual dynamics. Ann. Rev. Ecol. Syst. **28**: 571-592.

Hindar, K., and Jonsson, B. 1993. Ecological polymorphism in Artic charr. Biol. J. Linn. Soc. **48**: 63-74.

Hindar, K., Jonsson, B., Ryman, N., and Ståhl, G. (1991). Genetic relationships among landlocked, resident, and anadromous brown trout, *Salmo trutta* L. Heredity **66**: 83-91.

Hoar, W.S. 1976. Smolt transformation: evolution, behaviour and physiology. J. Fish. Res. Bd Can. **33**: 1233-1252.

Holtby, L.B., and Healey, M.C. 1990. Sex-specific life-history tactics and risk-taking in coho salmon. Ecology **71**: 678-690.

Houston, A.I., and McNamara, J.M. 1992. Phenotypic plasticity as a state-dependent life-history decision. Evol. Ecol. **6**: 243-253.

Hunt, J., and Simmons, L.W., 2001. Status-dependent selection in the dimorphic beetle *Onthophagus Taurus*. Proc. R. Soc. Lond. B Bio Sci. **268**: 2409-2414.

Hutchings, J.A., 1993. Adaptive life histories effected by age-specific survival and growth rate. Ecology **74**:673-684.

Hutchings, J.A., 1994. Age- and size-specific costs of reproduction within populations of brook trout, *Salvelinus fontinalis*. Oikos **70**: 12-20.

Hutchings, J.A., and Jones, M.E.B. 1998. Life history variation and growth rate thresholds for maturity in Atlantic salmon, Salmo salar. Can. J. Fish. Aquat. Sci. **55**(Suppl.1): 22-47.

Hutchings, J.A., and Morris, D.W. 1985. The influence of phylogeny, size and behaviour on patterns of covariation in salmonid life histories. Oikos **45**: 118-124.

Hutchings, J.A., and Myers, R.A. 1994. The evolution of alternative mating strategies in variable environments. Evol. Ecol. **74**: 673-684.

Hutchings, J.A., Pickle, A., McGregor-Shaw, C.R., and Poirier, L. 1999. Influence of sex, body size, and reproduction on overwinter lipid depletion in brook trout. J. Fish. Biol. **55**: 1020-1028.

Jenkins. T.M., Jr., Diehl, S., Kratz, K.W., and Cooper, S.D. 1999. Effect of population density on individual growth of brown trout in streams. Ecology **80**: 941-956.

Johnsson, J.I., and Åkerman, A. 1998. Intersexual differences in aggression in juvenile rainbow trout. J. Fish Biol. **52**: 1292-1294.

Jones, M.W., Danzmann, R.G., and Clay, D. 1997. Genetic relationships among populations of wild resident, and wild and hatchery anadromous brook charr. J. Fish. Biol. **51**: 29-40.

Jonsson, B. 1982. Diadromous and resident trout Salmo trutta: is their difference due to genetics? Oikos **38**: 297-300.

Jonsson, B. 1985. Life history patterns of freshwater resident and sea-run migrant brown trout in Norway. Trans. Am. Fish. Soc. **114**: 182-194.

Jonsson, B., and Jonsson, N. 1993. Partial migration : niche shift versus sexual maturation in fishes. Rev. Fish Biol. Fish. **3** : 348-365.

Keeley, E.R., and Grant, J.W.A. 2001. Prey size of salmonid fishes in streams, lakes and oceans. Can. J. Fish. Aquat. Sci. **58** : 1122-1132.

Krebs, J.R., and Davis, N.B. 1993. An introduction to behavioral ecology, 3rd edn. Blackwell Scientific Publ., Oxford.

Kurdziel, J.P., and Knowles, L.L. 2002. The mechanisms of morph determination in the amphipod Jassa: implications for the evolution of alternative male phenotypes. Proc. R. Soc. Lond. B **269**: 1749-1754.

L'Abée-Lund, J.H., Jensen A.J., and Johnsen, B.O. 1990. Inter-population variation in male parr maturation of anadromous brown trout (*Salmo trutta*) in Norway. Can J. Zool. **68**: 1983-1987.

Lahti, K., Laurila, A., Enberg, K., and Piironen, J. 2001. Variation in aggressive behaviour and growth rate between populations and migratory forms in the brown trout, *Salmo trutta*. Anim. Behav. **62**: 935-944

Lank, D. B., C. M. Smith, O. Hanotte, T. Burke, and T. Cooke. 1995. Genetic polymorphism for alternative mating behaviour in lekking male ruff *Philomachus pugnax*. Nature **378**: 59-62.

LeJeune, R. 1987. Survol de la documentation relative à l'omble de fontaine anadrome. Ministère du Loisir, de la Chasse et de la Pêche, Direction de la Faune Aquatique, Québec, Canada.

Lesueur, C. 1993. Détermination des caractéristiques biologiques de la population de truite de mer (*Salvelinus fontinalis*) de la rivière Éternité (Saguenay). M.Sc. Thesis, UQAC, Chicoutimi, Québec, Can.

Levins, R. 1963. Theory of fitness in a heterogeneous environment. II. Developmental flexibility and niche selection. Am. Nat. **97**: 75-90.

Lima, S.L., and Dill, L.M. 1990. Behavioral decisions made under the risk of predation: a review and prospectus. Ca. J. Zool. **68**: 619-640.

Ludwig, D., and Rowe, L. 1990. Life-history strategies for energy gain and predator avoidance under time constraints. Am. Nat. **135**: 686-707.

Lundberg, P. 1987. Partial bird migration and evolutionary stable strategies. J. theor. Biol. **125**: 351-360.

MacCrimmon, H.R., and Campbell, J.S. 1969. World distribution of brook trout, *Salvelinus fontinalis.* J. Fish. Res. Board Can. **28**: 452-456.

Mangel, M., and Clark, C.W. 1986. Towards a unified foraging theory. Ecology **67**: 1127-1138.

Mangel, M., and Stamps, J. 2001. Trade-offs between growth and mortality and the maintenance of individual variation in growth. Evol. Ecol. Res. **3**: 583-593.

Marschall, E.A., Quinn, T.P., Roff, D.A., Hutchings, J.A., Metcalfe, N.B., Bakke, T.A., Saunders, R.L., and LeRoy, P. 1998. A framework for understanding Atlantic salmon (*Salmo salar*) life history. Can. J. Fish. Aquat. Sci. **55**(Suppl.1): 1122-1132.

Maynard-Smith, J. 1982. Evolution and the theory of games. Cambridge University Press, Cambridge, U.K.

McCormick, S.D., and Naiman, R.J. 1982. Osmoregulation in the brook trout (*Salvelinus fontinalis*). The Matamek research program annual report for 1981. Technical Report WHO I-82-29, Woods Hole, Massachusetts. pp. 169-176.

McCormick, S.D., and Naiman, R.J. 1984. Osmoregulation in brook trout (*Salvelinus fontinalis*). II. Effect of size, age and photoperiod on seawater survival and ionic regulation. Comp. Biochem. Physiol., **79A**: 17-28.

McCormick, S.D., Naiman, R.J., and Montgomery, E.T. 1985. Physiological smolt characteristics of anadromous and non-anadromous brook trout (*Salvelinus fontinalis*) and Atlantic salmon (*Salmo salar*). Can. J. Fish. Aquat. Sci., **42**: 529-538.

McCormick, S.D., and Saunders, R.L. 1987. Preparatory physiological adaptations for marine life of salmonids: osmoregulation, growth and metabolism. Am. Fish. Soc. Symp. **1**: 211-229.

McDowall, R.M. 2001. Anadromy and homing: two life-history traits with adaptive synergies in salmonid fishes? Fish and Fisheries **2**: 78-85.

McNamara, J.M., and Houston, A.I., 1986. The common currency for behavioral decisions. Am. Nat. **127**: 358-378.

Metcalfe, N.B. 1998. The interaction between behaviour and physiology in determining life history patterns in Atlantic salmon (Salmo salar). Can. J. Fish. Aquat. Sci. **55**(Suppl.1): 93-103.

Metcalfe, N.B., Taylor, A.C., and Thorpe, J.E. 1995. Metabolic rate, social status and life-history strategies in Atlantic salmon. Anim. Behav. **49**: 431-436.

Metcalfe, N.B., and Thorpe, J.E. 1992. Early predictors of life-history events: the link between first feeding date, dominance and seaward migration in Atlantic salmon, *Salmo salar* L. J. Fish Biol. **41** (Suppl. B): 93-99.

Metcalfe, N.B., Wright, P.J. and Thorpe, J.E. 1992. Relationship between social status, otoliths size at first feeding and subsequent growth in Atlantic salmon (*Salmo salar*). J. Anim. Ecol. **61**: 585-589.

Moczek, A.P., Hunt, J., Emlen, D.J., and Simmons, L.W. 2002. Threshold evolution in exotic populations of a polyphenic beetle. Evol. Ecol. Res. **4**: 587-601.

Montgomery, W.L., McCormick, S.D., Naiman, R.J., Whoriskey, F.G, and Black, G. 1990. Anadromous behaviour of brook charr (*Salvelinus fontinalis*) in the Moisie River, Québec. Pol. Arch. Hydrobiol. **37**: 43-61.

Moran, N.A. 1992. The evolutionary maintenance of alternative phenotypes. Am. Nat. **139**: 971-989.

Morinville, G.R., and Rasmussen, J.B. 2003. Early bioenergetic differences between juvenile anadromous and resident brook trout (*Salvelinus fontinalis*). Can. J. Fish. Aquat. Sci. **60**. (In press.)

Morita, K. 2001. The growth history of anadromous white-spotted charr in northern Japan: a comparison between river and sea life. J. Fish. Biol. **59**: 1556-1565.

Morita, K., and Takashima, Y. 1998. Effect of female size on fecundity and egg size in white-spotted charr: comparison between sea-run and resident forms. J. Fish. Biol. **53**: 1140-1142.

Morita, K.,Yamamoto, S., and Hoshino, N., 2000. Extreme life history change of white-spotted char (*Salvelinus leucomaenis*) after damming. Can. J. Fish. Aquat. Sci., **57**: 1300-1306.

Nelson, M.L., McMahon, T.E., and Thurow, R.F., 2002. Decline of the migratory form of bull charr, Salvelinus confluentus, and implications for conservation. Envir. Biol. Fishes **64**: 321-332.

Nicieza, A.G., and Braña, F. 1993. Relationships among smolt size, marine growth, and sea age at maturity of Atlantic Salmon (*Salmo salar*) in Northern Spain. Can. J. Fish. Aquat. Sci. **50**: 1632-1640.

Nikolskii, G.V. 1963. The ecology of fishes. Academic Press, London, 352 p.

Nylin, S., and Gotthard, K. 1998. Plasticity in life-history traits. Annu. Rev. Entomol. **43**: 63-83.

Nordeng, H. 1983. Solution to the 'Char Problem' based on Arctic char (*Salvelinus alpinus*) in Norway. Can. J. Fish. Aquat. Sci. **40**: 1372-1387.

Northcote, T.G. 1978. Migratory strategies and production in freshwater fishes. *In* Ecology of freshwater fish production. *Edited by* S.D. Gerkins. John Whiley and Sons, New-York pp. 326-359.

Northcote, T.G. 1992. Migration and residency in streams salmonids - some ecological considerations and evolutionary consequences. Nord. J. Freshwater Res. **67**:5-17.

Økland, F., Jonsson, B., Jenssen, A.J., and Hansen, L.P. 1993. Is there a threshold size regulating seaward migration in brown trout and Atlantic salmon ? J. Fish. Biol. **42**: 541-550.

Parker, H.H., Noonburg, E.G., and Nisbet, R.M.. 2001. Models of alternative life-history strategies, population structure and potential speciation in salmonids fish stocks. J. Anim. Ecol. **70**: 260-272.

Pollock, K.H., and Otto, M.C. 1983. Robust estimation of population size in closed animal populations from capture-recapture experiments. Biometrics **39**: 1035-1049.

Power, G. 1980. The brook charr, *Salvelinus fontinalis*. *In* Charrs: salmonids fishes of the genus *Salvelinus*, a review. *Edited by* E.F. Bakon, Junk., The Hague. pp. 141-203.

Power, G. 2002. Charrs, glaciations and seasonal ice. Env. Biol. Fish. **64**: 17-35.

Randall, R.G., Healey, M.C., and Dempson, J.B. 1987. Variability in length of freshwater residence of salmon, trout and char. Am. Fish. Soc. Symp. **1**: 27-41.

Repka, J., and Gross, M.R. 1995. The evolutionary stable strategy under individual condition and tactic frequency. J. theor. Biol. **176**: 27-31.

Rexstead, E., and Burnham, K. 1991. User's guide for interactive program CAPTURE. Colorado Cooperative Fish and Wildlife Research Unit, Fort Collins, Colorado, U.S.A. http://www.mbr-pwrc.usgs.gov./software/doc/capture/capture.htm.

Ricker, W.E. 1938. 'Residual' and kokanee salmon in Cultus Lake. J. Fish. Res. Bd. Can. **4**: 192-218.

Rikardsen, A.H., and Elliott, J.M. 2000. Variations in juvenile growth, energy allocation and life-history strategies of two populations of Artic charr in North Norway. *J. Fish. Biol.*, **56** : 328-346.

Rikardsen, A.H., Svenning, M.A., and Klemetsen, A. 1997. The relationships between anadromy, sex ratio and parr growth of Artic charr in a lake in North Norway. J. Fish. Biol. **51**: 447-461.

Rodriguez, M.A. 1995. Habitat-specific estimates of competition in stream salmonids: a field test of the isodar model of habitat selection. Evol. Ecol. **9**: 169-184.

Roff, D.A. 1996. The evolution of threshold traits in animals. Quart. Rev. Biol. **71**: 3-35.

Roff, D.A. 1998. The maintenance of phenotypic and genetic variation in threshold traits by frequency-dependent selection. J. evol. biol. **11**: 513-529.

Roff, D.A., and Fairbairn, D.J. 1991. Wing dimorphism and the evolution of migratory polymorphisms among the Insecta. Am. Zool. **31**: 243-251.

Roff, D.A., and Fairbairn, D.J. 1993. The evolution of alternative morphologies: fitness and wing morphology in male sand cricket. Evolution **47**: 1572-1584.

Roff, D.A., Tucker, J., Stirling, G., and Fairbain, D.J. 1999. The evolution of threshold traits: effects of selection on fecundity and correlated response in wing dimorphism in the sand cricket. J. Evol. Biol. **12**: 535-546.

Ryan, M.J., Pease, C.M., and Morris, M.R. 1992. A genetic polymorphism in the swordtail *Xiphophorus nigrensis*: testing the prediction of equal fitness. Am. Nat. **139**: 21-31.

Saunders, R.L., Muise, B.C., and Henderson, E.B. 1975. Mortality of salmonids cultured at low temperature in sea water. Aquaculture **5**: 243-252.

Sato, H. 1998. Payoffs of the two alternative nesting tactics in the African dung beetle, *Scarabeus catenatus*. Ecol. Entom. **23**: 62-67.

Schaffer, W.M. 1979. The theory of life-history evolution and its application to Atlantic salmon. Symp. Zool. Soc. Lond. **44**: 307-326.

Sinervo, B., and Zamudio, K.R. 2001. The evolution of alternative reproductive strategies: fitness differential, heritability, and genetic correlation between the sexes. J. Heredity **92**: 198-205.

Smith, M.W., and Saunders, J.W. 1958. Movements of brook trout, *Salvelinus fontinalis* (Mitchill) between and within fresh and salt water., J. Fish. Res. Bd. Can. **15**: 1403-1449.

Snorrason, S.S., Skulason S., Jonsson, B., Malmquist, H.J., Jonasson, O., Sandlund, O.T., and Lindem, T. 1994. Trophic specialisation in Artic charr *Salvelinus alpinus* (Pisces; Salmonidae): morphological divergence and ontogenetic niche shifts, Biol. J. Linn. Soc. **52**: 1-18.

Spidle, A.P., Quinn, T.P., and Bentzen, P. 1998. Sex-biased marine survival and growth in a population of coho salmon. J. Fish. Biol. **52**: 907-915.

Stearns, S.C. 1992. The Evolution of Life Histories. Oxford University Press, New York.

Stearns, S.C. 2000. Life-history evolution: successes, limitations and prospects. Naturwissenschaften **87**: 476-486.

Sutterlin, A.M., Harman, P., and Barchard, H. 1976. The culture of brook trout in saltwater. Tech. Rep. Fish. Mar. Serv. (Can.) No. 636.

Svenning, M.-A., Smith-Nilsen, A., and Jobling, M. 1992. Sea water migration of Artic charr (*Salvelinus alpinus* L.) - Correlation between freshwater growth and seaward migration, based on back-calculation from otoliths. Nord. J. Fresh. Res. **67**: 18-26.

Taborsky, M. 2001. The evolution of bourgeois, parasitic, and cooperative behaviors in fishes. J. Heredity **92**: 100-110.

Thériault, V. 2001. Anadromie et résidence chez l'omble de fontaine (*Salvelinus fontinalis*): présence d'une stratégie conditionnelle basée sur la croissance? M.Sc. Thesis, Laval University, Québec, Canada.

Thériault, V., and Dodson, J.J. The role of size in determining anadromy or residency in brook charr (*Salvelinus fontinalis*). Submitted to J. Fish. Biol.

Thorpe J.E., 1987. Smolting versus residency : developmental conflict in salmonids. Am. Fish. Soc. Symp., **1**: 244-252.

Thorpe J.E., Mangel, M., Metcafle, N.B., and Huntingford, F.A. 1998. Modelling the proximate basis of salmonid life-history variation, with application to Atlantic salmon, Salmo salar L. Evol. Ecol. **12**: 581-599.

Thompson, J.D. 1991. Phenotypic plasticity as a component of evolutionary change. TREE **6**: 246-249.

Tucker, S., and Rasmussen, J.B. 1999. Using ^{137}Cs to measure and compare bioenergetic budgets of juvenile Atlantic salmon (*Salmo salar*) and brook trout (*Salvelinus fontinalis*). Can. J. Fish. Aquat. Sci. **56**: 875-887.

Werner, E.E., and Gilliam, J.F. 1984. The ontogenic niche and species interactions in size-structured populations. Ann. Rev. Ecol. Syst. **15**: 393-425.

White, G.C., and Burnhnam, K.P. 1999. Program MARK – survival estimation from populations of marked animals. Bird Study, **46**: 120-138.

White, H.C. 1940. Life-history of sea running brook trout, *Salvelinus fontinalis*, of the Moser River, Nova Scotia. J. Fish. Res. Bd Can. **5**: 176-186.

Whiteman, H.H. 1994. Evolution of facultative paedomorphosis in salamanders. Quart. Rev. Biol. **69**: 205-221.

Wilder, D.G. 1952. A comparative study of anadromous and freshwater populations of brook trout (*Salvelinus fontinalis* (Mitchill)). J. Fish. Res. Bd Can., **9**: 169-203.

Wootton, R.J. 1998. Ecology of teleost fishes. Second Edition. Kluwer Academic Publishers, Dordrecht, The Netherlands.

Zamudio, K.R., and Sinervo, B. 2000. Polygyny, mate guarding, and posthumous fertilizations as alternative male strategies. Proc. Natl. Acad. Sci. **97**: 14427-14432.

Zera, A.J., and Denno, R.F. 1997. Physiology and ecology of dispersal polymorphism in insects. Annu. Rev. Entomol. **42**: 207-231.

ZIP-Saguenay, 1998. Plan d'action et de réhabilitation écologique de la rivière Saguenay. Comité Zone d'Intervention Prioritaire (ZIP) Saguenay, La Baie, Canada.

Autorisation de co-auteur(s) pour un article inclu dans le mémoire ou la thèse

NOM DE L'ÉTUDIANT-E SOPHIE LENORMAND

NOM DU PROGRAMME DOCTORAT EN BIOLOGIE

TITRE DU MÉMOIRE OU DE LA THÈSE ÉVOLUTION DE L'ANADROMIE ET STRATÉGIE DE REPRODUCTION CHEZ L'OMBLE DE FONTAINE (SALVELINUS FONTINALIS)

Par la présente, le(s) soussigné(s), co-auteur(s) d'un article intitulé :

Seasonal and ontogenetic patterns in the migration of anadromous brook charr (Salvelinus fontinalis)

faisant partie du mémoire de maîtrise ou de la thèse de doctorat présentée à la Faculté des études supérieures de l'Université Laval, autorise(nt) l'insertion de l'article dans ce mémoire ou cette thèse et l'éventuel microfilmage selon les règles de la Bibliothèque nationale du Canada (Service des thèses canadiennes).

SIGNATURE	NOM EN CARACTÈRE D'IMPRIMERIE	DATE
Annie Ménard	ANNIE MÉNARD	6/04/2003

Annie Ménard ANNIE

Ce formulaire doit être remis à la Faculté des études supérieures au moment du dépôt initial.