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DYNAMIQUE DE L'ORGANISATION GÉOGRAPHIQUE DE LA DIVERSITÉ GÉNÉTIQUE CHEZ L'OMBLE DE FONTAINE *SALVELINUS FONTINALIS* MITCHILL.

Diversité des habitats et des histoires de vie.

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Résumé court

La structure de la diversité génétique d'une espèce devrait à terme refléter la structure du paysage. Comment alors expliquer que dans certains systèmes, la concordance puisse être si faible ? Une analyse des variations temporelles des patrons d'isolement par la distance le long d'un gradient de colonisation a révélé qu'une des causes de la faible concordance pouvait être l'évolution des patrons d'organisation de la diversité. De plus, la forme de dispersion de l'espèce semble avoir évolué au cours de la colonisation en fonction de l'intensité du fardeau de consanguinité, générant ainsi des variations spatiales des paramètres démographiques. La diversité génétique est donc clairement une variable dynamique dont la compréhension nécessite la prise en compte de facteurs biogéographiques. Les résultats de cette thèse mettent en évidence des variations spatiales et temporelles des contraintes de l'habitat qui compromettent l'utilisation de plusieurs méthodes d'inférence démographiques courantes. C'est pourquoi une approche strictement comparative est proposée comme alternative possible.

Résumé long

Bien que difficiles à identifier, bien que variables, les contraintes du paysage déterminent les possibilités de coalescence entre allèles. La structure de la diversité devrait donc à terme refléter la structure du paysage. Comment alors expliquer que dans certains systèmes, la concordance puisse être si faible ? D'une part, les espèces ont une histoire, souvent liée à celle de leur habitat. D'autre part, les espèces ne sont pas idéales, et leurs paramètres démographiques peuvent varier dans le temps et dans l'espace. Ainsi, les taux de migration peuvent varier d'un point à l'autre de l'aire de répartition sous l'effet des forces qui déterminent l'évolution des forces de dispersion. L'omble de fontaine en milieu côtier se prête particulièrement bien à l'étude empirique des écarts simples aux modèles de génétique des populations, parce que les contraintes de l'habitat sont généralement aisémement identifiables, que l'histoire du nord-est de l'Amérique du Nord est connue, et que la dynamique de la forme anadrome, la forme de dispersion de l'espèce en milieu côtier a été abondamment décrite dans le cadre de l'étude des migrations saisonnières. La faible concordance de la structure de la diversité avec la structure d'un habitat lacustre qui contraint pourtant fortement les patrons de migration a révélé la difficulté associé à cette tâche, particulièrement aux grandes échelles spatiales. Une analyse des variations temporelles des patrons d'isolement par la distance le long d'un gradient de colonisation a ensuite révélé qu'une des causes de la faible concordance pouvait être l'évolution toujours en cours des patrons d'organisation de la diversité. De plus, la forme de dispersion de l'espèce semble avoir évolué au cours de la colonisation en fonction de l'intensité du fardeau de consanguinité, générant ainsi des variations spatiales des paramètres démographiques. La diversité génétique est donc clairement une variable dynamique dont la compréhension nécessite la prise en compte de facteurs biogéographiques. Les résultats de cette thèse mettent en évidence des variations spatiales et temporelles des contraintes de l'habitat qui compromettent l'utilisation de plusieurs méthodes d'inférence démographiques courantes. C'est pourquoi une approche strictement comparative est proposée comme alternative possible.

Abstract

The expected concordance between landscape structure and geographic patterns of genetic structure is due to landscape constraints over potential coalescence among alleles. In the long run, a high level of concordance may thus be expected. Why then is concordance sometimes so weak? First, species have a history, such that landscape disturbances can affect geographic patterns of diversity. Second, species are seldom "ideal", as defined by population genetic models, such that their demographic properties can vary in space and in time. For instance, migration rates can vary within the species' range because the form of dispersal can evolve. Brook charr populations in coastal areas is an especially useful model system to empirically investigate the consequences of simple departures from population genetic models because landscape constraints can generally be easily identified, because recent disturbances of north-eastern North America have been extensively described, and because the dynamic of anadromy, brook charr's form of dispersal in coastal areas, has been ecologically characterized in the frame of seasonal migrations between freshwater and saltwater. Although lakes and rivers strongly constraint migration pathways, geographic patterns of diversity in lacustrine populations were only weakly correlated with landscape structure, especially at large geographic scales. Temporal variation of isolation by distance along a colonization gradient then revealed that spatial patterns of genetic diversity were still evolving toward stable equilibrium. The species' form of dispersal was also evolving along this gradient, according to variation of the inbreeding load. Our results thus revealed some aspects of the dynamics of genetic diversity in natural populations. Understanding its evolution requires that biogeographic considerations be included into the view of genetic variation in space. Because the accuracy of demographic inference methods would be impaired by spatial and temporal variations in habitat constraints, a strictly comparative approach is proposed as an alternative in empirical population genetics studies.

Avant-propos

Cette thèse a constitué une partie importante des quatre années que j'ai passées à Québec. De cette belle aventure académique, je retire le plaisir de m'être laissé guidé par un sujet au gré des questions qui se sont posées à moi. Si les périodes d'hésitation et de découragement n'ont pas manqué, cette expérience de recherche sera toujours restée stimulante par sa diversité. Existe-t-il beaucoup d'entreprises humaines dont le résultat dépende si complètement de ce qu'on a pu, su, ou voulu y mettre ?

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Introduction

1.1. Dynamique de la diversité biologique : quelle importance ?

Apparente à toutes les échelles de temps et d'espace, la diversité du monde vivant est un de ses aspects les plus remarquables. Au cœur de la biologie moderne, cette diversité est selon la théorie darwinienne de l'évolution par sélection naturelle la condition préalable à la possibilité d'une évolution, la quantité de variation présente en un lieu à un moment donné permettant ou ne permettant pas l'action de la sélection. La compréhension de la genèse et de la dynamique de la diversité a donc constitué un thème central de la biologie évolutive.

Depuis la diversité des communautés d'espèces jusqu'à la diversité moléculaire, un des aspects les plus frappants de la diversité est qu'elle n'est pas répartie aléatoirement dans l'espace. L'examen de la répartition géographique des communautés, des espèces, des individus et des allèles révèle en effet des patrons d'organisation souvent clairs. Ainsi, la composition des communautés varie d'une région géographique à l'autre, les espèces ont des aires de répartition souvent disjointes, les sous-espèces sont géographiquement délimitées, les fréquences des haplotypes mitochondriaux et des allèles nucléaires varient d'un point à l'autre de l'aire de répartition. Cette répartition géographique est importante à plusieurs points de vue. D'une part parce que la capacité d'adaptation de l'espèce dépend en partie de son échelle de structure si les pressions de sélection varient dans l'espace. En effet, cette structure détermine les unités fonctionnellement indépendantes sur lesquelles la sélection peut agir. D'autre part parce que, même dans un environnement sélectif homogène, la réponse d'une population structurée est différente de celle d'une population homogène (Whitlock 2002). La diversité génétique et ses patrons d'organisation géographique sont donc des aspects essentiels de la capacité des espèces à évoluer par sélection naturelle.

Quelles sont alors les forces et les événements qui déterminent l'organisation géographique de la diversité dans l'espace ? Cette question a été posée de multiples façons, souvent différente en fonction de l'échelle de temps et d'espace considérée. À une grande échelle, l'écologie des communautés a beaucoup insisté sur l'importance du régime de perturbation et les patrons de spécialisation des espèces dans un cadre biogéographique. A l'inverse, les études empiriques de génétique des populations ont mis l'accent sur les forces de mutation, de

migration et de dérive en considérant que l'effet du régime de perturbation était négligeable et qu'un état stationnaire était atteint (hypothèse d'équilibre). Si de récents travaux contribuent à réconcilier ces deux approches (Bell 2001, Hubbel 2001), elles sont encore largement disjointes. Le travail présenté dans cette thèse est une tentative de contribuer à la prise en compte de l'ensemble des facteurs contemporains et historiques responsables de l'organisation contemporaine de la diversité génétique d'une espèce.

1.2. Écologie du paysage

1.2.1. La structure du paysage contraint la généalogie des gènes

Dans un habitat structuré, tous les individus n'ont pas la même probabilité de se reproduire les uns avec les autres, ce qui modifie l'historique de coalescence des allèles. La première influence que subit la répartition spatiale de la diversité génétique est donc la structure du paysage dans lequel se trouve l'espèce. Cette structure se définit par la taille et l'organisation spatiale des patchs d'habitat ainsi que par la nature de la matrice qui les sépare (Fahrig et Merriam 1997). La structure du paysage freine ou facilite le mouvement des allèles d'une génération à la suivante, ce qui caractérise sa connectivité et détermine la distribution de probabilité de la date des événements de coalescence entre allèles. Cette distribution détermine à son tour la répartition spatiale de la diversité génétique de l'espèce dans le paysage. Par exemple, dans un habitat comportant de nombreux patchs de petite taille fortement isolés les uns des autres, la probabilité que deux allèles dans un même patch aient un ancêtre commun à la génération précédente sera élevée et leur temps moyen de coalescence sera court. La distribution des temps de coalescence intra- et inter-patchs se reflétant dans l'organisation géographique de la diversité génétique, on devra s'attendre à trouver de faibles niveaux de diversité à l'intérieur des patchs et de fortes différences entre patchs. A l'extrême opposé, pour un nombre identique d'individus, un habitat comportant quelques grands patchs interconnectés par une matrice propice à la migration, rendra la probabilité de coalescence entre deux allèles plus faible, le temps d'attente avant coalescence plus long et diminuera la diversité inter-patchs au profit de la diversité intra-patchs. La contrainte de l'habitat sur les probabilités de coalescence entre allèles est donc à l'origine de la concordance attendue entre la structure de l'habitat et la structure de la diversité génétique d'une espèce qui s'y trouve. Les vérifications empiriques de cette prédiction théorique sont nombreuses, notamment chez les poissons, où

des niveaux plus élevés de structure sont observés chez les espèces d'eau douce confrontées à un habitat fortement structuré (lacs, rivières) que chez les espèces anadromes et marines, pour lesquelles les barrières au flux géniques sont de plus faible intensité (milieu marin ou côtier; Ward 1984, Hendry et al. 2002). À une plus courte échelle temporelle, l'accroissement marqué des niveaux de structure suite à la détérioration des possibilités de migration confirme également cette prédiction. Globalement, les études empiriques ont montré que la nature du paysage avait une forte influence sur les niveaux de différenciation génétique et leur organisation géographique (p. e. Avise and Felley 1979, Pounds & Jackson 1981, Caccone & Sbordoni 1987, King 1987, Arter 1990, Kane et al. 1992, Preziosi & Fairbairn 1992, Napolitano & Descimon 1994, Britten et al. 1995, Johnson & Black 1995, Neve et al. 1996, Johannesen et al. 1996, Van Dongen et al. 1998, Keyghobadi et al. 1999).

Cette concordance est la base conceptuelle des méthodes d'inférences démographiques (Slatkin 1993, Rousset 1997) qui se sont rapidement diffusées dans la littérature empirique (voir par exemple Bohonak 1999). Étant donné un habitat dont la contrainte sur le mouvement des allèles est homogène dans l'espace et constante dans le temps, il est possible d'obtenir la relation théorique entre la probabilité d'identité par descendance de deux allèles (Wright 1943, Kimura & Weiss 1964, Sawyer 1977, Barton et al. 2002), ou la densité de probabilité de leur temps de coalescence (Slatkin 1991) et la distance qui les sépare. Ces résultats étant disponibles, il suffit alors de procéder à rebours, la répartition des allèles dans l'espace nous fournissant ces probabilités d'identité qui nous permettent d'inférer la distance de dispersion qui leur aurait donné forme (encadré 1).

Encadré 1.

Méthode d'estimation du flux de gènes dans un habitat unidimensionnel.
(Rousset 1997)

Soit un grand nombre de populations de N individus diploïdes chacune disposées linéairement. Les échanges entre populations se font par les gamètes, un gène pouvant se trouver par migration dans une population différente de celle de ses parents. La variance de la position d'un allèle d'une génération à la suivante est σ^2, le second moment de la distance entre un allèle et son parent à la génération précédente. Prenant deux populations séparées par une distance de j unités, sous l'hypothèse d'un faible taux de mutation,

$$\frac{F_{ST}}{1-F_{ST}} \approx \frac{A_1}{4N\sigma} + \frac{j}{4N\sigma^2}$$

Une relation linéaire est donc attendue entre $F_{ST}/(1-F_{ST})$ et la distance séparant deux populations. La pente de cette relation linéaire est $1/(4N\sigma^2)$, ce qui fournit une estimation de $N\sigma^2$. Une propriété particulièrement attractive de cette méthode est que seul $N\sigma^2$ a une influence sur la pente : ce paramètre est donc indépendant de la forme exacte de la distribution de dispersion, qui est généralement difficile à estimer en populations naturelles donc mal connue dans les études empiriques.

Parmi les hypothèses sous-jacentes à cette procédure d'estimation :

- le système est à l'équilibre. Cette hypothèse est nécessaire pour que les propriétés asymptotiques de l'équilibre puissent être utilisées et que F_{ST} ,estimé sur des marqueurs moléculaires, reflète bien les probabilités d'identité par descendance
- le taux de mutation est négligeable devant le taux de migration
- toutes les sous-populations ont même taille efficace N
- l'habitat est homogène : le flux de gènes est inversement proportionnel à la distance et ne dépend que d'elle.

1.2.2. Identification des contraintes de l'habitat

Cette concordance attendue entre la structure du paysage et la structure génétique des populations nécessite cependant que les contraintes du paysage soient bien identifiées. La distance géographique n'est en effet parfaitement corrélée à la probabilité d'identité par

descendance que dans un habitat stable, homogène et isotrope. Cette relation est donc faussée dès que des contraintes supplémentaires de l'habitat sont prises en compte, et les caractéristiques de la matrice peuvent alors s'avérer importantes. La structure des populations peut alors contribuer à identifier les facteurs qui constituent, pour une espèce donnée, une contrainte du paysage (Parsons 1996). Ainsi, dans un ensemble de populations lacustres de daphnies *Daphnia ambigua* connectées par des rivières, Michels et al. (2001) ont montré que les niveaux de différenciation entre lacs n'étaient corrélés à la distance entre lacs que lorsque l'intensité des courants des rivières étaient pris en compte dans la mesure de distance. Dans cet exemple, il est clair que l'intensité du flux de gènes dépend fortement d'autres facteurs que de la seule distance géographique. Cette approche a également été utilisée par King (1987) et par Arter (1990) pour identifier parmi plusieurs facteurs liés aux flux génique ceux dont l'influence était la plus importante en confrontant plusieurs matrices de distances possibles, chacune basée sur une caractéristique particulière de l'habitat. Un lien entre la structure du paysage et la structure génétique des populations devrait dont être attendu si les contraintes du paysage sont bien comprises et identifiées. Cette contrainte peut être la possibilité de migration entre patchs au sein d'un habitat, comme je l'ai rapidement détaillé, mais peut également être une autre caractéristique du paysage. Ainsi, la taille physique d'un patch d'habitat peut s'avérer un très mauvais critère pour prédire la taille de la population qui s'y trouve. La nature, la quantité et la disponibilité de la ressource présente, peuvent également jouer un rôle majeur, tout comme le nombre de sites de reproduction appropriés.

En plus d'être parfois difficiles à identifier, ces contraintes dépendent fortement de l'espèce considérée, une contrainte pour l'une n'est pas nécessairement une contrainte pour l'autre. Il en résulte que les dynamiques démographiques de deux espèces trouvées au sein d'un même habitat ne sont pas nécessairement couplées. Deux espèces peuvent ainsi avoir dans un même habitat des niveaux différents de structure si leurs capacités de dispersion sont différentes. Là encore, les organismes marins fournissent un exemple éloquent, la durée de la phase larvaire étant hautement corrélée au niveau de différentiation entre localités (p. e. Waples 1987), il apparaît clairement qu'un même habitat (côtier dans ce cas) impose des contraintes différentes aux différentes espèces en fonction de leurs capacités de dispersion larvaire. De la même façon, des variations spatiales ou temporelles des capacités de dispersion d'une espèce

amèneraient certaines populations à réagir différemment aux contraintes de l'habitat auxquelles elles sont confrontées, même si celui-ci est constant.

1.2.3. Structure du paysage et dépression de consanguinité

En plus de contribuer à l'organisation spatiale de la diversité génétique, la structure du paysage modifie un ensemble de propriétés génétiques, comme l'efficacité de la sélection. Celle-ci peut être modifiée de deux façons opposées (Whitlock 2002). D'une part, le patron non aléatoire de reproduction que génère la structure de l'habitat augmente l'exposition des allèles récessifs à l'action de la sélection en modulant le niveau d'homozygotie pour un locus donné via le degré d'apparentement entre partenaires de reproduction. La sélection peut alors être rendue plus efficace dans une population structurée. À l'inverse, si le niveau d'apparentement entre individus au sein d'un patch d'habitat est élevé, les niveaux de diversité locale seront plus faibles et le faible polymorphisme disponible peut alors limiter l'action de la sélection. Ces effets se traduisent en particulier dans la capacité d'une espèce à se débarrasser des mutations délétères qui s'accumulent au sein de son génome. Pour des niveaux de structure réalistes, la fréquence moyenne des allèles délétères est diminuée, le fardeau de mutation est réduit et le niveau attendu de dépression de consanguinité est plus faible que dans une population homogène (Whitlock 2002, encadré 2).

Encadré 2

Dépression de consanguinité dans une population structurée

(Whitlock 2002)

Dans une population constituée d'un grand nombre de patchs partiellement isolés, soit un locus à deux allèles (fréquences pi et qi) dont le deuxième est délétère. Les fitness relatives des trois génotypes possibles sont alors 1, 1+hs, 1+s, où h est le coefficient de dominance et s $\in$ [-1,0]. La fitness moyenne relative d'un patch est alors $\overline{w_i} = 1 + 2hsp_iq_i + sq_i^2$.

Sous de faibles valeurs du taux de mutation et de faibles valeurs de F_{ST}, la fréquence de l'allèle délétère est plus faible dans une population structurée que dans une population panmictique lorsque $h < \frac{1 - F_{ST}(1-2b)}{3 - 2b - F_{ST}(1-2b)}$, où b mesure la position sur un continuum allant d'un régime de sélection soft (b=0, pas de régulation locale de la démographie) à hard (b=1, les patchs contribuent à hauteur de leur fitness relative). Sous sélection soft pure (b=0), cette condition se réduit à h<1/3 tandis que pour b=1, elle se réduit à h<1, ce qui est toujours réalisé. En d'autres termes, la structure des populations diminue la fréquences des allèles délétères sous une vaste gamme de coefficients de dominance.

Ce résultat se traduit directement dans l'intensité de la dépression de consanguinité, définie comme la fitness relative des individus issus de croisements consanguins expérimentaux par rapport aux individus issus de croisements aléatoires dans le même patch. A titre d'exemple, pour des F_{ST} de l'ordre de 0,10 - 0,15 tels qu'observés entre certaines populations de salmonidés, la dépression de consanguinité peut être réduite de 20 à 50 % par rapport à une même population qui ne serait pas structurée (figure 2.1).

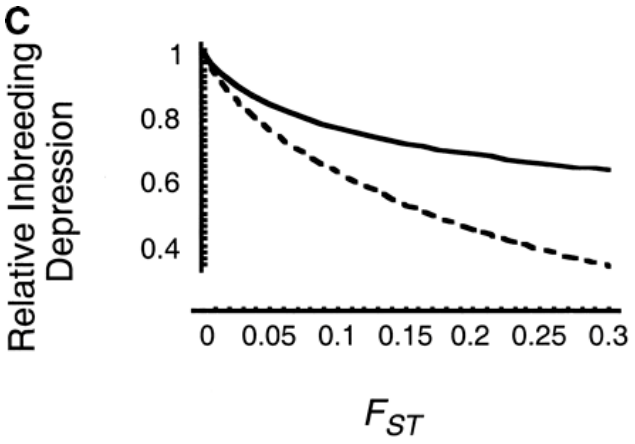

Figure 2-1Dépression de consanguinité attendue dans une population structurée en fonction de la différenciation entre les populations. La ligne ligne continue représente un régime de sélection soft pur et la ligne pointillée un régime de sélection hard, les deux types extrèmes de régimes de sélection. La dépresssion est mesurée relativement à une population panmictique, indicée 1.

1.3. Variations des paramètres démographiques : évolution de la dispersion

Bien que la majorité des études génétique des populations empirique emploient des modèles de basés sur des paramètres démographiques homogènes dans l'espace et constants dans le temps, un champ d'étude vaste et dynamique s'est attaché à comprendre l'évolution de la dispersion considérée comme trait d'histoire de vie (Clobert et al. 2001). Un examen des quatre classes principales de modèles d'évolution de la dispersion permet de comprendre l'origine des variations des capacités de migration au sein de l'aire de répartition d'une espèce.

1.3.1. Dispersion sous l'effet de la stochasticité démographique

Une espèce dont toute capacité de dispersion serait absente est vouée à l'extinction, non seulement dans un habitat instable, mais aussi dans un habitat stable en raison de stochasticité de la dynamique démographique de ses populations. Un premier facteur qui favorise l'évolution et le maintien d'une forme de dispersion, peut-être le plus intuitif est donc la stochasticité démographique, les individus qui dispersent étant les seuls à n'avoir pas une fitness nulle dans le cas extrême de l'extinction de la population. Cet argument verbal a été développé théoriquement (Van Valen 1971), particulièrement dans le cadre de la théorie des métapopulations (Levin et al. 1984). Olivieri et al (1995) ont montré que la proportion d'individus disperseurs pouvait varier avec l'age du patch d'habitat considéré, les patchs les plus récents contenant une plus forte proportion d'individus dispersant et cette proportion diminuant au fil des générations en raison du coût à la dispersion. Des données empiriques ont montré que cette première source de variation des capacités de dispersion pouvait être observée dans des populations naturelles (Cody et Overton 1996).

1.3.2. Dispersion sous l'effet de la variabilité spatiale

Mais la dispersion peut également évoluer même si la probabilité d'extinction des populations est nulle, en réponse à une variabilité spatiale de la qualité de l'environnement. Si les patchs d'habitat sont de qualité variable, McPeek et Holt (1992) ont montré qu'un génotype capable d'ajuster sa décision de dispersion pour rester sur les patchs de bonne qualité et quitter les patchs de mauvaise qualité serait favorisé par la sélection. De même, un cycle de vie dont les stades successifs de développement ont des comportement de dispersion différents

peut être évolutivement stable même si l'environnement est stable mais qu'il est hétérogène (Greenwood-Lee et Taylor 2001). Là encore, différents patchs peuvent donc avoir des taux de dispersion différents en fonction, par exemple, de leur « qualité ». À une plus grande échelle, deux régions caractérisées par des variations spatiales plus ou moins prononcées de la qualité de l'habitat, devraient théoriquement être caractérisées par des contrastes dans l'intensité de la dispersion.

1.3.3. Dispersion sous l'effet de la sélection de parentèle

Troisièmement, même dans un habitat temporellement stable et géographiquement homogène, la dispersion peut évoluer sous l'effet de la sélection de parentèle. En effet, dans un habitat structuré, les individus d'un même patchs ont de fortes chances d'être apparentés. Si la densité locale est limitée par compétition, cette compétition s'exercera principalement entre individus apparentés. La dispersion, même si elle est coûteuse en terme de survie et/ou de probabilité de reproduction, peut alors permettre à un individu d'augmenter sa fitness inclusive en diminuant l'intensité de la compétition locale, favorisant ainsi indirectement ses apparentés (Hamilton et May 1977). L'intensité de la compétition, liée par exemple à la quantité de ressources disponibles peut donc être directement liée à l'intensité de la dispersion, ce que des études empiriques ont contribué à confirmer (voir Lambin et al. 2001 pour une revue critique).

1.3.4. Dispersion sous l'effet de la dépression de consanguinité

Enfin, la dispersion peut évoluer sous l'effet de la dépression de consanguinité. En effet, puisque les apparentés sont géographiquement groupés dans une population structurée, la probabilité est faible pour un individu migrant dans un patch dont il n'est pas lui-même issu de se reproduire avec un apparenté. La dispersion est donc un moyen d'échapper avec certitude aux éventuelles conséquences délétères des croisements consanguins, et les migrateurs obtiennent un gain en fitness qui peut contrebalancer le coût associé à la dispersion (Motro 1991). L'ampleur du gain en fitness des migrateurs dépendant de l'intensité de la dépression de consanguinité, dispersion et fardeau de consanguinité évolueront conjointement. À ma connaissance cependant, les modèles actuels d'évolution de la dispersion sous l'effet de la dépression de consanguinité considèrent que le fardeau de consanguinité est fixe dans l'espace

et dans le temps, tandis que les modèles d'évolution du fardeau considèrent soit une population homogène (Pollack 1995), auquel cas la notion de dispersion n'a pas de sens, soit que la dispersion est invariable en fixant la structure des populations (Whitlock 2002). Le modèle complet n'existe donc pas à l'heure actuelle (Gandon et Michalakis, 2001, Perrin et Goudet 2001, Ronce et al. 2001, S. Gandon comm. pers. 2002) et des données empiriques permettraient de mettre cette lacune en évidence.

1.3.5. Multiples facteurs pour l'évolution de la dispersion

Les forces responsables de l'évolution d'une forme de dispersion ont été considérées de façon isolée, chacune des quatre forces décrites précédemment (1.3.1 à 1.3.4) ayant été décrite dans un cadre formel relativement indépendant des autres. L'effort de formalisation permettant de traiter l'ensemble de ces forces dans un même cadre théorique pour comparer la magnitude de leurs effets est récent (Gandon et Michalakis, 2001, Perrin et Goudet 2001) et reste partiellement incomplet. Ces études ont cependant montré que les forces relatives de la variabilité temporelle de l'environnement, de la variabilité spatiale, de la compétition entre apparentés et de la dépression de consanguinité sont inégales. Ainsi, la variabilité temporelle semble être un puissant moteur de l'évolution de la dispersion, tandis que l'évitement de la dépression de consanguinité semble avoir un effet mineur s'il n'est pas accompagné d'une réduction de la compétition entre apparentés. L'effet principal de la dépression de consanguinité semble être de biaiser la dispersion entre mâles et femelles, la dispersion d'un seul des deux sexes étant suffisante pour éviter à l'autre sexe tout risque de croisement consanguin. Comme mentionné plus haut cependant, l'effet de la dispersion sur le fardeau de mutations délétères lui-même n'est pas pris en compte par ces modèles, bien que ce lien ait été démontré par Whitlock (2002).

1.3.6. La dispersion chez les salmonidés côtiers

1.3.6.1. L'anadromie comme trait permettant la dispersion

Les modèles théoriques considèrent généralement la dispersion comme un trait d'histoire de vie dont l'évolution est indépendante des autres traits d'histoire de vie. Cette non-spécification des contraintes de développement et des corrélations génétiques sous-jacentes est importante car elle les rend polyvalents et applicables à toutes les situations dès lors que les

capacité de dispersion sont variables et héritables (Roff et Fairbairn 2001). Mais la dispersion est un trait avec des composantes physiologiques, comportementales, et d'histoire de vie qui toutes contribuent à la probabilité qu'un individu disperse. Il est donc probable que les traits de dispersion soient corrélés directement ou indirectement à de nombreux autres traits liés à la fitness. C'est par exemple le cas chez le criquet *Grillus firmus* où le développement des ailes est génétiquement corrélé à la fécondité des femelles (Roff et al. 1999). C'est également le cas chez les salmonidés en milieu côtier où la dispersion implique l'expression d'une tolérance à l'eau salée qui ne se produit que chez une partie des individus (migration partielle). Le milieu côtier est en effet constitué de rivières (eau douce, habitat obligatoire pour de la reproduction et les jeunes stades de vie) disposées linéairement et séparées par une masse d'eau salée, barrière infranchissable pour les individus non-tolérants à l'eau salée. La (les) population(s) de chacune des rivières ne peut alors échanger de matériel génétique que si une fraction des individus est capable de traverser la barrière d'eau salée. Cette tolérance est conférée par un ensemble de modifications physiologiques associées aux migrations saisonnières anadromes entre l'eau douce et l'eau salée. Il convient ici de distinguer clairement la dispersion (appelée *égarement* chez les salmonidés) de la migration saisonnière anadrome sous l'angle de laquelle la tolérance à l'eau salée a été considérée presque exclusivement. Si l'expression de l'anadromie est une condition nécessaire à la dispersion, elle n'est pas suffisante, de nombreux individus regagnant leur rivière à l'issue de leur séjour en eau salée. La tolérance à l'eau salée confère cependant un potentiel de dispersion, qui peut alors s'interpréter à la lumière des modèles d'évolution de la dispersion formulés sous la simple hypothèse que la dispersion est un trait variable et héritable. La connaissance relativement précise des conséquences physiologiques et écologiques liées à l'expression de la tolérance font des salmonidés un modèle de choix pour étudier l'évolution de la dispersion jusque dans ses détails mécanistiques.

1.3.6.2. Expression de l'anadromie : physiologie, écologie et facteurs déclencheurs

L'expression de la tolérance à l'eau salée s'accompagne chez les salmonidés d'un ensemble de modifications physiologiques importantes. Le passage d'un milieu hyper-osmotique à un milieu hyposmotique nécessite l'inversion du système d'osmorégulation, permise par le développement des cellules à chloride et l'augmentation des niveaux d'expression de

l'enzyme Na^+K^+ATPase dans les branchies (revue dans Bœuf 1993). Ces modifications s'amorcent tôt dans la vie des futurs migrateurs, le contact avec l'eau salée constituant la dernière étape d'un long processus physiologique de préadaptation (smoltification). Souvent négligée chez l'omble de fontaine parce que moins évident que chez d'autres salmonidés, ce processus de smoltification a été mis en évidence tant chez des individus captifs (Besner et Pelletier 1991) qu'en populations naturelles (Boula et al. 2002).

De nombreux traits sont associés à l'expression de la tolérance à l'eau salée, et les individus non migrateurs et migrateurs des populations côtières de salmonidés ne diffèrent pas uniquement par leur tendance à migrer. Ces derniers ont aussi généralement une croissance juvénile plus faible, une plus grande longévité, des comportements territoriaux sur les frayères, et un patron d'itéroparité différent. Ils sont de livrée plus argentée, de forme générale plus longiligne, moins agressifs, et exposés à des communautés de parasites et de prédateurs plus vaste. En d'autres mots, l'anadromie est un événement majeur dans l'histoire de vie d'un salmonidé : exprimer la tolérance à l'eau salée, c'est modifier un vaste ensemble de paramètres d'histoire de vie liés directement ou indirectement à la fitness.

La migration anadrome semble déclenchée par plusieurs facteurs proximaux. Le processus de smoltification s'accompagne de variations hormonales importantes, impliquant les hormones thyroïdiennes (T_3, T_4, Boula et al. 2002), hypophysaires (Bœuf et al. 1994), et interrénales (cortisol, Boula et al. 2002). La productivité des eaux douces pendant les stades juvéniles semble également jouer un rôle, ainsi que la température de l'eau. Ces deux derniers facteurs, liés à la croissance juvénile, pourraient intervenir dans le cadre d'un système à seuil, la croissance étant alors corrélée à la « condition ».

Les bénéfices associés à la migration saisonnière sont généralement interprétés à la lumière de la forte productivité du milieu marin par rapport au milieu dulçaquicole (Gross et al. 1988). La valeur sélective de l'un et l'autre phénotype s'établit selon le rapport des bénéfices liés à l'accès aux réserves de nourriture abondantes par rapport aux coûts physiologiques (inversion du système d'osmorégulation), aux coûts énergétiques des déplacements, et aux risques de prédation et de parasitisme.

En résumé, la connectivité des populations de salmonidés côtiers est due à l'intensité de la dispersion. Cette dispersion ne peut se produire sans l'expression d'une tolérance à l'eau salée, qui est corrélée à un ensemble de traits d'histoire de vie. Pour comprendre les variations de la connectivité des populations, il faudrait idéalement s'intéresser à l'ensemble des relations complexes entre tous ces traits. Si cette tâche est pour l'instant impossible, une chose est pourtant certaine : la connectivité des populations peut évoluer dans le temps et varier dans l'espace. Il s'agit donc bien d'une variable dynamique, pour laquelle la relativement bonne connaissance des traits liés à la dispersion chez les salmonidés peut être mise à profit pour mettre empiriquement en évidence quelques aspects de cette dynamique.

1.4. Diversité d'aujourd'hui, histoire d'hier.

Les populations naturelles peuvent s'écarter de plusieurs façons des prémisses des modèles simples basés sur les propriétés asymptotiques de l'équilibre. L'organisation géographique de la diversité génétique résulte des contraintes que fait peser la structure de l'habitat sur les probabilités de coalescence entre allèles (1.2). Ceci n'est cependant vrai qu'en autant que ces événements de coalescence ont eu le temps de se produire. En effet, l'organisation de la diversité résulte de l'intégration au cours du temps de l'influence du paysage. La structure de la diversité ne reflètera donc la structure de l'habitat que si cet habitat est resté stable sur une période de temps suffisamment étendue. Les probabilités d'identités par descendance pourront alors être considérées comme stables dans le temps, toute trace des états transitoires de départ étant effacée.

1.4.1. Dynamique des habitats

Peu d'habitats restent cependant stables sur de très grandes périodes de temps, et ce à toutes les échelles spatiales. Ainsi, les aires de répartition sont des ensembles dynamiques qui fluctuent sous l'effet de multiples facteurs (Brown et al. 1996), dont les variations climatiques. Celles-ci se produisant en raison d'un forçage externe du climat par des variations, même légères, de l'orbite terrestre, cette observation s'applique à l'ensemble des espèces vivantes et a eu lieu de tout temps (Dynesius et Jansson 2000). Si l'effet des variations climatiques sur les aires de répartition a sans doute été moindre dans les régions tropicales, elle est incontournable dans les régions tempérées et polaires, où les fluctuations climatiques se sont traduites par

l'avancée et le retrait successif des calottes de glace (Davis and Shaw 2001). En Amérique du Nord, les habitats disponibles (non couverts de glace) ont ainsi constamment fluctué de façon importante, et l'habitat actuellement occupé par l'omble de fontaine dans l'est du Canada a donc connu d'importantes perturbations (Fig 2.2).

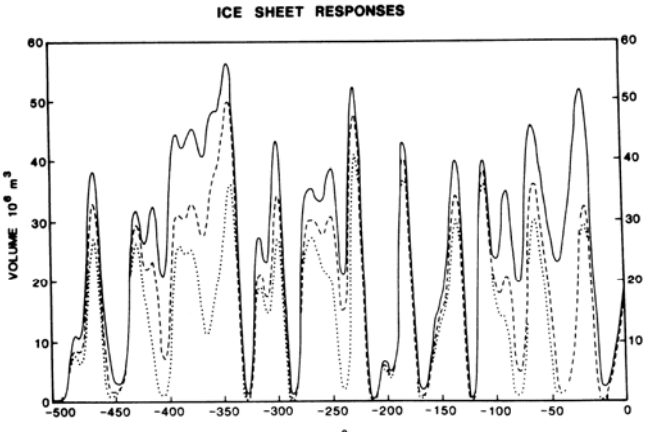

Figure 2-1. Variations du volume de la calotte glaciaire Laurentienne au cours des 500,000 dernières années (d'après Budd et Smith 1987). Remarquer la courte durée des interglaciaires, au cours desquelles les habitats nordiques son disponibles.

Les populations de l'espèce ont ainsi été à de nombreuses reprises repoussées au sud vers leurs refuges glaciaires puis décalées vers le Nord à la faveur du rétablissement de conditions propices à leur survie et leur reproduction. Il ne subsiste que peu de restes permettant de caractériser directement la dynamique de recolonisation de l'omble de fontaine suite au dernier événement de colonisation car il existe peu de sites archéologiques dans la région et que peu d'entre eux ont été fouillés (M. Courtemanche, Ostéothèque de Montréal, comm. pers.). Le rétablissement des conditions modernes de climat et de végétation peut cependant être inféré par les analyses paléoclimatiques et paléoécologiques basées sur les signatures isotopiques, biosédimentaires et palynologiques d'échantillons datés (voir par exemple de Vernal et Marcel-Hillaire 1987). Ces analyses révèlent que le retrait du glacier des régions entourant le Golfe du St-Laurent s'est amorcé vers –13,500 ans pour s'achever vers –10,000 ans. Les conditions climatiques modernes se sont alors rapidement établies entre –11,000 et –10,500 ans, suivies par les conditions de salinité vers –10,000 ans. Les premières traces de toundra boréale sont détectée entre 11,000 et 9,500 ans, tandis que les *Picea* s'établissaient lentement entre 9,500 et 6,500 pour finalement dominer entièrement la région entre 6,500 et

3,750 (de Vernal et al. 1993). S'il n'y a pas de données précises sur la colonisation par les proies invertébrés à la base de l'alimentation de l'omble de fontaine, la colonisation n'a pas pu se produire avant que l'écosystème dans son ensemble ne lui fournisse des conditions propices. S'il est difficile d'identifier avec précision ces conditions, quelques dates butoirs peuvent tout de même être avancées, la colonisation ne pouvant physiquement pas s'être produite avant le retrait du glacier. En tout état de cause, la colonisation est un phénomène récent et l'aire de répartition actuelle n'est occupée que depuis un maximum de 10,000 ans, qui, sous certaines hypothèses restrictives sur les conditions nécessaires, peut être ramené à 3,750 ans.

Si l'avancée d'une calotte de glace de 2000m d'épaisseur constitue un cas extrême de variation des caractéristiques de l'habitat, une espèce peut également être soumise à un régime de perturbations sein d'une aire de répartition aux contours stables. Il en résulte pour les populations d'une espèce une probabilité non nulle de s'éteindre à court ou à long terme, encore augmentée par le caractère stochastique de la dynamique des populations. Il semble alors évident que pour beaucoup d'espèces et de populations, l'histoire des perturbations qu'elles ont subi ont pu fortement marquer l'organisation géographique de leur diversité. Nous disposons pour l'omble de fontaine d'une relativement bonne connaissance des événements récents qui ont perturbé sa distribution dans l'est du Canada. Cette connaissance peut être mise à profit pour documenter avec précision les conséquences génétiques du décalage de l'aire de répartition suite au retrait du glacier.

1.4.2. Conséquences génétiques de la dynamique des habitats

1.4.2.1.Dynamique d'extinction/colonisation.

La colonisation d'un patch d'habitat peut soit augmenter soit diminuer l'intensité de sa différenciation avec les autres populations. Le paramètre critique est ici le nombre et l'origine des colonisateurs (Slatkin 1977). Avec peu de migrants provenant d'un petit nombre de patchs (propagule-pool model), la différenciation est accrue par rapport à une population stable. À l'inverse si les migrants sont issus d'un nombre important de patchs et qu'ils sont nombreux, leur composition génétique reflétera la composition génétique moyenne de la population générale, ce qui tendra à homogénéiser l'ensemble des patchs plus fortement que dans une

population stable. Ces deux situations extrêmes ont été développées par Slatkin (1993, Good's model of stepwise colonization) et par LeCorre et al. (1998) dans le cas de la colonisation progressive d'un habitat linéaire (chaque patch est colonisé à partir de migrants du patch voisin). Ces résultats montrent qu'un événement de colonisation peut perturber (en les augmentant ou en les diminuant) les niveaux de différenciation entre populations au sein d'une espèce. La concordance entre la structure du paysage et celle de la diversité génétique d'une espèce pourra donc être faible et dépendra en grande partie de la vitesse à laquelle les populations atteignent à nouveau leur niveau stable de différenciation.

1.4.2.2. Vitesse d'atteinte de l'équilibre migration / dérive.

En l'absence de toute migration et de mutation, un ensemble de populations isolées se dirigera vers la fixation de l'un des allèles présents à une vitesse déterminée uniquement par la taille *N* de chacune des populations.

$$t_{50} = \frac{-\ln 2}{\ln(1 - \frac{1}{2N})},$$

où t_{50} représente le temps nécessaire pour atteindre la moitié de la différenciation attendue à l'équilibre (Crow et Kimura 1970). Lorsque ces populations sont connectées par un taux de migration m, cette valeur devient

$$t_{50} = \frac{1}{2m + \frac{1}{2N}}$$

La vitesse de mise en place d'un patron d'isolement par la distance tel que décrit dans l'encadré 1 n'a à ma connaissance pas reçu de traitement analytique similaire. En conséquence, l'absence de signal d'isolement par la distance est généralement pris par les études empiriques de génétique des populations comme une indication que le système n'a pas atteint l'équilibre migration / dérive (par exemple Hellberg 1995, Baer 1998, Hutchison et Templeton 1999, Ehrich et Stenseth 2001).

1.4.3. Entre biogéographie et génétique des populations

Les données empiriques ont contribué peut-être plus clairement encore que les approches procédant par modélisation, à révéler la place importante des phénomènes historiques dans l'organisation géographique de la diversité génétique chez de nombreuses espèces. La répartition spatiale de certains polymorphismes (en particulier mitochondriaux) révèle en effet des patrons d'organisation largement indépendants de la structure de l'habitat et qui s'interprètent plus aisément dans un cadre biogéographique. Ce « pont » phylogéographique établi par les travaux de Avise et collaborateurs (1987) entre génétique moléculaire des populations et biogéographie, a été emprunté à l'occasion de nombreux travaux dans un grand nombre de taxons (revue dans Avise 2000). Il a contribué à la prise de conscience par de nombreux généticiens des populations que la diversité génétique est à certaines échelles géographiques plus un héritage historique qu'un reflet de l'interaction d'une espèce avec son environnement. Génétique des populations et biogéographie ont chacune beaucoup profité de ce rapprochement conceptuel. Le développement de marqueurs nucléaires plus variables s'est accompagné du raffinement des méthodes d'analyses, qui sont progressivement devenues moins descriptives et plus quantitatives. Des essais de formalisation de l'impact conjugué des effets écologiques et historiques ont été développés par Hutchison et Templeton (1999) et Templeton (1998).

1.5. Dynamique de l'organisation de la diversité génétique

Au cours de cette thèse de doctorat, je me suis efforcé de comprendre de façon aussi large que possible l'organisation spatiale de la diversité génétique chez l'omble de fontaine. J'ai opté pour une approche empirique aux bases comparatives, en cherchant à dégager à chaque échelle géographique les variables à l'origine des différences observées. Ainsi, au cours du premier chapitre de cette thèse, je me suis attaché à une description détaillée des patrons de concordance entre la structure de l'habitat et l'organisation de la diversité dans un ensemble de lacs et de rivière dans le Maine (USA). L'approche employée était donc de type « écologie du paysage » et se basait sur l'examen des corrélations observées. Le second chapitre de cette thèse était dédié à l'analyse spécifique de l'une de ces corrélations, observée entre la taille des lacs et l'intensité du déficit en hétérozygotes. Ce chapitre était structuré comme un test d'hypothèses dont l'objectif était d'évaluer la pertinence de trois explications proposées. Nous

proposions dans ce cadre une méthodologie originale basée sur l'analyse de données empiriques de génétique des populations. Le troisième chapitre profitait de l'existence d'un gradient temporel de colonisation postglaciaire de l'omble de fontaine le long de la côte est du Canada pour examiner la vitesse d'établissement des patrons d'organisation spatiale de la diversité chez des populations côtières anadromes d'omble de fontaine. L'évolution du patron d'isolement par la distance était particulièrement concernée car il existe peu de systèmes empiriques permettant ce type d'analyses sur des populations naturelles. De plus, les analyses des patrons d'isolement par la distance révélant généralement beaucoup de dispersion des observations autour de la régression linéaire théorique, il semblait important de chercher à déterminer si la mise en place progressive du patron ne permettrait pas d'expliquer une partie de cette dispersion. Si les analyses présentées dans ce chapitre mettent comme prévu en évidence une évolution progressive vers l'état d'équilibre, cette mise en place initiale n'est pas suivie de la stabilisation des patrons d'organisation. Une interprétation possible à cette observation inattendue est l'évolution de la forme de dispersion de l'espèce, la forme anadrome. Nous avons alors cherché à l'occasion du quatrième chapitre à comparer les individus migrateurs (anadromes) aux individus non migrateurs (résidents) de quatre rivières situées le long du gradient de colonisation. Globalement, ces résultats mettent en évidence quelques aspects de la dynamique de la diversité génétique chez l'omble de fontaine. Les variations que nous avons révélées des paramètres démographiques dans le temps et dans l'espace peuvent rendre contestable l'utilisation des outils statistiques d'analyse des données basés sur des modèles. Je propose donc dans le cinquième chapitre de procéder de manière strictement comparative pour identifier les variables responsables des contrastes dans les patrons d'organisation de la diversité génétique chez l'omble de fontaine et le saumon atlantique échantillonnés au sein des mêmes rivières.

2. Landscape structure and hierarchical genetic diversity in the brook charr *Salvelinus fontinalis* Mitchill

2.1. Résumé

Pour comprendre comment les espèces évoluent lorsque elles sont confrontées à un environnement particulier, il est nécessaire de mettre en évidence l'intensité, les causes et les conséquences de la distribution spatiale de la diversité génétique. Pourtant, l'identification des barrières intrinsèques à la migration liées à la structure de l'habitat demeure une tâche difficile pour le biologiste des populations. Dans cette étude, trente populations (771 individus) d'omble de fontaine (*Salvelinus fontinalis*, Salmonidae) issues de six bassins versants majeurs du Maine (É-U) ont été caractérisées à six locus microsatellites pour quantifier le rôle de différents aspects de l'habitat, tels sa taille, son altitude, sa connectivité contemporaine et historique dans les patrons d'organisation de la diversité génétique à trois échelles spatiales: celle des lacs, celle des bassins versants, et celle de l'ensemble des bassins versants. L'hétérozygotie attendue dans les populations était négativement corrélée à l'altitude mais pas à la taille des lacs. À l'inverse, l'intensité du déficit en hétérozygotes à l'intérieur des lacs était négativement corrélée à la taille de l'habitat. L'analyse hiérarchique de la variance génétique a révélé que l'intensité que la différenciation entre les bassins versants était étonnamment faible par rapport à la différenciation entre les populations d'un même bassin versant. Les bassins versants voisins St. John et Penobscot étaient caractérisés par des effets inverses de l'altitude et de la distance géographique sur les patrons de différenciation entre populations. Le patron de différenciation entre les bassins versants ne s'accordait ni à un modèle d'isolement par la distance ni à modèle de recolonisation graduelle. Globalement, cette étude a permis de mettre en évidence le rôle des aspects contemporains du paysage sur les patrons d'organisation de la diversité génétique à une petite échelle géographique (dans les populations et entre les populations d'un même bassin versant). À une échelle plus importante, le rôle de la structure contemporaine du paysage dans la différenciation observée entre les bassins versants semble mineur. Ce résultats s'ajoutent à un corpus empirique croissant tendant à montrer la généralité de l'absence d'atteinte des conditions d'équilibre migration-dérive dans une vaste gamme de taxons. Le développement de descriptions théoriques plus réalistes des systèmes hors d'équilibre apparaît donc comme une étape importante de notre compréhension des influences conjuguées de l'histoire et des facteurs écologiques dans l'organisation géographique de la diversité génétique, particulièrement dans les habitats jeunes tels les régions récemment déglacées.

2.2. Abstract

Explaining the extent, causes, and consequences of biotic distributions in space is fundamental to our understanding of how species evolve and cope with particular environments. Yet, identifying extrinsic barriers to migration imposed by landscape structure and predicting their impacts on intraspecific genetic diversity remains a major challenge in population biology. In this study, 30 populations (771 individuals) of brook charr (*Salvelinus fontinalis,* Salmonidae) representing six major river drainages from Maine, USA, were characterized at six microsatellite loci to quantify the role of landscape features, such as habitat size, altitude, contemporary and historical connectivity, in shaping genetic diversity at three spatial scales: within lakes, within river drainages, and among river drainages. Within-population expected heterozygosity was negatively correlated with altitude, whereas no significant correlation was observed with lake size. Conversely, the extent of heterozygote deficiency within lakes was negatively associated with habitat size. The hierarchical analysis of genetic variance revealed that the extent of among-drainage differentiation was unexpectedly low relative to the pronounced population structuring within drainage. Geographically proximate St. John and Penobscot River drainages were characterized by opposite effects of altitude and geographic distance in shaping the pattern of population differentiation within drainages. The geographic pattern of differentiation among drainages could not be accounted for either by an isolation by distance or by a stepwise range expansion model. Overall, this study provided evidence for the role of contemporary landscape features in shaping the observed pattern of genetic diversity at smaller geographic scales (within and among populations within river drainage). On a broader geographic scale, contemporary landscape structure appeared to be only a minor factor determining the observed pattern of genetic structuring among drainages. These results add to the increasing evidence for nonequilibrium conditions between drift and migration in a wide array of animal taxa. The development of more realistic theoretical descriptions of nonequilibrium population structure thus appears to be important to better understand the relative influence of historical and ecological factors in shaping genetic variation in young habitats, such as recently deglaciated areas.

2.3. Introduction

In species composed of large numbers of mobile individuals, extrinsic barriers to migration imposed by landscape features are particularly important in determining population genetic structure. Yet, the identification of such barriers and the prediction of their impacts in shaping intraspecific genetic diversity remain a major challenge in population biology (Slatkin 1985 ; Sork et al. 1999 ; Wiegand et al. 1999). Studies dealing with the effect of landscape in shaping population structure have largely focused on the consequences of habitat fragmentation caused by recent anthropogenic disturbance (e.g., Aldrich et al. 1998 ; Gibbs 1998 ; Van Dongen et al. 1998). Although obviously relevant, such studies generally lack a historical perspective on the influence of landscape structure on temporal dynamics of genetic connectivity among natural populations (but see Fahrig and Merriam 1994 ; McCauley 1995 ; McCauley et al. 1995). Consequently, there is a need for detailed empirical studies that simultaneously quantify the effects of individual landscape features at various geographic scales (Shaw et al. 1994 ; Kudoh and Whigham 1997 ; Keyghobadi et al. 1999 ; Sork et al. 1999).

In this study, we use microsatellite loci to test specific hypotheses about the role of historical and contemporary landscape features in shaping the hierarchical pattern of genetic diversity in the brook charr, *Salvelinus fontinalis* Mitchill. This salmonid is endemic to eastern North America (McCrimmon and Campbell 1969) and inhabits lakes connected by streams, which are themselves potential habitats for the species (Power 1980). Thus, opportunities for migration are highly constrained by patterns of hydrographic networks. The extensive life history (Hutchings 1990) and genetic (Angers and Bernatchez 1998) differences found at all geographic scales in brook charr suggest that genetic exchanges are extremely reduced among populations from different lakes, which therefore act as discrete and independent demographic units. Assuming that habitat and effective population size are correlated, we first tested the hypothesis that lake area should be positively correlated with the levels of intrapopulation genetic diversity (Crow and Kimura 1970 ; Frankham 1996 ; Hanfling and Brandl 1998).

Although rarely taken into account (but see Hernandez-Martich and Smith 1990 ; Shaw et al. 1991, 1994 ; Angers et al. 1999), altitude may also influence the levels of diversity in freshwater habitats. High-altitude populations are expected to be more physically isolated, either because of increased probability of physical barriers to gene flow (e.g., impassable

waterfalls) and/or due to more pronounced founder effects, assuming that the number of colonists decreased with altitude. Therefore, a second hypothesis was that the extent of genetic divergence among populations should correlate with the altitudinal difference in their locations. Because movements of brook charr have been shown to be geographically restricted in riparian habitats (Gowan and Fausch 1996), we also tested the hypothesis that isolation by distance should contribute to population differentiation within river drainages. Migration among river drainages can only be achieved by anadromous individuals. Direct (Smith and Saunders 1958) as well as indirect estimates (V. Castric, unpubl. data) suggest that dispersal of anadromous individuals is limited to coastal waters and geographically restricted. Therefore, isolation by distance is also predicted to occur among drainages.

North American biota have been extensively influenced by the last glacial age (Pielou 1991). No freshwater habitats were available in Maine until the region was deglaciated, approximately 12,700–13,000 years ago (Borns et al. 1985 ; Dyke and Prest 1987). Following glacier retreat, a marine invasion (saltwater intrusions) in the coastal plain prevented establishment of freshwater fish communities until at least 12,100–11,000 years ago (Stuiver and Borns 1975). Recolonisation from the closest glacial refugia (so-called Acadian and Atlantic; Danzmann et al. 1998 ; Fig. 1) was therefore impossible before this time. Eurhyaline fishes, such as brook charr, most likely took advantage of their physiological tolerance to saltwater to reinvade previously ice-covered areas via coastal dispersal (Black et al. 1986). Thus, given the relatively short evolutionary time since the postglacial settlement of brook charr populations, we tested the hypothesis that the patterns of genetic differentiation among brook charr from different drainages still reflect the sequence of successive founding events from one river drainage to another.

2.4. Materials and Methods

2.4.1. Sampling Design

A total of 771 individuals were collected from Maine at 30 locations (22 lakes and eight brooks) representing six major river drainages during summers 1997 and 1998 (Table 1 , Fig. 1). There is no record that these populations have ever been stocked, so we considered them to be native. Adipose fins were removed non-destructively and preserved in 95% ethanol.

2.4.2. Detection of Microsatellite Polymorphism

Total DNA was extracted following a quicklysis protocol (Olsen et al. 1996). Quantification of genetic variation was performed using six microsatellite loci specifically developed for brook charr (SFO-8, SFO-12, SFO-18, SFO-23; Angers et al. 1995), brown trout (*Salmo trutta,* MST-85; Presa and Guyomard 1996), or Atlantic salmon (*Salmo salar,* SSA-197; O'Reilly et al. 1996). Two simultaneous triplex polymerase chain reactions (PCRs; SFO-8, SFO-12, MST-85 and SFO-18, SFO-23, SSA-197) were conducted using 1 l of the DNA extract (Hébert et al. 2000) . A volume of 0.8 l of each PCR product was mixed with 2 l of blue formamide containing 10% of GS350 internal size standard (TAMRA 350 bp) and loaded on a 5% polyacrylamid gel for a 2.25-h electrophoresis at 3000 V using an ABI 377 automated DNA sequencer (Perkin-Elmer, Foster City, CA). The fragment sizes were determined in reference to a size standard run in each lane using the softwares GENESCAN version 2.1 and GENOTYPER version 2.0 (Perkin-Elmer). A reference brook charr sample with known allele size (Angers and Bernatchez 1997) was run on each gel to ensure homogeneity of results across gels and to avoid scoring bias when comparing our results to previously published datasets (Angers and Bernatchez 1998 ; Hébert et al. 2000).

2.4.3. Genetic Data Analysis

For each hierarchical level (within population, among populations within drainage, among drainages), we first estimated the parameters of genetic polymorphism and then quantified the correlation between these estimates and landscape physical features.

2.4.3.1.Intrapopulation genetic diversity

Within-population genetic diversity was quantified as the number of alleles per locus (A), observed heterozygosity (H_O), and the unbiased estimate of heterozygosity corrected for the sampling bias (H_E; Nei 1987). Deviations from Hardy-Weinberg equilibrium (HWE) in each site were investigated using an approximation of an exact test based on a Markov chain iteration as implemented in GENEPOP version 3.1 (Raymond and Rousset 1995). Multilocus values of significance for HWE tests were obtained following Fisher's method to combine probabilities of exact tests. Critical significance levels for multiple testing were corrected following the sequential Bonferroni procedure (Rice 1989).

The extent of deviation from HWE proportions was quantified by Weir and Cockerham's (1984) estimator of $F_{IS}(f)$ at each locus and at each site using GENETIX version 4.0 (Belkhir et al. 1998). We tested whether the same loci consistently exhibited stronger f using Kendall's concordance method (Sokal and Rohlf 1981).

We then considered the possible impact of habitat size and altitude on population parameters estimates H_E and f (whenever f was positive). Because it was impossible to reliably quantify habitat size for brooks, this parameter was only quantified for lakes. Because H_E and f may not be distributed normally, all correlations were nonparametrically tested using Spearman R available in STATISTICA version 4.5 (Statsoft 1993).

2.4.3.2.Hierarchical population structure

The null hypothesis of homogeneity in allele frequencies was tested using the exact test for population differentiation in GENEPOP. The extent of population differentiation was then quantified by Weir and Cockerham's (1984) estimator of $F_{ST}(\theta)$, based on the variance in allele frequencies and Michalakis and Excoffier's (1996) estimator of $\rho_{ST}(\Phi_{ST})$, incorporating variance in allelic size. These two parameters behave differently with regard to drift and mutation and their comparison can provide insights into the historical time frame involved in population differentiation (Rousset 1996 ; Goodman 1998). We then performed a hierarchical analysis of genetic variation (AMOVA) implemented in ARLEQUIN version 1.1 (Schneider et al. 1997) to quantify the amount of genetic variance imputable to drainage subdivision.

Cavalli-Sforza and Edwards's (1967) chord distance (D_{CE}) was used to construct a population phenogram using Saitou and Nei's (1987) neighbor-joining algorithm. D_{CE} was chosen because it leads to a higher probability of depicting the correct tree topology (Takezaki and Nei 1996) and because this measure involves no assumption regarding constant population size or equal mutation rates among loci. Previously published data for brook charr from La Mauricie National Park, Canada (Angers and Bernatchez 1998) were also included in this analysis to compare the congruence in overall pattern of population structuring between geographically remote areas. SEQBOOT, GENEDIST, NEIGHBOR, and CONSENSE computer programs implemented in PHYLIP version 3.5 (Felsenstein 1993) were used to build the tree from allele frequencies data obtained from GENETIX. Confidence in tree topology was assessed by bootstrapping over loci (2000 iterations).

2.4.3.3.Patterns of differentiation within drainages

As shown in Rousset (1997) , a linear relationship is expected between waterway distance and $F_{ST}/(1-F_{ST})$ when dispersal is geographically limited in a linear array of populations. Mantel tests (Mantel 1967) were thus used to test the significance of this correlation in St. John and Penobscot, the two drainages in which a sufficient number of sites were sampled. Probability values for no correlation were estimated using the permutation procedure (n = 2000) in GENETIX. To assess whether populations were at migration-drift equilibrium under isolation by distance in one dimension, we computed the slope of $\log[F_{ST}/(1-F_{ST})]$ against log(distance). Equation (7) in Rousset (1997) predicts a positive slope of approximately one under equilibrium conditions.

Physical barriers to migration, such as impassable waterfalls, are expected to have a strong impact on genetic exchanges among populations. We assumed that such barriers were more frequent among sites separated by high altitudinal differences, and consequently defined the sum of altitude differences as the sum of altitude variation along the shortest waterway between each population pair. Thus, if populations 1 and 2 have elevation h_1 and h_2, respectively, and their first common node on the hydrographic network has elevation h_N, the sum of altitude differences between populations 1 and 2 is $(h_1-h_N) + (h_2-h_N) = h_1 + h_2-2h_N$. This distance would be greatest between two populations located on mountain tops, moderate

between one population of high altitude and one of low altitude, and lowest between two low-altitude populations. It is unclear, however, what relationship should be expected between the sum of altitude differences and genetic differentiation, because there is no specific theoretical background to support the use of $F_{ST}/(1-F_{ST})$ in such circumstances. Consequently, we used D_{CE} genetic distance, for which basic assumptions are less restrictive than for F_{ST}. Mantel tests were used to test the correlation between D_{CE} and the sum of altitudinal differences (2000 permutations).

2.4.3.4.Differentiation patterns among drainages

We also tested whether isolation by distance occurred among drainages. Genetic differentiation among drainages (subscript D) was estimated by F_{DT}, the hierarchical *F*-statistic associated with this component of genetic variance in the AMOVA framework based on allele frequency data. Coastal distances were measured on 1:50,000 topographic maps by closely following the contemporary coastline from one river mouth to the other. Mantel tests were used to test the significance of the regression of pairwise $F_{DT}/(1-F_{DT})$ on coastal distances (2000 permutations).

Brook charr populations in Maine most likely originated from either an Atlantic or an Acadian refugium (Danzmann et al. 1998) and probably recolonized previously ice-covered areas via coastal dispersal (Black et al. 1986). Therefore, we tested whether the observed patterns of genetic differentiation among drainages could be explained by a postglacial recolonization from these putative refugia. Slatkin (1993) provides one of the only available frameworks to predict the expected patterns of genetic differentiation under nonequilibrium conditions. A directional and gradual stepwise range expansion, referred to as Good's model in Slatkin (1993) , is expected to result in greater divergence among earlier founded populations than among more recently founded ones, independently of the geographic distance among them. For example, assuming that recolonization of Maine watersheds by brook charr occurred from southwest to northeast, Androscoggin drainage (see Fig. 1) would have been colonized first and one would predict southwestern populations to be most highly differentiated because they underwent genetic drift for a longer time. Good's model was thus used to assess whether the observed pattern of genetic differentiation fitted the alternative expectations of either

southwest-northeast recolonization from an Atlantic refugium or a northeast-southwest recolonization from an Acadian refugium. Under the hypothesis of an Atlantic origin of Maine populations, we plotted for each pair of drainages $(1/F_{DT}-1)/4$ against *i,* the coastal distance between the oldest drainage of a given pair and the Androscoggin River (the drainage that would have settled first under this scenario). Mantel's test was used to test the significance of the correlation (2000 iterations). Conversely, under the hypothesis of an Acadian origin, we considered the regression of $(1/F_{DT}-1)/4$ against *j,* the coastal distance between the oldest drainage of a given pair and the St. John River.

2.5. Results

2.5.1. Intrapopulation Genetic Diversity

All six microsatellite loci were highly polymorphic, with the number of different alleles observed across all populations (*A*) ranging from 10 (SSA-197) to 57 (SFO-8) and mean within population unbiased heterozygosity H_E ranging from 0.40 (SFO-12) to 0.81 (SFO-8; Appendix). The exact test of HWE showed a significant global trend toward heterozygote deficiency (f = 0.0807, $P < 0.001$). Seven populations exhibited significant departures from Hardy-Weinberg proportions following sequential Bonferroni correction (P = 0.0017, = 0.05, k = 30). Details on *f*-values are presented in Appendix. This global deficiency was not caused by one particular locus, as four out of the six screened loci deviated significantly from Hardy-Weinberg expectations following Bonferroni correction (P = 0.008, = 0.05, k = 6; Appendix). Furthermore, Kendall's test of concordance showed that the ranks of all loci according to *f*-values were not consistent across populations (P = 0.4653).

2.5.2. Intrapopulation Diversity Versus Landscape Features

We observed a significant negative correlation (P = 0.0381) between altitude and mean expected heterozygosity (H_E), whereas no significant association (P = 0.7110) between lake size and H_E was apparent (Fig. 2A, B , respectively). Conversely, the extent of heterozygote deficiency (f) was not associated with altitude (P = 0.2017) but was negatively correlated (P = 0.0145) with lake size (Fig. 2C, D , respectively). No correlation was found between lake size and altitude (P = 0.312), which ensured the independence of altitude and lake size effects. Noticeably, three out of the four populations exhibiting the highest allelic diversity (J1, J2, J7) were from riparian habitats (stream, river, and brook, Appendix).

2.5.3. Hierarchical Population Structure

Highly significant heterogeneity in allele frequencies was found in all pairwise comparisons for at least one locus ($P < 0.001$; data not shown), which confirmed that brook charr found in different locations compose genetically distinct populations. Overall F_{ST} and

ρ_{ST} estimates were very similar but pairwise comparisons were highly variable (mean F_{ST} = 0.216, range = 0.016–0.465; mean ρ_{ST} = 0.208, range = 0.011–0.718).

The hierarchical analysis of genetic variance revealed that a significant (F_{DT} = 0.037, P = 0.002) component of allelic variance was explained by drainage structure. However, the extent of among-drainage differentiation was very low relative to the pronounced interpopulation structuring within drainage (F_{SD} = 0.203). When assuming a stepwise mutation model, the estimate of differentiation among drainages was lower than F_{DT} (ρ_{DT} = 0.024) and not significantly different from zero (P = 0.2082).

The population phenogram inferred from D_{CE} distance further illustrated the overall lack of population grouping by drainage or any other type of hierarchical clustering among Maine populations. The tree was starlike, with all branches of approximately equal length, and generally poorly supported (Fig. 3). When compared with La Mauricie National Park, Maine populations tightly clustered together and were genetically more similar as illustrated by shorter branch lengths, despite the fact that they were sampled over a much broader geographic scale (Maine: 86,156 km^2 vs. La Mauricie: 544 km^2).

2.5.4. Contrasting Patterns of Differentiation within Drainages

The Penobscot and St. John River drainages were characterized by differential effects of landscape features on the genetic structure. In the St. John drainage, a strong positive correlation was observed between D_{CE} and the sum of altitudinal differences (Fig. 4A ; Mantel test, Z = 3423, P = 0.0055). However, no pattern of isolation by distance was apparent, as the extent of population differentiation did not depart significantly from a randomized association between $F_{ST}/(1-F_{ST})$ and waterway distance (Fig. 4B ; Mantel test, P = 0.533). The Penobscot drainage populations showed the reverse pattern. Genetic divergence was not correlated with the sum of altitudinal differences (Fig. 4C ; Mantel test, Z = 5306, P = 0.576), whereas waterway distance was marginally correlated with $F_{ST}/(1-F_{ST})$ (Fig. 4D ; Mantel test, Z = 5458, P = 0.0556). The slope (0.33) of $\log[F_{ST}/(1-F_{ST})]$ on log(distance) in this drainage was far from the value of one expected at migration-drift equilibrium.

2.5.5. Patterns of Differentiation among Drainages

The geographic pattern of differentiation among drainages could not be accounted for either by isolation by distance or by a stepwise range expansion model. We observed, however, a statistical trend (Mantel test, $Z = 2.3032$, $P = 0.0755$) for a reversed isolation by distance pattern, that is, greater genetic similarity with increased coastal distance among drainages. Good's model yielded nonsignificant outcomes for the two alternative hypotheses of gradual recolonization from an Atlantic or an Acadian refugium (Mantel tests $Z = 734$, $P = 0.424$ and $Z = 910$, $P = 0.286$, respectively).

2.6. Discussion

The main objective of this study was to test specific hypotheses regarding the role of historical and contemporary landscape features in shaping the pattern of genetic diversity in the brook charr, *S. fontinalis* Mitchill. Overall, this study provided evidence for the role of contemporary landscape in shaping the observed pattern of genetic diversity at smaller geographic scales (within and among populations within river drainage). The detected consequence of habitat features, however, generally differed from a priori predictions. On a broader geographic scale, the role of contemporary landscape features appeared to be only a minor factor determining the observed pattern of genetic structuring among drainages.

The finding of lower heterozygosity in populations of higher elevation was congruent with the results of recent empirical studies in other fishes, such as the guppy *Poecilia reticulata* (Shaw et al. 1994); mosquitofish, *Gambusia holbrooki* (Hernandez-Martich and Smith 1990); and brown trout, *Salmo trutta* (Hamilton et al. 1989). At higher altitude, populations are more likely to be isolated by waterfalls, whereby unidirectional downstream gene flow is more likely to occur. Habitats at higher altitudes may also have become isolated earlier. As for all regions covered by glaciers, an isostatic rebound (crustal upheaval) occurred in Maine following removal of the weight of the 2.2-km thick ice sheet (Stuiver and Borns 1975). This in turn may have caused a lag in the timing of population settlement in habitats of different altitudes. Although habitat size is commonly used to infer population census size and thus diversity, such a trend was not detected in this study. This could first reflect the difficulty of reliably quantifying habitat size. Namely, surface lake area alone may not accurately reflect the complex ecological interactions that determine the carrying capacity of lacustrine habitats for brook charr. For instance, the availability of spawning grounds (Blanchfield and Ridgway 1997) and the relative abundance of other species (Magnan 1988) could also influence charr abundance in different lakes. Alternatively, the absence of correlation between habitat size and genetic diversity may indicate the persistent effect of founder events. Freshwater communities in Maine are approximately 11,000 years old (Stuiver and Borns 1975) and brook charr populations may be even younger because they could not become established prior to their invertebrate preys. Consequently, it is likely that mutation-drift equilibrium may not have been reached yet. As such, the levels of intrapopulation diversity may be more reflective of the

allelic diversity in founding populations of differential abundance, rather than contemporary censuses.

Highest allelic diversity was observed in stream populations despite much smaller habitat size, as was recently observed for brook charr populations (Angers et al. 1999 ; Hébert et al. 2000). This suggests that lacustrine and stream populations are characterized by contrasting demographic dynamics. For instance, restricted gene flow among genetically differentiated subpopulations within streams would lead to increased genetic diversity relative to a single panmictic population of the same census size (Whitlock and Barton 1997). A more detailed comparison of fine-scale genetic and demographic structure between lacustrine and riverine populations is required to confirm this hypothesis.

Our data revealed a significant heterozygote deficiency, which was mainly attributed to a significant trend toward higher heterozygote deficiencies in smaller lakes. Technical artifacts were unlikely to cause this pattern, as the observed deficit was not locus-specific. Moreover, previous studies using the same loci (Angers and Bernatchez 1998 ; Hébert et al. 2000) found no evidence of departures from Hardy-Weinberg equilibrium. At least two alternative explanations could account for this observation, the most likely being admixture of differentiated gene pools. Dynes et al. (1999) recently provided evidence for a slight genetic differentiation between benthic and limnetic lacustrine forms of brook charr in another area of the species range. The possible existence of such sympatric forms in Maine is reinforced by the fact that this area is a known zone of secondary contact between genetically and morphologically differentiated glacial races of other fishes, such as whitefish, *Coregonus clupeaformis* (Bernatchez and Dodson 1990), and rainbow smelt, *Osmerus mordax* (Taylor and Bentzen 1993). Also of note, sympatric pairs of lake whitefish are known to occur mainly in smaller lakes (G. Lu, pers. comm.). Increased probability of relatedness among sampled individuals could also conceivably explain the more pronounced heterozygote deficiencies in smaller lakes. Limited number of spawners could generate a Wahlund effect due to genetic differences among fish using different spawning grounds at a given reproduction event in smaller lakes. Increased availability of spawning areas in larger lakes may potentially buffer this effect. We are currently investigating this possibility.

The overall level of differentiation observed in brook charr populations from Maine was relatively modest when compared to that reported in previous studies. For example, the overall F_{ST}-value was 40% lower than that reported by Angers and Bernatchez (1998) in La Mauricie National Park at a much smaller spatial scale (F_{ST} = 0.37 with the greatest linear geographic distance of 42 km compared to a maximum of 375 km in this study). The observed level of population differentiation more resembled that observed recently on a much smaller geographic scale (F_{ST} = 0.28, maximum linear distance = 13 km) by Hébert et al. (2000) . Furthermore, starlike tree topology, low bootstrap support, and the hierarchical analysis of molecular variance all indicated that hierarchical population structuring by drainage was very weak. These results are also in sharp contrast with most studies of genetic variation in freshwater fishes, which generally reported that drainage structure represent a major constraint to gene flow (Gyllenstein 1985 ; Currens et al. 1990 ; Carvalho et al. 1991 ; Ward et al. 1994 ; Estoup et al. 1998 ; but see Avise and Felley 1979 ; Hernandez-Martich and Smith 1990). Lack of structuring by drainage could result from extensive gene flow via coastal dispersal among drainages. However, highly significant population differentiation has been recently observed among neighboring (less than 10 km) anadromous populations in other areas (V. Castric, unpubl. data), suggesting that this factor alone would be insufficient to homogenize allele frequencies among drainages in Maine. Artificial stocking with populations from one drainage into another cannot be entirely ruled out. However, such practices have not been reported in the region (F. Bonney, unpubl. data) and thus appear unlikely to have heavily weakened a signal of drainage differentiation.

Paleodrainages have been deeply modified by the isostatic rebound since the glacial retreat. Consequently, temporal instability in drainage isolation could also reduce genetic differentiation among populations from separate river systems. For instance, although their river mouths are separated by approximately 200 km, the headwaters of the St. John and Penobscot drainages are geographically proximate in central Maine. Thus, hydrographic changes such as drainage capture or disrupted stream connections could have intermittently allowed genetic exchanges among populations from different drainages. In such a case, however, formerly connected populations should cluster together, which was clearly not the case here. Finally, it is also possible that the apparent lack of structuring by drainage partly

reflect departure from migration-drift equilibrium, implying that time since population founding (approximately 2000 generations) has been insufficient for genetic differences to accumulate at this spatial scale.

Another salient feature of this study was the observation that geographically proximate drainages (Penobscot and St. John River) were characterized by differential effects of landscape features on genetic structure. Isolation by distance was responsible for shaping population differentiation in the Penobscot River drainage, whereas a correlation between genetic divergence and altitudinal differences was observed within the St. John drainage. The sum of altitude differences was used as a surrogate for the number of impassable falls and thus for the intensity of physical isolation. A significant effect of this parameter on population structuring in the St. John River therefore indicates that restricted gene flow caused by these barriers may be mainly responsible for population divergence within the St. John relative to the Penobscot River drainage. Because the variance around F_{ST} estimates is not known under pure isolation by distance models, the lack of correlation between $F_{ST}/(1-F_{ST})$ and distance does not entirely rule out the possibility that dispersal is not geographically restricted within the St. John drainage. However, the sharp contrast between both drainages strongly suggested that the landscape features shaping genetic structure are not concordant.

At a larger scale of landscape structure, Good's model failed to detect a signature of progressive recolonization, either from a northern or from a southern refugium. Given the rarity of empirical tests of this model (Jackman and Wake 1994 ; Hutchison and Templeton 1999), and the relatively small number of comparisons we used to apply it, we cannot rule out the possibility that limited statistical power was responsible for this outcome. Alternatively, rapid range expansion (Slatkin 1993), rather than stepwise recolonization, could possibly account for the unexpected trend for increased genetic similarity among more geographically distant drainages. Under this scenario, isolation by distance is expected among nearby but not among distant populations until the system reaches migration-drift equilibrium. Sampling over a broader geographical scale may be needed to clarify this issue.

In summary, this study revealed substantial variation in the influence of landscape features on contemporary patterns of genetic structure in brook charr, both spatially and temporally.

Other empirical studies in freshwater fishes (Ryman 1983 ; McClenaghan et al. 1985 ; Crozier and Ferguson 1986 ; Moran et al. 1995 ; Baer 1998 ; Hansen and Mensberg 1998) also reported limited correlations between indirect estimates of gene flow and potential for dispersal among populations within structured habitats. Similarly, nonequilibrium conditions between drift and migration are increasingly reported for a wide array of animal taxa, particularly when considering population structure over a broad geographic scale (e.g., Larson et al. 1984 ; Boileau et al. 1992 ; Hellberg 1995 ; Baer 1998). The development of more realistic theoretical descriptions of nonequilibrium population structure thus appears to be important for a better understanding of the relative influence of environmental and ecological factors in shaping genetic variation in young habitats, such as recently deglaciated areas (Slatkin 1993 ; Templeton 1998 ; Beerli and Felsenstein 1999 ; Hutchison and Templeton 1999).

2.7. Acknowledgments

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Table 2-1 Location and physical features of the sampling sites in Maine. Habitat size was not quantified for streams, rivers and brooks.

Population	Code	Drainage	*N*	Latitude	Longitude	Altitude (m)	Size (ha)
Kennebago Lake	A1	Androscoggin	25	70°46′21″	45°08′08″	359	688
Upper Flood Lake	C1	Ste. Croix	22	67°53′22″	45°22′36″	183	100
Trout Lake	C2		30	67°49′05″	45°22′05″	241	20
B-Stream	J1	St. John	32	67°54′41″	46°11′54″	183	—
Little Machias River	J2		30	68°33′10″	46°43′18″	207	—
Brown Brook Pond	J3		30	68°54′24″	46°25′02″	414	24
Third Wallagrass Lake	J4		18	68°49′16″	47°06′44″	301	182
Deboullie Lake	J5		23	68°51′21″	46°57′54″	344	1060
Third Pelletier Brook Lake	J6		31	68°53′25″	47°02′00″	379	336
McQueen Brook	J7		34	69°07′15″	46°54′12″	293	—
Robbins Brook Pond	J8		28	69°10′01″	46°43′27″	405	109
Ross Lake	J9		26	69°37′21″	46°29′36″	366	1171
Johnson Pond	J10		22	69°34′54″	46°19′10″	319	797
Lost Pond	J11		17	69°47′32″	46°06′44″	599	182
Rock Pond	K1	Kennebec	22	70°23′29″	45°27′42″	499	502
Massachussets Bog	K2		16	70°47′27″	45°20′37″	509	121
Round Pond	K3		30	69°45′38″	45°24′54″	449	243
Prick Pond	K4		23	70°31′02″	45°26′43″	753	2
Clark Meadow Brook	N1	Narraguagus	15	68°08′44″	44°40′49″	84	—
Narraguagus Lake	N2		8	68°08′41″	44°39′29″	68	1724
Little Moxie Pond	P1	Penobscot	31	69°43′28″	45°18′35″	397	295
Horseshoe Pond	P2		23	69°24′10″	45°30′30″	448	648
Baker Pond	P3		28	69°24′45″	45°32′12″	503	4
Beaver Pond	P4		22	69°09′27″	45°48′12″	320	12
Sourdnahunk Lake	P5		31	69°05′47″	46°02′30″	421	565
Bean Pot Pond	P6		20	69°42′42″	46°03′20″	407	210
Clish Pond	P7		29	70°15′33″	46°01′10″	550	85
Hathorn Pond	P8		29	68°46′01″	46°00′22″	274	61
Hay Pond	P9		29	68°45′09″	46°10′03″	195	542
Fourth Lake	P10		19	69°10′06″	46°16′13″	298	26

Table 2-2 Microsatellite polymorphism and departures from Hardy-Weinberg proportions. A, number of alleles observed in the sample; H_E and H_O, expected and observed heterozygosities; *f*, Weir and Cockerham (1984)'s F_{IS} estimate; P(HW) is the combined P-value of exact tests of HWE using Fisher's method. Significant values following Bonferroni correction are in bold (k=30 for multilocus values and k=6 for single-locus values).

		Populations										
		A1	C1	C2	J1	J2	J3	J4	J5	J6	J7	J8
SFO-12	*A*	3	3	4	6	4	3	4	2	1	5	6
	H_E	0.15	0.50	0.57	0.57	0.64	0.50	0.67	0.05	0	0.64	0.71
	H_o	0.16	0.36	0.39	0.47	0.60	0.53	0.50	0.05	0	0.74	0.57
	f	−0.049	0.282	**0.314**	0.185	0.064	−0.058	0.261	0	—	−0.146	0.197
SFO-18	*A*	5	5	3	9	6	2	5	3	4	7	7
	H_E	0.48	0.67	0.65	0.80	0.75	0.50	0.64	0.27	0.31	0.71	0.71
	H_o	0.32	0.62	0.57	0.84	0.77	0.30	0.75	0.20	0.32	0.53	0.57
	f	0.34	0.078	0.124	−0.052	−0.025	0.408	−0.176	0.273	−0.053	0.255	0.201
SFO-23	*A*	15	4	9	15	13	9	11	11	4	21	9
	H_E	0.87	0.59	0.79	0.90	0.89	0.79	0.86	0.87	0.69	0.95	0.87
	H_o	0.80	0.59	0.83	0.83	0.78	0.83	0.75	0.95	0.63	0.91	0.78
	f	0.083	−0.007	−0.044	0.075	0.124	−0.057	0.137	−0.105	0.082	0.043	0.111
SFO-8	*A*	14	7	8	13	15	8	10	12	4	21	12
	H_E	0.87	0.79	0.68	0.88	0.93	0.73	0.89	0.84	0.57	0.95	0.78
	H_o	0.88	0.77	0.38	0.70	0.87	0.57	0.80	0.74	0.27	0.81	0.58
	f	−0.015	0.023	**0.438**	0.206	0.071	0.224	0.106	**0.118**	**0.54**	**0.153**	**0.254**
SSA-197	*A*	2	2	3	3	3	3	4	5	4	5	6
	H_E	0.04	0.50	0.54	0.23	0.42	0.63	0.60	0.55	0.59	0.66	0.71
	H_o	0.04	0.59	0.43	0.19	0.38	0.69	0.61	0.52	0.64	0.58	0.58
	f	0	−0.182	0.198	0.181	0.099	−0.099	−0.019	0.041	−0.098	0.127	0.193
MST-85	*A*	12	5	6	9	11	5	6	5	6	11	7
	H_E	0.88	0.42	0.56	0.77	0.87	0.76	0.77	0.61	0.70	0.82	0.76
	H_o	0.88	0.20	0.45	0.88	0.83	0.73	0.67	0.39	0.71	0.74	0.71
	f	−0.004	**0.532**	**0.202**	−0.136	0.046	0.041	0.132	**0.365**	−0.013	0.104	0.058
Global	*A*	8.5	4.33	5.5	9.16	8.66	5	6.66	6.33	3.83	11.67	7.83
	H_E	0.55	0.58	0.63	0.69	0.75	0.65	0.74	0.53	0.48	0.79	0.76
	H_o	0.51	0.52	0.51	0.65	0.70	0.61	0.68	0.48	0.43	0.72	0.63
	f	0.0648	0.0993	**0.1962**	**0.0605**	0.0629	0.0678	0.0826	0.1036	**0.1002**	0.0937	**0.1671**
	P(HW)	0.1606	0.0046	<0.0001	0.0004	0.0705	0.1812	0.1812	0.0004	0.0005	0.0049	0.0054

		Populations									
		J9	J10	J11	K1	K2	K3	K4	N1	N2	P1
SFO-12	*A*	3	3	1	4	3	2	3	3	2	3
	H_E	0.33	0.57	0	0.69	0.51	0.34	0.56	0.58	0.50	0.16
	H_o	0.35	0.60	0	0.73	0.50	0.21	0.22	0.60	0.50	0.14
	f	−0.034	−0.056	—	−0.062	0.012	0.379	**0.619**	−0.041	0	0.155
SFO-18	*A*	7	6	3	3	3	6	3	2	4	3
	H_E	0.77	0.69	0.47	0.46	0.55	0.72	0.09	0.13	0.68	0.38
	H_o	0.73	0.79	0.24	0.55	0.56	0.73	0.09	0.13	0.25	0.37
	f	0.052	−0.156	0.506	−0.18	−0.015	−0.018	−0.011	−0.037	0.646	0.028
SFO-23	*A*	11	14	5	15	12	11	5	8	7	8
	H_E	0.87	0.86	0.70	0.89	0.74	0.82	0.74	0.79	0.87	0.75
	H_o	0.88	0.89	0.71	0.86	0.81	0.73	0.70	0.71	1.00	0.69
	f	−0.13	−0.041	−0.003	0.037	−0.096	0.103	0.062	0.103	−0.167	0.084
SFO-8	*A*	13	13	4	14	14	15	5	8	7	9
	H_E	0.87	0.92	0.51	0.85	0.93	0.92	0.70	0.75	0.85	0.80
	H_o	0.77	0.88	0.59	0.86	0.87	0.88	0.84	0.60	0.75	0.63
	f	0.117	0.048	−0.151	−0.006	0.071	0.034	−0.208	0.208	0.125	0.218

Tableau 2 continued.

		Populations									
		J9	J10	J11	K1	K2	K3	K4	N1	N2	P1
SSA-197	A	5	4	2	4	2	3	4	2	3	3
	H_E	0.57	0.34	0.30	0.66	0.44	0.24	0.60	0.50	0.64	0.18
	H_o	0.54	0.29	0.24	0.59	0.38	0.27	0.64	0.80	0.63	0.13
	f	0.049	0.152	0.22	0.1	0.159	−0.105	−0.063	−0.647	0.028	0.294
MST-85	A	10	6	2	6	6	6	4	3	7	9
	H_E	0.78	0.81	0.49	0.69	0.80	0.61	0.67	0.25	0.85	0.83
	H_o	0.84	0.65	0.41	0.73	0.69	0.53	0.64	0.27	1.00	0.82
	f	−0.083	0.197	0.158	−0.062	0.145	0.122	0.05	−0.077	−0.191	0.005
Global	A	8.17	7.67	2.83	7.67	6.67	7.17	4	4.33	5	5.83
	H_E	0.70	0.70	0.41	0.71	0.66	0.61	0.56	0.50	0.73	0.52
	H_o	0.68	0.68	0.36	0.72	0.63	0.56	0.52	0.52	0.69	0.46
	f	0.0196	0.0193	0.123	−0.0173	0.0455	00776	0.0741	−0.0409	0.0629	0.1069
	P(HW)	0.1076	0.2440	0.2180	0.9949	0.9656	0.3971	0.0123	0.0304	0.4617	0.0223

		Populations									
		P2	P3	P4	P5	P6	P7	P8	P9	P10	Global
SFO-12	A	5	2	2	4	2	2	2	3	3	14
	H_E	0.50	0.04	0.51	0.20	0.50	0.19	0.22	0.24	0.42	0.29
	H_o	0.41	0.04	0.10	0.21	0.35	0.21	0.10	0.17	0.37	0.26
	f	0.171	0	**0.817**	−0.06	0.307	−0.102	0.525	0.279	0.128	**0.1508**
SFO-18	A	7	5	6	6	3	4	6	6	4	14
	H_E	0.76	0.59	0.71	0.46	0.19	0.43	0.76	0.82	0.70	0.59
	H_o	0.48	0.36	0.59	0.38	0.20	0.45	0.70	0.78	0.53	0.42
	f	**0.371**	**0.398**	0.171	0.158	−0.063	−0.049	0.072	0.048	0.254	**0.1176**
SFO-23	A	10	13	17	13	7	11	11	6	7	45
	H_E	0.78	0.90	0.93	0.89	0.81	0.82	0.89	0.59	0.84	0.85
	H_o	0.66	0.93	0.91	0.90	0.75	0.66	0.79	0.64	0.95	0.87
	f	0.161	−0.038	0.019	−0.011	0.07	0.207	**0.106**	−0.085	−0.135	0.0339
SFO-8	A	9	9	14	15	7	10	19	12	7	57
	H_E	0.77	0.76	0.87	0.90	0.71	0.64	0.94	0.86	0.70	0.78
	H_o	0.78	0.68	0.79	0.90	0.65	0.38	1.00	0.95	0.84	0.86
	f	−0.009	0.104	0.095	0.001	0.092	**0.423**	−0.069	−0.114	−0.205	**0.0952**
SSA-197	A	2	2	2	4	4	2	6	4	2	10
	H_E	0.22	0.04	0.47	0.51	0.43	0.17	0.67	0.54	0.10	0.42
	H_o	0.24	0.04	0	0.52	0.50	0.18	0.62	0.67	0.11	0.41
	f	−0.116	0	**1**	−0.007	−0.159	−0.08	0.069	−0.242	−0.029	0.0473
MST-85	A	8	7	9	7	4	6	9	8	6	24
	H_E	0.77	0.67	0.82	0.52	0.58	0.62	0.80	0.77	0.77	0.82
	H_o	0.72	0.59	0.82	0.55	0.47	0.50	0.48	0.91	0.89	0.89
	f	0.064	0.119	0.004	−0.059	0.194	0.194	**0.402**	−0.186	−0.163	**0.0684**
Global	A	6.83	6.33	8.33	8.17	4.5	5.83	8.83	6.5	4.83	6.61
	H_E	0.63	0.50	0.72	0.58	0.54	0.48	0.71	0.64	0.59	0.61
	H_o	0.55	0.44	0.53	0.58	0.49	0.40	0.62	0.69	0.61	0.65
	f	**0.1347**	0.1207	**0.262**	0.0049	0.0963	0.1778	**0.1334**	−0.0823	−0.0425	**0.0807**
	P(HW)	<0.0001	0.0069	<0.0001	0.4094	0.3083	0.0059	<0.0001	0.2830	0.1467	<0.0001

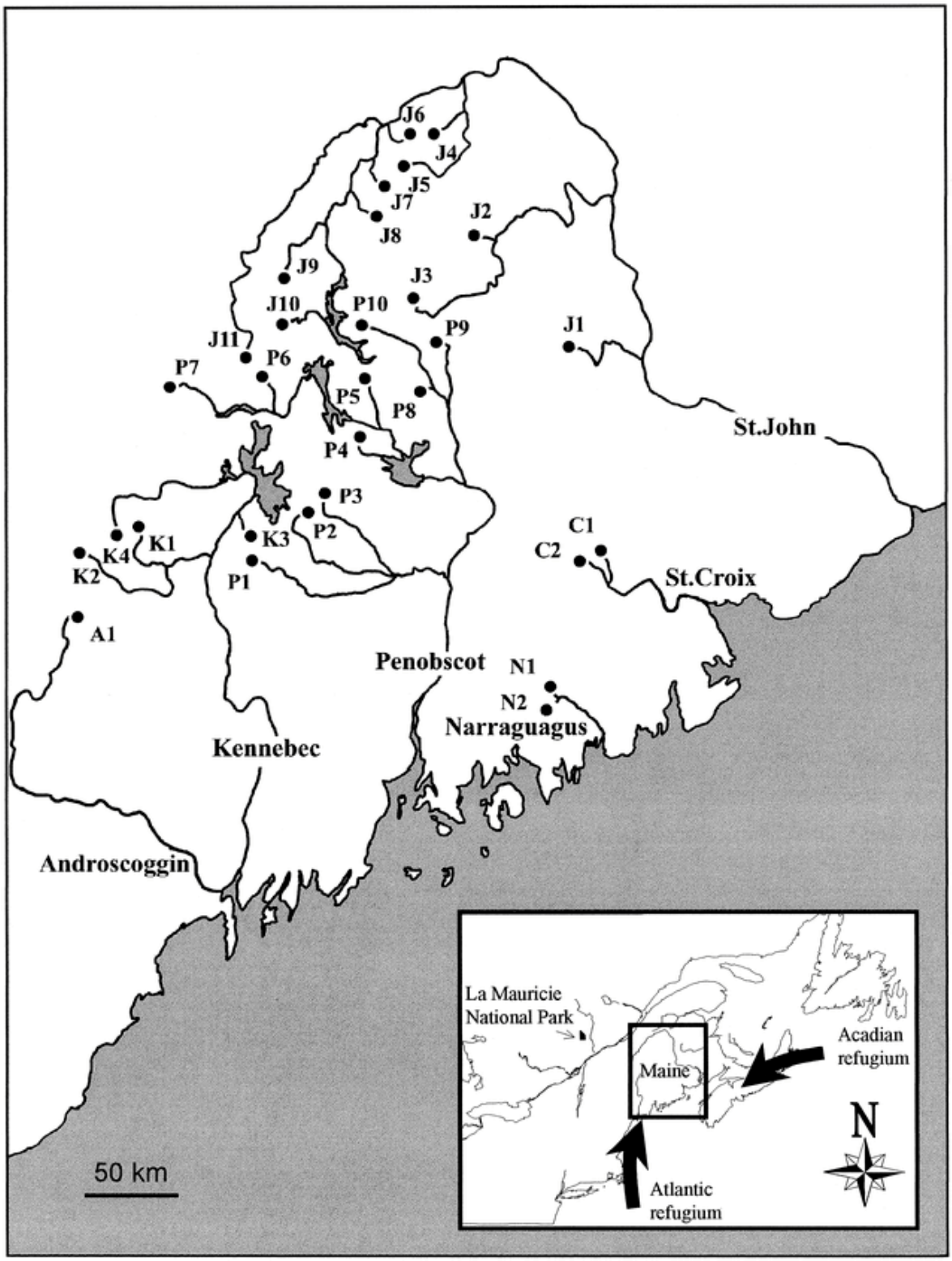

Figure 2-1 Sampling sites in Maine. Population codes correspond to locations in Table 1. Approximate locations for glacial réfugia are from Schmidt (1986)

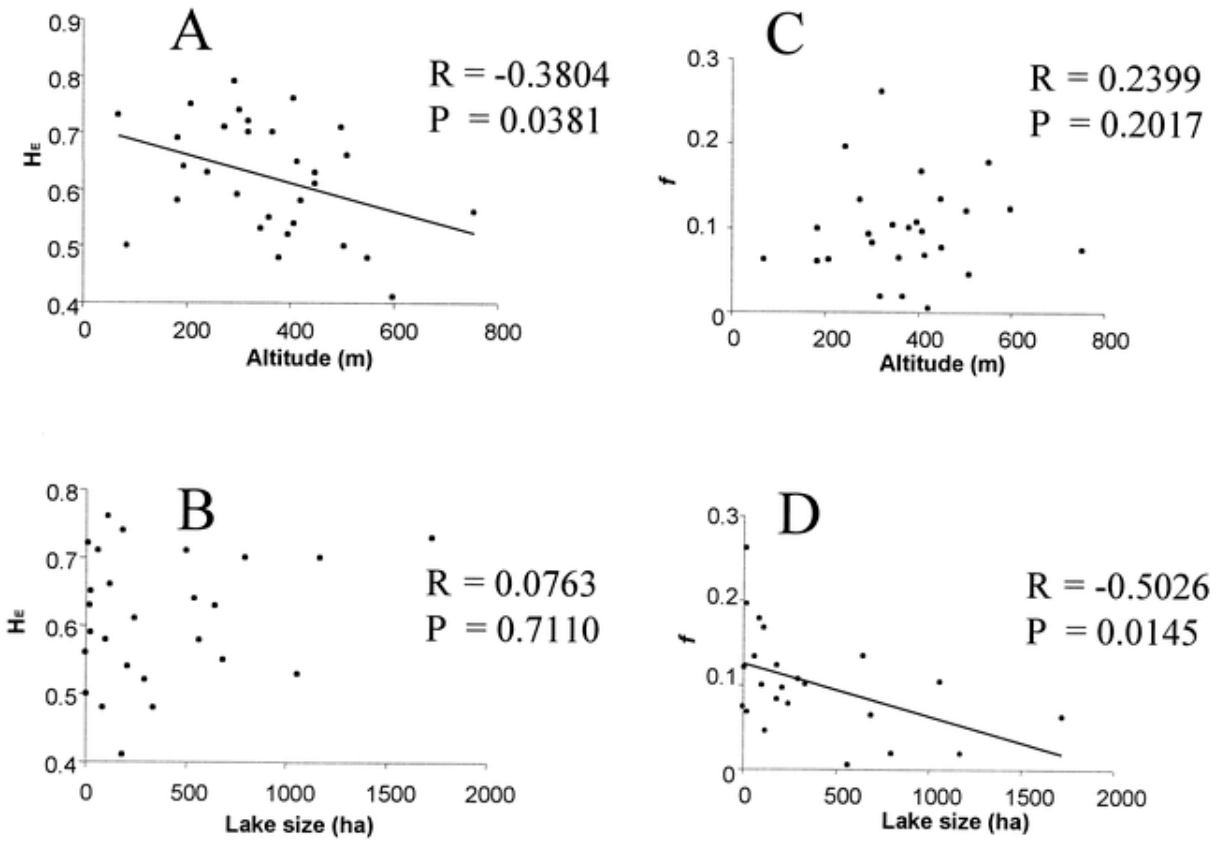

Figure 2-2 Relationships between physical features of lakes (lake size and altitude), expected heterozygosity (A, B) and *f*, F_{IS}estimate (C, D). Correlations were tested using Spearman's R.

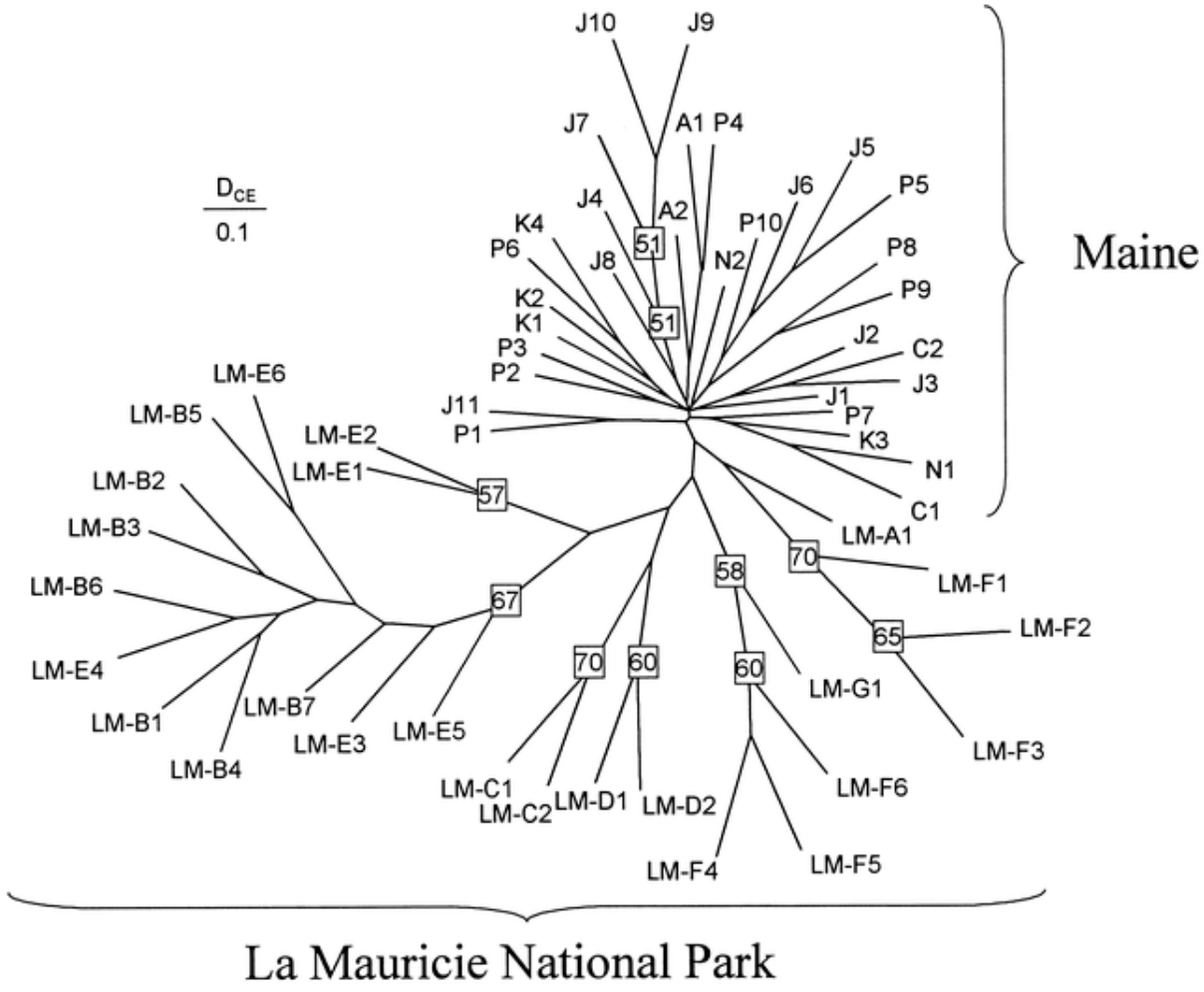

Figure 2-3 Neighbour-joining tree relating the 30 populations sampled in Maine and also incorporating La Mauricie National Park (Québec, Canada) populations. Codes for La Mauricie (prefix LM) are as indicated in Angers and Bernatchez (1998). The tree was constructed using the chord distance of Cavalli-Sforza and Edwards (1967). Bootstrap values are based on 2000 replicates.

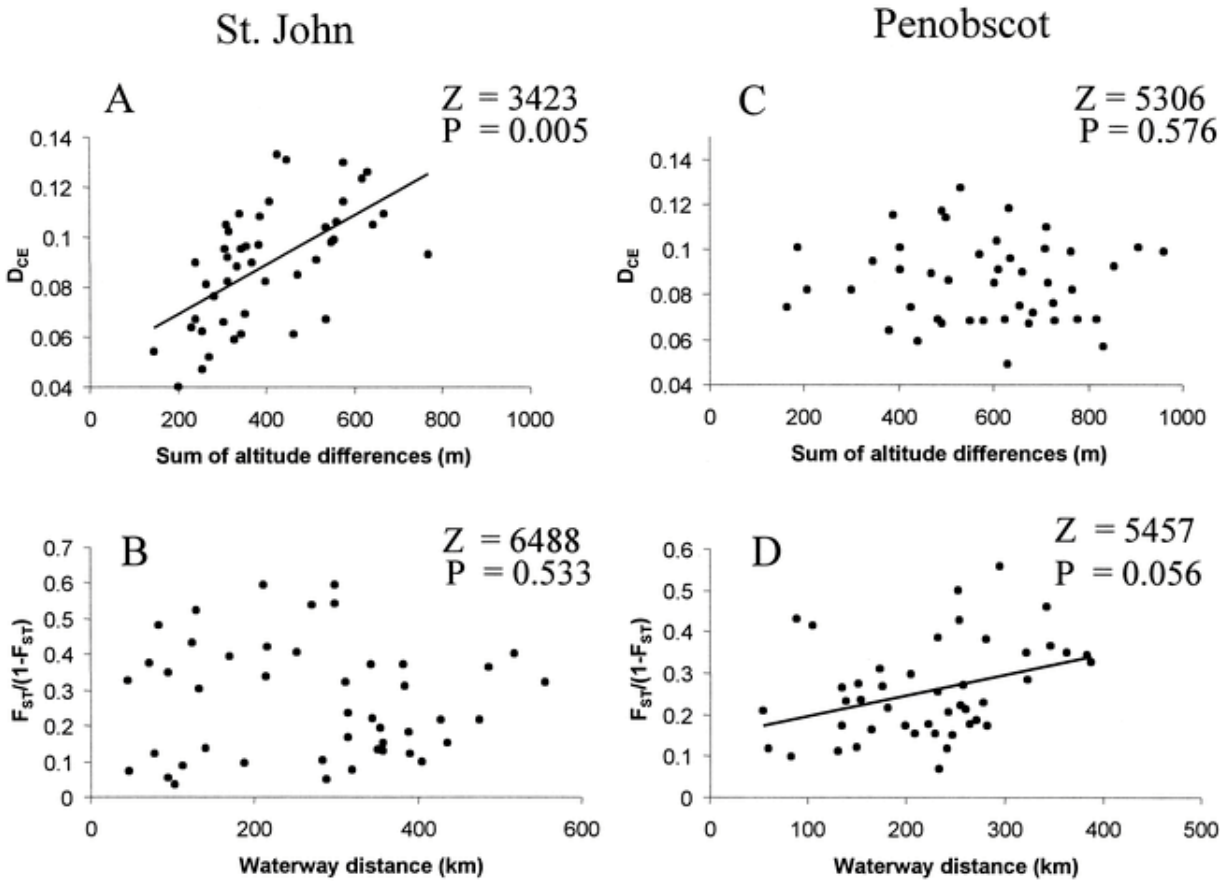

Figure 2-4 Genetic divergence among populations as a function of sum of altitudinal différences and waterway distance winch St. John (A, B, respectivement) and Penobscot River drainage (C, D, respectivement).

3. Heterozygote deficiencies in small lacustrine populations of brook charr *Salvelinus fontinalis* Mitchill (Pisces, Salmonidae) : a test of alternative hypotheses.

3.1. Résumé

L'observation d'écarts aux proportions prédites d'individus hétérozygotes dans une population est courante dans les études empiriques en populations naturelles. Des progrès récents des outils statistiques disponibles en génétique des populations permettent maintenant d'exploiter les génotypes individuels multilocus pour tester plus rigoureusement les différentes sources possibles de déficit en hétérozygote. Dans une étude précédente chez l'omble de fontaine (*Salvelinus fontinalis*) en lacs, nous avions observé de plus forts déficits dans les lacs de plus petite taille. Dans cette article, nous proposons une méthodologie pour tester empiriquement des hypothèses alternatives et identifier la cause des déficits observés dans trois des plus petits lacs analysés (85, 109 and 182 ha).

Premièrement, comme plusieurs autres salmonidés, l'omble de fontaine peut développer un polymorphisme trophique au sein des lacs tempérés nordiques. Si les morphes divergent génétiquement, l'échantillonnage indifférencié de l'un et l'autre morphe aboutirait à l'observation de moins d'individus hétyérozygotes qu'attendu dans une population à reproduction aléatoire (effet Walhund). En utilisant une méthode individuelle destinée à détecter une structure de population cryptique, nous avons pu rejeter l'hypothèse que cette seule explication pouvait être à l'origine des déficits dans chacun des trois lacs. Deuxièmement, la reproduction entre apparentés pourrait aussi être plus fréquente dans les petits lacs, ce qui mènerait à un déficit accru. Un nombre significativement accru de poissons avaient une hétérozygotie multilocus accrue dans deux des lacs, ce qui suggère que des poissons consanguins ont été échantillonnés. Troisièmement, l'échantillonnage de poissons apparentés peut aussi être à l'origine d'écarts aux proportions de Hardy-Weinberg. Dans les deux mêmes lacs, la distribution des coefficients d'apparentement par paire s'écartait de sa distribution nulle aléatoire, ce qui suggére de plus que des individus plus apparentés qu'au hasard ont été inclus dans les échantillons.

3.2. Abstract

Empirical studies of natural populations have commonly reported departures from Hardy-Weinberg expected proportions of heterozygote individuals. Recent advances in statistical population genetics now offer the potential to exploit individual multilocus genotypic information to test more rigorously for possible sources of heterozygote deficiencies. In a previous study in lacustrine brook charr (*Salvelinus fontinalis*), we reported stronger deficits in small than in large lakes. In the present paper, we propose a methodology for empirically testing alternative hypotheses to identify the cause of the deficits observed in three of the smallest lakes (85, 109 and 182 ha) analysed.

First, as in several salmonid species, brook charr may exhibit a trophic polymorphism in north temperate lakes. If morphs are genetically divergent, indiscriminate sampling of both forms would result in less heterozygote individuals than expected in a randomly mating population (Wahlund effect). Using an individual-based method aiming at detecting cryptic population structure, we can reject this explanation as the sole source of deficits for all three lakes. Secondly, mating among relatives could also be frequent in small lakes and lead to heterozygote deficiencies. Significantly more fish than expected at random had low individual multilocus heterozygosity in two of the lakes, suggesting that inbred fish may have been present. Thirdly, sampling of genetically related fish would also lead to departures from Hardy-Weinberg proportions. In the same two lakes, the distribution of pairwise relatedness coefficients departed from its random expectation, suggesting that non-random sampling of kin may have occurred.

3.3. Introduction

In large and randomly mating populations of diploid species, the pairing of alleles within individuals can be predicted using binomial sampling properties according to Hardy-Weinberg equilibrium (HWE). Interpretations of departures from these expected genotypic proportions have been a recurrent theme of both theoretical and empirical population genetics studies since their first formal stating by Hardy (1908) and Weinberg (1908). Once artefactual sources of deficits have been discarded (e.g. entirely or sporadically non-amplifying alleles : Callen, 1993; Pemberton *et al.*, 1995; Brookfield, 1996; Van Treuren *et al.*, 1998; Wattier *et al.*, 1998), heterozygote deficiencies may be used to infer various aspects of breeding systems *sensu lato*, such as quantifying the rate of selfing (Jarne & Charlesworth, 1993 and e.g. in snails, Viard *et al.*, 1997; in plants, Enjalbert & David 2000) or the levels of consanguineous matings in natural and captive populations of non-selfing organisms (Wright, 1921; Thornhill, 1993). In largely outcrossing species, heterozygote deficits have commonly been interpreted as indirect evidence of the mixing of differentiated gene pools (Wahlund effect; Wahlund, 1928), while, on the other hand, heterozygote excesses have been used to quantify the effective number of breeders in small populations (Pudovkin *et al.*, 1996; Luikart and Cornuet, 1999).

Overall, heterozygote deficiency in non-selfing, diploid populations is relatively common (see e.g. Waldman & McKinnon 1993 for a review in fishes, amphibians and reptiles ; Zouros & Foltz, 1984 in marine bivalves). Yet very few studies have been specifically aimed at systematically testing the possible causes of deficiencies (but see Christein *et al.*, 1979; Zouros & Folz, 1984; David *et al.*, 1997). Typically, a biologically plausible explanation is suggested as the most likely source of heterozygote deficits, but there is often a lack of rigorous testing of the various alternative hypotheses (but see Overall *et al.* 2001). The recent advances in statistical population genetics prompted by the use of highly polymorphic markers such as microsatellites now offer the potential of quantifying departures from HWE with high precision (Chakraborty & Zhong, 1993; Raymond & Rousset, 1995) and exploiting individual multilocus genotypic information to test more rigorously for possible sources of heterozygote deficiencies.

Heterozygote deficiencies have been recently documented in lake populations of the brook charr (Castric *et al.*, 2001), a freshwater salmonid whose movements in riverine habitats are restricted (Bélanger & Rodriguez 2001). Deficiencies were negatively correlated with lake size (i.e. they were stronger in smaller lakes), so we focused here on three small lakes (size < 200ha) whose census size was sufficiently large to allow a temporal comparison by resampling in 1999. Since technical artefacts, such as non-amplifying (null) alleles or selective amplification of shorter alleles would be systematic for all the analysed samples, they could not account for the relationship with lake size and could be ruled out (Castric *et al.* 2001). We thus focus here on three competing hypotheses related to the biology of brook charr inhabiting small lakes.

First, heterozygote deficiency could result from a subdivision of the local population into isolated and differentiated reproductive units (Wahlund effect). The coexistence of genetically isolated populations of the same species in single lakes is a common feature of many northern temperate freshwater fishes (reviewed in Taylor, 1999). Typically, genetic differentiation among such populations is accompanied by differences in trophic related traits. Dynes *et al.* (1999) recently documented that such a differentiation of sympatric lacustrine populations may also occur in brook charr. However, the extent of morphological differentiation between the two forms (benthic and pelagic) appears much subtler than that reported in other species. Consequently, the occurrence of sympatric but differentiated populations of brook charr in our samples may have remained undetected. Although the underlying mechanisms are still debated (Kondrashov & Kondrashov, 1999; Diekman & Doebeli, 1999), intraspecific competition is believed to be one of the major causes of the divergence of sympatric populations of northern temperate lacustrine fishes (reviewed in Schluter 2000). If intraspecific competition is increased in smaller lakes because of more limited resources, the probability and intensity of population divergence could be higher in smaller lakes, thereby explaining the observed correlation between lake size and heterozygote deficiency due to Wahlund effect.

A second possible cause for the observed heterozygote deficiency is the mating of close relatives (Wright, 1921). Although little is known about brook charr reproductive behaviour under natural conditions (but see Blanchfield and Ridgway, 1996), kin recognition has been

shown to occur in controlled environments (Hiscock and Brown, 2000) and could potentially bias the reproductive system towards inbreeding.

Finally, a third hypothesis could be the non-random sampling of members from a limited number of families. When few parents contribute to a given sample, the discreteness of the number of possible different genotypes leads to a slight heterozygote excess in the progeny relative to HW proportions in an infinite population with the same allele frequencies (Crow & Kimura 1970 pp55-56; Robertson, 1965; Pudovkin *et al.*, 1996; Luikart & Cornuet, 1999). However, when several familial groups are sampled, each involving only a limited number of progenitors, allele frequencies are expected to vary among such groups, even if progenitors are drawn from the same source population. Hence, when the progeny of several reproductive groups are pooled, heterozygote excess may be counterbalanced by a "family" Wahlund effect, whose relative magnitude is not known (Pudovkin *et al.*, 1996). More specifically, it is unclear how the number of pooled reproductive groups may affect heterozygote proportions in the next generation. Because larger lakes potentially provide more suitable spawning grounds, the number of reproductive groups may be an important factor to consider in explaining the relationship between lake size and heterozygote deficiencies. Specifically, fish from small lakes could be derived from a few families only, and consequently the probability of sampling two related individuals is higher than expected in a randomly mating population .

In this study, we used an individual-based approach to analyse multilocus genotypic data from six microsatellite loci in order to test the above three competing explanations for the observed heterozygote deficiencies. We first tested the possibility of detecting a Wahlund effect using a maximum likelihood method and quantified the detection power of that method using permutation techniques. We then assessed the distribution of pairwise relatedness coefficients to test for the existence of a limited number of effective breeders producing a given cohort. Finally, we performed computer simulations to explore how the number of spawning grounds could influence departures from HWE.

3.4. Materials and methods

3.4.1. Lake size and interlocus variance of F_{IS}

We first extended the data analysis from the 22 lakes sampled in 1997 and included in Castric *et al.* (2001), which provided evidence of stronger heterozygote deficiency in smaller lakes. A systematic investigation of variation in F_{IS} estimates *f* (in what follows, F_{IS} and F_{ST} will stand for their estimates by *f* and θ respectively, Weir & Cockerham, 1984) across loci was not performed in that study. We therefore plotted interlocus variance in *f*-values against lake size and tested the correlation using Spearman's R.

3.4.2. Sampling and microsatellite data

If deficiencies proceed from a single cause, then it should be easier to identify in small lakes in which the signal is expected to come out stronger. Thus, with the aim of identifying the cause of heterozygote deficiencies and their variance across loci in small lakes, all further analyses focused on three selected lakes in which additional sampling could be performed in 1999. These lakes (Clish Pond, Robbins Brook Pond and Third Wallagrass Lake) were small (85, 109 and 182 ha) and differed in the distribution of heterozygote deficiencies among loci (Fig 1). Clish Pond was representative of most small lakes in Castric *et al.* (2001) with strong and highly variable heterozygote deficiencies across loci. Robbins Brook Pond exhibited a slightly different pattern, with constantly strong deficits for all six loci. The third lake, named Third Wallagrass Lake, exhibited slightly positive but non-significant F_{IS} estimates. In addition to those fish sampled in 1997 in Clish Pond (n =28), Robbins Brook Pond (n = 28), and the Third Wallagrass Lake (n= 18), 34, 50 and 51 additional fish were respectively collected by successive trap net attempts at different locations of the same lakes in 1999. Total DNA was extracted from white muscle tissue using phenol-chloroform protocol and fish were genotyped at six microsatellite loci as detailed in Castric *et al.* (2001).

3.4.3. Wahlund effect ?

Fewer heterozygotes are expected than under random mating when differentiated gene pools are sampled together (cryptic population structure). This hypothesis was tested using a maximum likelihood (ML) method aiming at unravelling cryptic population structure. The null

hypothesis was that fish from each lake are a representative sample of a single Hardy-Weinberg population, and the alternative hypothesis is that the sample is a mixture of two differentiated populations (benthic and limnetic in the present case, Dynes *et al.* 1999). If fish collected in a lake actually belong to two differentiated subpopulations, the likelihood of a partition in two panmictic clusters should depart from its expected distribution under the hypothesis of no structure (a single panmictic population). We thus searched for the best (i.e. most likely) possible partition in two independent panmictic clusters for each lake sample using a "Simulated Annealing" procedure (Kirkpatrick *et al.*, 1983). The present ML-based algorithm (PartitionML, available at http://www.univ-montp2.fr/~genetix/partitionml.htm) provides the opportunity to compare conveniently the likelihood of different configurations and is a fast and complementary alternative to other approaches to the same problem that use more complex Bayesian statistics (Pritchard *et al.* 2000; Dawson & Belkhir, 2001). Following Paetkau *et al.* (1995) and Rannala and Mountain (1997), the likelihood criterion for a monolocus genotype being drawn from a cluster is calculated as $p = x_i^2$ for homozygotes and $p = 2\ x_i.x_j$ for heterozygotes (where x_i is the frequency of the ith allele at this locus in the target cluster, the unknown x_i values being estimated by their observed value in the cluster). These values are calculated for each locus and are then multiplied to give the likelihood of the individual's multilocus genotype. For a given partition of a sample into two clusters, the likelihood of the partition is given by the product of the likelihoods in the two clusters. This latter is the product of individual multilocus likelihoods calculated for each individual of the cluster. If fish sampled in single lakes actually belonged to two differentiated entities, this algorithm should sort individuals into these subpopulations. But because a model with two clusters (and hence more parameters) will tend to have a higher likelihood (i.e. the algorithm will favour partitions with two clusters rather than one in any data set regardless of its relevance), the likelihood of partitions with one and two clusters cannot be directly compared. We thus tested whether the resulting clusters were significantly more likely than those found in the absence of subdivision. To this end, we generated the null distribution of the log-likelihood of the partitions proposed by the ML algorithm in each of 100 panmictic pseudo-samples generated by random permutation of monolocus genotypes of the real samples using GENETIX 4.02 (Belkhir *et al.* 2001).

Because an eventual lack of significance of the partitions could be due to insufficient statistical power of the algorithm, we empirically tested its ability to disentangle accurately individuals from composite populations at a given threshold of divergence (θ). To that end, simulations were performed using Easypop 1.7. (Balloux, 1999). Genetic drift was simulated for 60 generations between two populations of varying size (50-100-200-400-800 and 1000) to generate various levels of divergence starting from randomly generated populations at 6 loci with 9 alleles each. Individuals were then pooled into a single composite population and the percentage of correctly classified individuals by the ML partitioning algorithm was plotted against θ. To ensure concordance of the present ML-approach with Bayesian methods (Pritchard *et al.* 2000), we ran the same analysis using both methods on the same simulated datasets.

3.4.4. Inbreeding ?

When individuals differ in their inbreeding history, inbred individuals are more homozygous over all loci than expected based on their single-locus genotype frequency, and we should expect identity disequilibrium (Haldane, 1949; Bennet & Binet, 1956). The hypothesis that heterozygote deficiencies are due to the presence of inbred fish in samples was therefore tested by comparing the distribution of MLH (multilocus heterozygosity), i.e. the number of individuals heterozygous at 0, 1, 2...6 loci (Sved, 1968; Brown *et al.*, 1980) with its expectation under random mating using a permutation test. The number of fish in each MLH interval in the sampled population was compared to its random distribution obtained from 1000 randomised populations in which alleles were randomly associated within individuals. Linear interpolation was used to include fish not analysed at all six loci, thus intervals rather than classes were used. A fish heterozygous at 5 loci over the 6 possible was included in the]4,5] interval, while a fish heterozygous at 5 loci over 5 genotyped was considered fully heterozygote and thus included in the]5,6] interval. Probabilities of observing fewer individuals in a given MLH interval than expected at random were then combined across the six samples using Fisher's method (Sokal & Rohlf, 1995). Biparental inbreeding should result in a significant over-representation of low MLH classes compared to random expectations, that is a higher proportion of fish homozygous at several loci than expected by random mating.

3.4.5. Sampling from a limited number of families ?

Genetic relatedness of every pair of fish in each lake was estimated according to the pairwise identity coefficient of Mathieu *et al.* (1990), which computes the probability of identity by state at a locus of a pair's offspring weighted across loci.

$I_{xy} = \frac{i_{xy}}{\sqrt{i_{xx} i_{yy}}}$, where $i_{xy} = \frac{\sum_j n_{jx} n_{jy}}{2}$, where n_{jx} is the number of copies of allele j in individual x. The multilocus estimate is obtained by weighting loci by $1/\sum_j (p_j)^2$, p_j being the sample frequency of allele j.

Identity was chosen over other available measures of genetic relatedness (e.g. that of Queller & Goodnight, 1989 and that of Lynch & Ritland, 1999) because of its substantially reduced variance (Belkhir *et al.* in prep). Following a testing procedure first proposed by Blouin et al (1996) to classify individuals as full, half sibs or unrelated, we tested whether the relatedness pattern of fish collected in a given lake significantly differed from its null expectation in a panmictic population. The mean Identity among all pairs of fish in a sample was compared to its expected distribution under the hypothesis of no relatedness obtained by random permutation of genotypes in 1000 randomised populations. Our approach thus differed from that of Blouin *et al.* (1996) in that relatedness was here considered at the population rather than at the individual level.

We also simulated the behaviour of heterozygote deficiency when only a few progenitors reproduce in each generation using Maple version 5.4 (Waterloo Inc., 1999). One to 25 discrete spawning grounds (S) were generated, each composed of 5 males and 5 females (Quinn, 1995; Blanchfield and Ridgway, 1997, 1999) whose genotypes were randomly drawn at a biallelic locus with frequency p and q. Fifty progeny were produced from each spawning ground using random drawings from male and female genotypes. All progenies were then pooled, and global heterozygosity of the system was computed and compared to Hardy-Weinberg expectations using observed allele frequencies in the progeny. F_{IS} was estimated by $(H_E-H_O)/H_E$. Because we were mainly interested in the change of F_{IS} and var(F_{IS}) across loci with S, 250 independent biallelic loci ($p = q = 0.5$) were replicated for each value of S.

3.5. Results

3.5.1. Lake size and interlocus variance of F_{IS}

When including all 22 lakes previously reported in Castric *et al.* (2001), a significant correlation (P=0.0041) was found between lake area and var(F_{IS}) indicating that F_{IS} were not only higher but also more variable among loci in smaller lakes (Fig. 1).

3.5.2. Heterozygote deficiencies in the 3 lakes

Contrasted levels of heterozygote deficiencies were observed among lakes as well as among sampling years (Table 1). Clish Pond had the strongest and most variable levels of heterozygote deficiencies both in 1997 (f=0.178, P=0.001) and 1999 (f=0.157, P=0.007). Robbins Brook Pond also revealed strong positive f-values in 1997 (f=0.167, P<0.001), but no significant departure (P=0.469) was observed in this lake in 1999. The Third Wallagrass Lake exhibited positive global heterozygote deficiencies, but they were not significantly different from zero following sequential Bonferroni correction either in 1997 (f=0.083, P=0.068) or in 1999 (f=0.049, P=0.05).

No evidence for allele frequency variation between sampling years was detected in Clish Pond and Robbins Brook Pond (F_{ST} =0.0051, P=0.132 and F_{ST} =0.0051, P=0.201), whereas both samples differed significantly -though slightly- in the Third Wallagrass Lake (interannual F_{ST} =0.026, P= 0.004).

3.5.3. Wahlund effect

Using simulated pools of distinct populations with known levels of divergence, the partitioning algorithm could classify individuals to their population of origin without error when θ approximately reached 0.10 (Fig. 2), in accordance with previous results (see Fig 3. in Cornuet *et al.*, 1999). At θ =0.05, over 90% of individuals were still correctly classified (Fig 2). Results provided by the software Structure (Pritchard *et al.* 2000) were very similar (Fig 2.), suggesting that both methods have similar efficiency in such simple situations. Because $(1-F_{IT})=(1-F_{IS})(1-F_{ST})$, a given F_{ST} between two pooled and panmictic (F_{IS}=0) differentiated units translates into a F_{IT} of equal magnitude (regardless of the estimation bias of the

parameter F_{ST} when only two populations are considered, Weir & Cockerham, 1984). Because the observed multilocus heterozygote deficiencies were superior to 0.10 in Robbins Brook Pond in 1997 and Clish Pond in 1997 and 1999, this suggests that the algorithm used should have been able to unambiguously detect a partition if the observed heterozygote deficiency resulted from a Wahlund effect between two differentiated entities.

Permutation tests indicated that this was not the case. In none of the lakes did the log-likelihood value depart clearly from that created by the partitioning algorithm in homogenised populations (Fig 3, P>0.05 in all cases). These results therefore argued against a Wahlund effect as a systematic explanation for the observed deficiencies.

3.5.4. Inbreeding

Evidence was found for a global shift of MLH towards lower individual heterozygosity than expected in randomly mating populations (Table 2). More fish heterozygous at three or less loci were observed than would have been expected if mating had been random (Fisher's method, d.f.=12; P=0.0022, P=0.0001 and P=0.0025 respectively for the three lowest MLH intervals), while no such departure was observed in the three highest MLH intervals (P=0.8259, P=0.9467 and P=0.3834). This global trend was mostly due to fish sampled in 1997 in Robbins Brook Pond and in 1999 in Clish Pond (Table 2), indicating that a higher proportion of inbred fish than randomly expected may have been collected in those two samples.

3.5.5. Relatedness

Evidence for relatedness was found in Robbins Brook Pond in 1997 and Clish Pond in 1999. The mean pairwise identity coefficient departed significantly from its expected distribution under the hypothesis of a random association of monolocus genotypes within individuals, as would be the case in a panmictic population (Fig 4; two-tailed test, P= 0.006 and P=0.024, respectively).

3.5.6. Sampling from a limited number of families ?

Computer simulations showed that F_{IS} was slightly negative (heterozygote excess) for low numbers of spawning grounds (S). There was however a rapid increase in F_{IS} with S, closely approaching 0 when S reached approximately 3 (Fig 5). The main effect of an increase in the number of spawning grounds was to asymptotically decrease the variance in F_{IS} across independent loci, while the effect on mean F_{IS} itself was much weaker unless S was very small. For any S, mean F_{IS} was at least one order of magnitude smaller than its standard deviation. An increase in the number of spawning grounds with lake size could thus account for the correlation between lake size and variance of F_{IS} estimates across loci (Fig 1B).

3.6. Discussion

The objective of this study was to find a biological explanation for the relationship between lake size and heterozygote deficiencies found in lacustrine brook charr populations in Maine. To that end, we focused on three relatively small lakes and tested three alternative hypotheses using multilocus microsatellite data. On the one hand, computer simulations provided support to the hypothesis that the observed decrease in variance of F_{IS} estimates across loci with lake size could be explained by an increase in the number of reproductive groups involved in producing each cohort. On the other hand, none of the proposed explanations for increased F_{IS} in smaller lakes could be given full support in all three lakes we used for hypothesis testing. A Wahlund effect was rejected in both years in all three lakes, while the presence of inbred fish (MLH distribution) in the samples, together with departures from the expected pairwise relatedness distribution, were detected in Robbins Brook Pond in 1997 and in Clish Pond in 1999, but not in any other sample. Although based on a restricted number of loci, our data thus suggested that no single explanation could account for both above-mentioned correlations.

Fish sampled in Robbins Brook Pond in 1997 and in Clish Pond in 1999 exhibited strong heterozygote deficiencies (Fig 1). Significant departures from the expected relatedness were also detected, indicating that the progeny of a limited number of families only may have been sampled at these locations. A significant shift toward lowered individual heterozygosity further suggested that the relatedness detected may be associated with mating among relatives. Small population size alone cannot account for both observations, as random mating even in a small isolated population would not lead to lowered individual multilocus heterozygosity compared to random expectations (just as ambient inbreeding is different from consanguinity). Shoaling behaviour of kin, whereby genetically related individuals swim in cohesive groups, could possibly account for the observed relatedness and has already been reported in other fish species (Brown and Brown, 1996; Pouyaud *et al.*, 1999; Krause *et al.*, 2001; Gerlach *et al.*, 2001). As fish were collected in successive trap net attempts, kin swimming together in a shoal may have been sampled together. Kin recognition has recently been documented in the brook charr (Hiscock and Brown, 2000) and may provide further support to this explanation. Additional sampling and field behavioural observations in lakes of different size together with

relatedness estimates would however be required to address this question, more specifically to compare brook charr shoaling and mating behaviour in lakes of different size.

A restricted number of spawning grounds in those two lakes may also potentially explain increased relatedness. If fish remain in the vicinity of their hatching location until maturity (see e.g. Allendorf & Phelps, 1981; Hansen *et al.*, 1997), most individuals collected in those two small lakes could likely be derived from a small number of progenitors only. Mating could then be biased toward relatives if most dispersal opportunities are restricted to the close surroundings of the lakes. Such consanguineous matings would thus be more frequent in small than in larger lakes with numerous tributaries, because fish have access to a lower number of unrelated mates. This explanation is more parsimonious in that it only implies a limitation in dispersal opportunities in small lakes rather than a change in the pattern of mate choice. Because Hardy-Weinberg is an underlying assumption of the method aiming at detecting population substructure, such groups of related individuals (within which this assumption is not met, Fig 5) may have remained undetected.

Although samples analysed in the present study were all collected in small lakes, relatedness and consanguinity were detected in Robbins Brook Pond in 1997 and in Clish Pond in 1999 only. In all other samples, heterozygote deficiencies, when present, were not consistently associated with significant departures in individual multilocus heterozygosity or relatedness. A lack of power of the analytic tools we used could maybe account for this. Population geneticists' attention was drawn by Chakraborty (1984) to the loss of information due to the use of as summary a statistic as individual multilocus heterozygosity. We used a non-parametric approach (permutation test) to circumvent the low power of chi-square tests in this context. Although several outcomes are non-significant, the combined tests were significant and the three highest MLH classes were underrepresented in most instances when compared to random expectations ($P>0.5$ in 13/18 cases), while the three lowest classes were overrepresented ($P<0.5$) in 17/18 instances. Altogether, this suggested that there may still exist a trend for lowered individual heterozygosity in our data. A second possible weakness of our analysis lies in the lack of precise knowledge of the detection power of methods designed to detect relatedness in natural populations. Identity, however, has been shown to exhibit considerably less variance than other published (Queller & Goodnight, 1989; Lynch &

Ritland, 1999) estimators of pairwise relatedness (Belkhir *et al.*, in prep). A systematic evaluation of the power of methods based on pairwise estimates would however be required to address this issue more conclusively.

Beside the potential weaknesses of analytic tools, the contrasting results we obtained between lakes and between years for the same lake may reflect spatial and temporal variations in ecological conditions. Namely, the number of suitable spawning grounds in a lake was found to be non-significantly correlated with lake size in a study of 9 lakes (10 to 986 ha) from Ontario, Canada (Rigdway & Blanchfield, 1998). Lake size alone may hence be an inaccurate predictor of the number of available spawning habitats, and some small lakes (such as e.g. Third Wallagrass Lake) may potentially behave as lakes of a much larger area. Finally, inter-year variations in ecological conditions may also explain why the patterns in Robbins Brook Pond in 1997 and in Clish Pond in 1999 were not found again in 1999 and 1997, respectively. Ridgway & Blanchfield (1998) documented important inter-year variations in site use (less than 25% of all sites were used more than two out of the four years of the study despite strong competition for suitable spawning grounds) which may reflect extensive fluctuations in ecological conditions among years. If effects vary both among lakes and among years, a wider sampling design would be required to characterize finely the variation patterns in the specific mechanisms involved.

Altogether, the present test of alternative hypotheses allowed us to conclusively reject a Wahlund effect as the prime source of heterozygote deficiency, while providing indications that unexpected levels of relatedness and consanguinity occurred among fish in two of these small lakes. We therefore suggest that the correlation we observed between lake size and both heterozygote deficiencies and variance of heterozygote deficiencies across loci proceeds from two mechanisms. First, a direct increase in interlocus variance in F_{IS} estimates, because lakes of limited size generally -but not necessarily- provide a small number of suitable spawning sites. Second, an indirect increase in F_{IS} estimates, because fish that emerged in smaller lakes have less opportunities for dispersal and have therefore a higher probability of mating with relatives when compared to fish emerged in larger lakes. Because this signal was only detected in two of the six samples analysed in the present study and because only six loci were used, care should be taken before extending the phenomenon to all small lakes. Following this

analysis, however, it remains as the most coherent explanation for the increase in both F_{IS} estimates and interlocus variance in F_{IS} estimates observed in small lakes.

3.7. Acknowledgements

We thank C. Lemaire and N. Bierne from F.B.'s lab for having initiated several basic ideas at initial stages of data analysis, as well as P. Duchesne for help with Maple programming. Discussions with N. Raufaste helped us overcome some of our mathematical limitations and greatly helped clarifying several issues. We are also grateful to F. Bonney, Maine Department of Inland Fisheries and Wildlife for samples collection. Constructive comments by B. Guinand and two anonymous reviewers significantly improved a previous version of the manuscript. This is a contribution to the research program of GIROQ.

Table 1. Number of alleles (A), expected (Hnb) and observed (Ho) heterozygosity, Fis estimate and exact test probability of HW-equilibrium (P(HW))

		Third Wallagrass Lake		Robbins Brook Pond		Clish Pond	
		1997	1999	1997	1999	1997	1999
	N	18	51	28	50	28	34
SFO-12	A	4	5	6	7	2	2
	Hnb	0,671	0,586	0,709	0,666	0,195	0,317
	Ho	0,500	0,600	0,571	0,740	0,214	0,323
	Fis	0,261	-0,044	0,197	-0,082	-0,102	-0,017
	P(HW)	0,119	0,802	0,637	0,025	1,000	1,000
SFO-18	A	5	6	7	10	3	5
	Hnb	0,641	0,626	0,712	0,685	0,389	0,414
	Ho	0,750	0,588	0,571	0,604	0,429	0,226
	Fis	-0,176	0,068	0,201	0,138	-0,049	0,341
	P(HW)	0,742	0,395	0,053	0,010	0,299	0,013
SFO-23	A	11	14	9	10	9	8
	Hnb	0,865	0,845	0,874	0,850	0,810	0,831
	Ho	0,750	0,776	0,778	0,800	0,643	0,735
	Fis	0,137	0,068	0,111	0,059	0,207	0,117
	P(HW)	0,007	0,178	0,244	0,243	0,015	0,283
SFO-8	A	10	15	12	12	10	7
	Hnb	0,890	0,863	0,778	0,832	0,645	0,332
	Ho	0,800	0,750	0,583	0,809	0,375	0,273
	Fis	0,106	0,135	0,254	0,005	0,423	0,579
	P(HW)	0,252	<0.0005	0,006	0,249	0,009	0,000
SSA-197	A	4	5	6	4	2	2
	Hnb	0,600	0,734	0,712	0,706	0,166	0,268
	Ho	0,611	0,700	0,577	0,771	0,179	0,250
	Fis	-0,019	0,058	0,193	-0,093	-0,080	0,072
	P(HW)	0,373	0,247	0,037	0,484	1,000	0,551
Mu-85	A	6	9	7	10	5	5
	Hnb	0,765	0,812	0,758	0,681	0,607	0,678
	Ho	0,667	0,833	0,714	0,688	0,482	0,594
	Fis	0,132	-0,019	0,058	-0,001	0,194	0,125
	P(HW)	0,558	0,475	0,425	0,709	0,606	0,349
Global	A	40	54	47	53	31	29
	Hnb	0,739	0,744	0,757	0,736	0,469	0,473
	Ho	0,680	0,708	0,633	0,735	0,387	0,400
	Fis	0,083	0,049	0,167	0,002	0,178	0,157
	P(HW)	0,068	0,050	<0.0005	0,469	0,001	0,007

Table 2. Permutation test of the distribution of multilocus heterozygosity
Percentage of 1000 randomized populations in which a MLH class is underrepresented when compared to the real population.

		Multilocus heterozygosity					
		]0,1]	]1,2]	]2,3]	]3,4]	]4,5]	]5,6]
Clish Pond	1997	0,105	0,036	0,304	0,963	0,796	0,120
	1999	0,019	0,006	0,974	0,644	0,736	0,083
Robbins Brook Pond	1997	0,081	0,004	0,001	0,732	0,969	0,719
	1999	0,197	0,086	0,224	0,583	0,649	0,301
Third Wallagrass Lake	1997	0,044	0,125	0,029	0,605	0,303	0,867
	1999	0,152	0,176	0,132	0,150	0,629	0,887
Combined test (df=12)		0,0022	0,0001	0,0025	0,8259	0,9467	0,3834

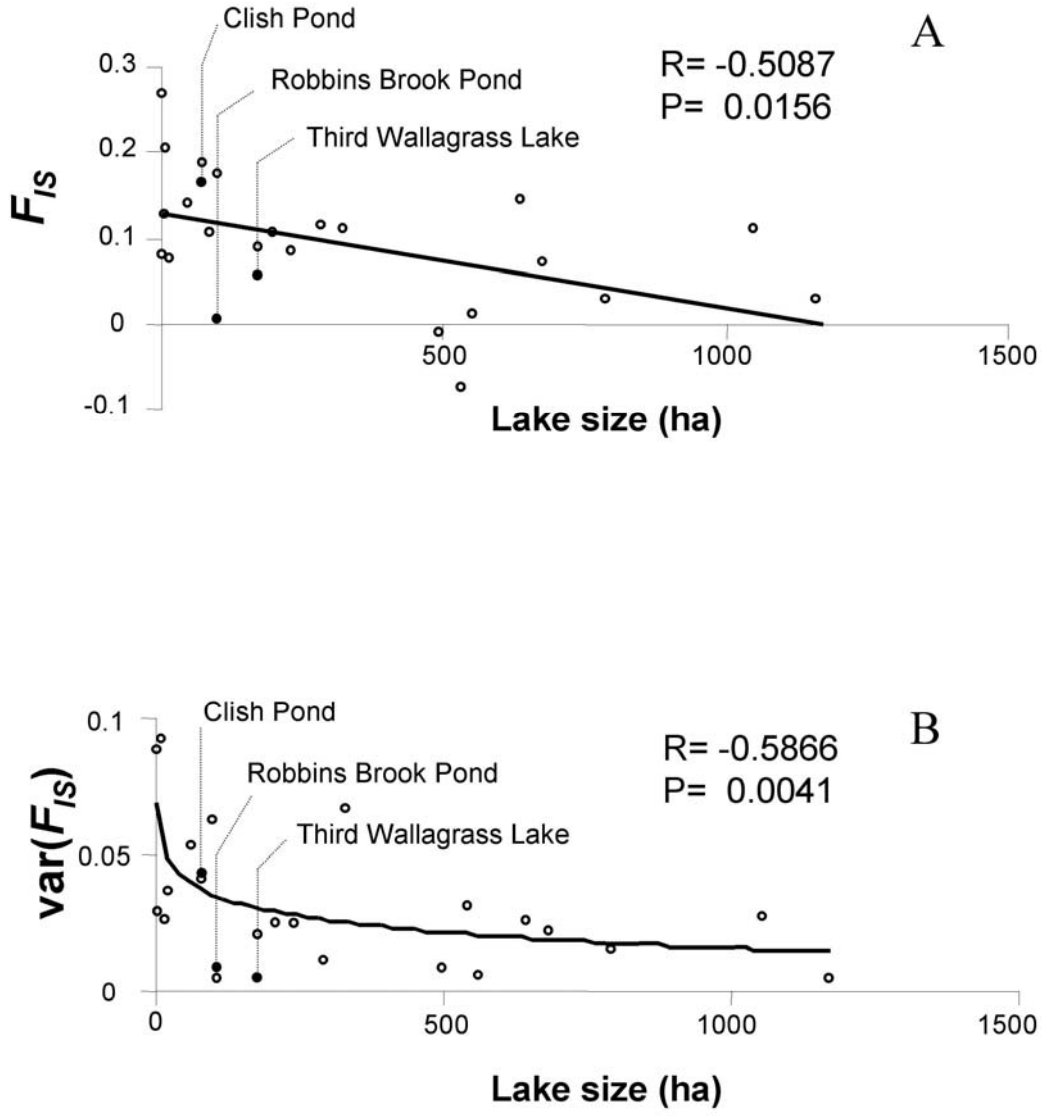

Figure 3-1 Correlations between lake size and A) heterozygote deficiencies (f) B) variance in f across six microsatellite loci. R is Spearman's non-parametric correlation coefficient. A log-linear curve was fitted on B. Open circles are from Castric et et (2001).

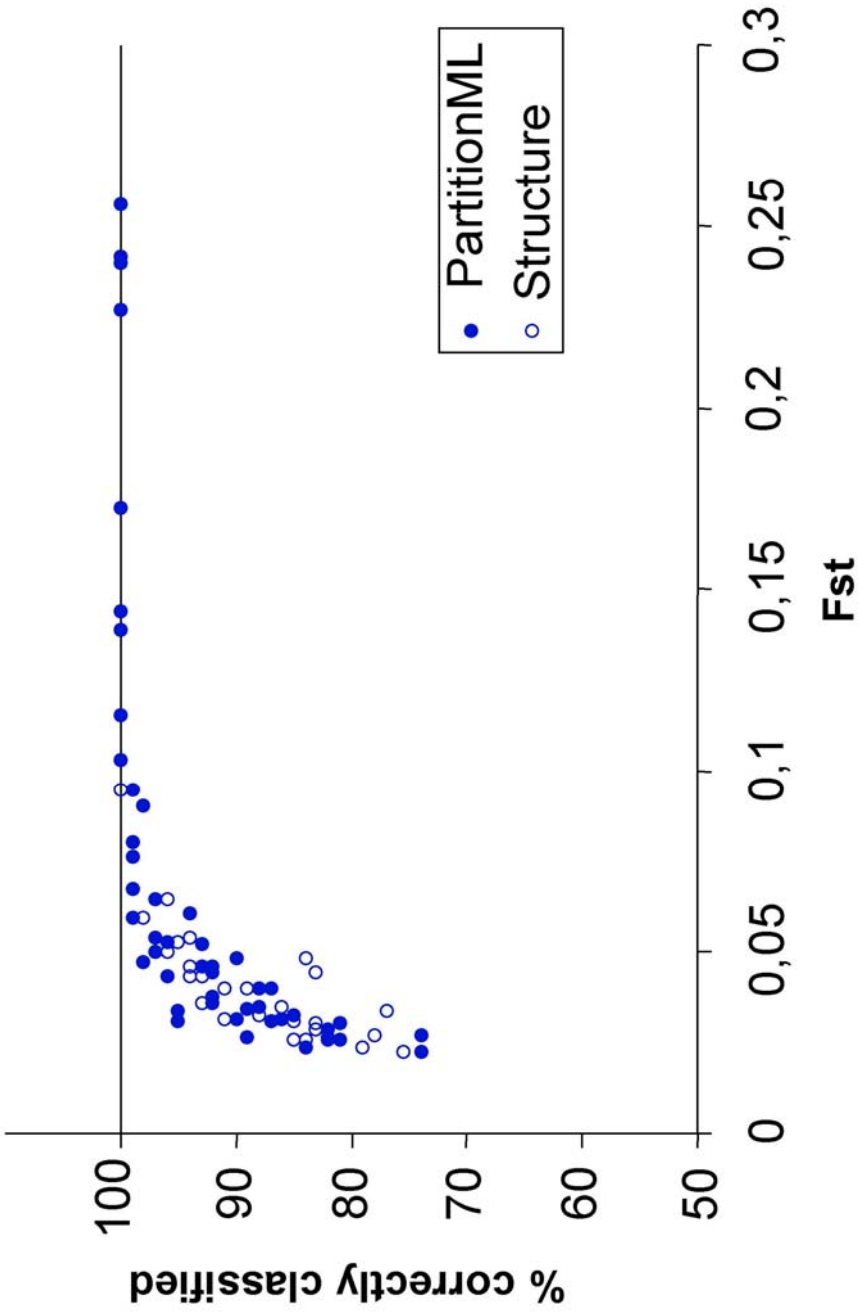

Figure 3-2. Proportion of correctly classified individuals by the ML-algorithm (PartitionML) and Structure (Pritchard *et al.* 2000) as a function of population divergence F_{ST}. Further details on simulation parameters are provided in the text.

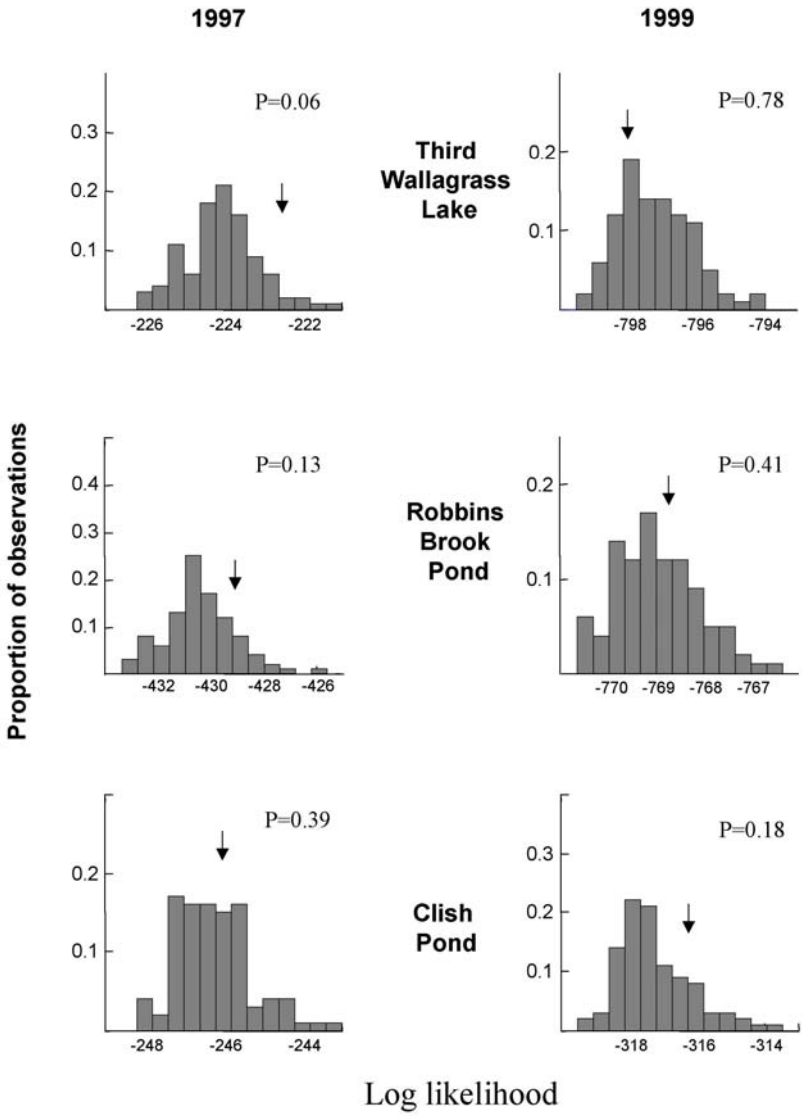

Figure 3-3 Distribution of loglikelihood of ML-partitions found in randomised populations. Arrows indicate observed values.

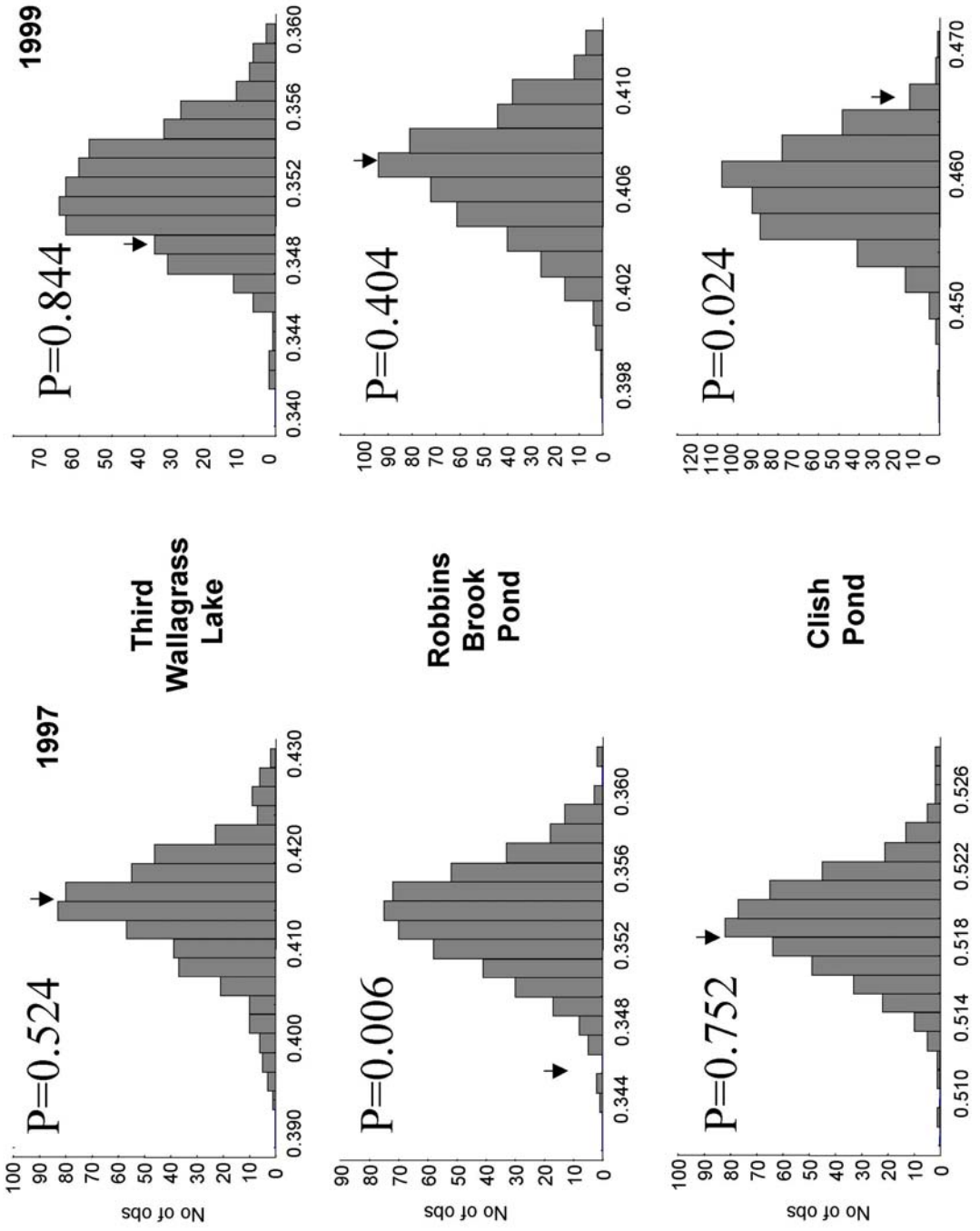

Figure 3-4 Distribution of pairwise relatedness coefficients estimated by Mathieu *et al.* (1990)'s identity coefficient assuming random association of monolocus genotypes. Arrows indicate observed values.

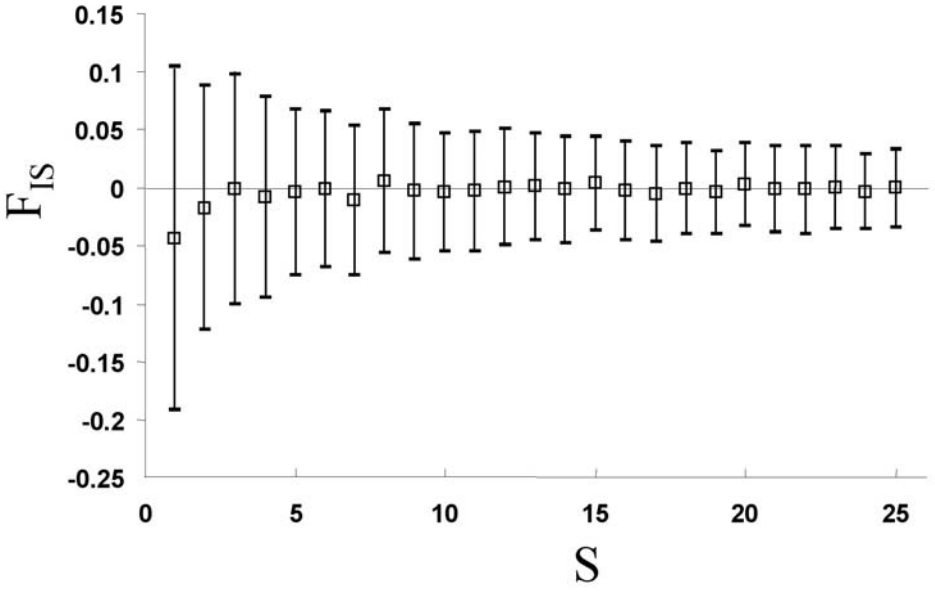

Figure 3-5 Deviation from Hardy-Weinberg proportions (Mean F_{IS} ± SD) as a function of S, the number of spawning grounds (see text for details).

4. The rise and fall of isolation by distance in the anadromous brook charr *Salvelinus fontinalis* Mitchill.

4.1. Résumé

Les patrons géographiques de la diversité génétique dépendent des propriétés démographiques d'une espèce évoluant au sein d'un habitat donné. Comme pour beaucoup d'espèce l'environnement et les propriétés démographiques peuvent tous deux évoluer dans le temps, la structure de la diversité génétique ne correspond souvent pas à ce qui pourrait être prédit par un simple examen de leur habitat. Il est alors crucial de connaître la vitesse à laquelle les patrons d'organisation approchent leur état d'équilibre stable. L'omble de fontaine *Salvelinus fontinalis* (Salmonidae) occupe des patchs d'habitat (rivières) organisés linéairement le long des aires côtières et connait des mouvements marins d'ampleur limitée. Un patron constant d'isolement par la distance devrait donc être observé tout du long de laire de répartition de l'espèce. Cette aire de répartition s'est cependant, récemment déplacée vers le nord suite au retrait de la calotte glaciaire de l'est du Canada. Les populations nordiques sont donc présentes depuis moins longtemps et peuvent donc être encore en chemin vers l'équilibre migration-dérive. Nous avons documenté les variations temporelles des patrons d'isolement par la distance, de différenciation génétique et de richesse allélique le lon,g de 4992 km d'une côte linéaire sur la route probable de recolonisation post-glaciaire en nous basant sur les génotypes à six locus microsatellite de 2087 ombles de fontaine anadromes issues de 59 populations. Nous avons observé un déclin la richesse allélique concomitant d'une augmentation des niveaux de différenciation et d'un déclin du signal d'isolement par la distance dans les populations les plus récemment colonisées au nord. Suite à cette progression initiale vers l'équilibre, cependant, les patrons d'organisation ne se maintenaient pas parmi les populations du sud. À la place, la richesse allélique diminuait, les populations étaient de plus en plus différenciées, et l'intensité des patrons d'isolement par la distance diminuait à nouveau, suggérant une fragmentation accrue des populations les plus anciennes. Nous proposons que la perte des capacités de dispersion associées à l'expression de l'anadromie est responsable de cette fragmentation accrue des populations du sud. Cette étude démontre donc que les patrons d'organisation géographique de la diversité génétique ne dépendent pas uniquement des propriétés démographiques d'une espèce dans un habitat donné : l'évolution de l'aire de répartition et de la forme de dispersion ont également une importance majeure. Ces considérations d'ordre biogéographique mènent au constant que la fenêtre temporelle à l'intérieur de laquelle les patrons spatiaux de diversité génétique reflètent l'interaction à long

terme d'une espèce avec son habitat peut être très réduite. Nos résultats introduisent donc une note de précaution quant à l'inférence de paramètres démographiques sur la seule base des patrons d'isolement par la distance. Plus généralement, ils argumentent pour une prise en compte plus générale d'une perspective biogéographique dans les études de génétique des populations.

4.2. Abstract

Geographic patterns of genetic variation depend on a species' demographic properties in a given habitat. Since both their environment and demographic properties evolve in time, many species will not fit the structure that would be predicted by a simple examination of their habitat. The rate at which patterns of genetic structure approach a stable equilibrium thus becomes pivotal in our understanding of spatial patterns of diversity. The brook charr *Salvelinus fontinalis* (Salmonidae) inhabits habitat patches (rivers) linearly organized along coastal areas and has limited movements at sea, such that a stable one-dimensional isolation by distance pattern should be observed over the whole range. The distribution range, however, recently shifted northward after the ice cap last retreated from eastern Canada, such that northern populations have been settled more recently and may still be on the process of reaching equilibrium. We investigated temporal variation in isolation by distance patterns, genetic divergence and allelic richness along 4992 km of a linear coast along the most likely northward postglacial colonization route of eastern Canada using individual genotypes of 2087 anadromous brook charr from 59 rivers at six microsatellite markers. We observed a decline in allelic richness, together with an increase in differentiation and a decrease in isolation by distance patterns in the most recently colonized populations in the North. Yet, after this initial rise towards equilibrium, spatial patterns did not stabilize among the most southern populations. Instead, allelic richness decreased, populations became increasingly divergent and isolation by distance patterns decreased in intensity again, suggesting increased fragmentation of older populations. We propose that the loss of dispersal capabilities associated with anadromy may be responsible for this increased fragmentation in the southern area of the range. This study thus demonstrated that geographic patterns of genetic variation depend not only on a species' demographic properties in a given habitat: the evolution of the species range and the evolution of the form of dispersal are also of prime importance. When taking such biogeographic considerations into account, the temporal window within which geographic patterns of genetic diversity reflect the long-term interaction of a species with the habitat it inhabits may actually be narrow. Our results thus provide a cautionary note for the inference of demographic parameters from the sole isolation by distance patterns and, more generally, they call for the inclusion of a biogeographic perspective in population genetics studies.

4.3. Introduction

With few exceptions (e.g. Whitlock 1992, Dybdahl 1994, Giles and Goudet 1997), population geneticists have considered that the current partitioning of genetic diversity in space reflects a species' long-term interaction with the habitat it reproduces in. Theoretical results have been obtained for increasingly realistic models of populations, among which isolation by distance (thereafter IBD) models are widely used because they account for the common observation that dispersal capabilities of many species are limited in most habitats. Obviously, this model should result in the increase of genetic differences with geographic distance (Wright 1943). This pattern of increase has been analytically derived using asymptotic properties of the equilibrium, i.e. after sufficient time has elapsed for patterns to be established and stabilized (Sawyer 1977). This equilibrium pattern should be most obvious when dispersal occurs along a linear transect than across a two-dimensional area (Kimura and Weiss 1964) and has been included within inference frameworks designed to estimate demographic parameters such as $N\sigma^2$ or Nm, the products of effective population size N by either the mean square of parent-offspring distance σ^2 (Rousset 1997) or by the fraction of a population replaced by migrants each generation m (Slatkin 1993). These methods are commonly used in the empirical literature of both plants and animals species (e.g. Neigel 1997, Bohonak 1999, Pogson et al. 2001 and references therein).

Such inferences, however, neglect that ecosystems are dynamic by nature (McArthur and Wilson 1967, Avise, 2000) and that species' ranges expand and shrink, sometimes at a fast pace (Brown et al. 1996, Kirkpatrick and Barton 1997, Davis and Shaw 2001). The last ice age in particular was one of tremendous periodic shifts in the range of most northern temperate species (Hewitt 2000). During this period, species followed the ice border, successively advancing and retreating, such that one may question the assumption that the time scale of these fluctuations was very large relative to the time required for equilibrium patterns to establish. Indeed, although the latter is quantitatively poorly known (but see Sawyer 1976, Slatkin 1993, Hardy and Vekemans 1999 for IBD patterns), the geographic distribution of genetic diversity of many species still bears the footprint of recent natural disturbances they

each experienced (reviewed in Hewitt 2000), thus providing empirical evidence that the rate of approach to equilibrium may be slow in comparison with the disturbance regime. This is problematic since contemporary spatial patterns of diversity should then be viewed as reflecting primarily past disturbances rather than current population dynamics and would therefore interfere with our understanding of the interaction between evolutionary processes and spatial patterns of genetic diversity. From a practical point of view, this is also of concern since reliable estimates of migration rates or dispersal distances are increasingly demanded as integral elements of applied management and conservation decisions.

Slatkin (1993) theoretically showed that in a species expanding its range instantaneously to a new bare habitat, the correlation between genetic and geographic distances should be first be low and then increase progressively until the pattern of increase reaches its stationary value. The pattern of increase should be most obvious in a one-dimensional habitat and be first attained at short geographic distances before the pattern spreads over larger geographic distances. The size of the region where IBD should be evident should increase with the parameter $\sqrt{2Nm\tau}$, where τ is the time since the foundation of the population, m is the fraction of migrants each generation and N is the subpopulation size. Thus, with small Nm values (low number of migrants each generation) and recent foundation (small τ), the observed rate of increase of genetic differences with distance in recently settled systems may reflect foundation processes rather than contemporary demographic parameters, especially at wider geographic scales.

Empirical studies monitoring the evolution of spatial patterns of genetic diversity provide an important contribution to our understanding of the origin of geographic patterns of genetic diversity (Boileau et al. 1992, Whitlock 1992, Dybdahl 1994, Hossært-McKey et al. 1996, Giles and Goudet 1997). Yet, they remain rare in the literature, mainly because dealing analytically with spatial and temporal heterogeneity in demographic parameters is inherently difficult. Populations located at the expanding edge of a species' range typically show a high occurrence of dispersing phenotypes (Thomas et al. 2001), low allelic richness (e.g. Taberlet et al. 1998, Frydenberg et al. 2002), while differentiation can be either decreased (e.g. Dybdahl 1994, Green et al. 1996, Comps et al. 2001, Wilcock et al. 2001, Bernatchez and Wilson 1998) or increased (Berlocher 1984, Johnson 1988, Whitlock 1992, McCauley et al.

1995, Ingvarsson and Giles 1999) depending on the dynamic of colonization (Slatkin 1977, Ibrahim et al. 1996, Austerlitz et al. 1997, 2000, Le Corre & Kremer 1998). Empirical data on the evolution of IBD patterns during the early settlement of a species in a new habitat remain even more scarce (but see Leblois et al. 2000, Barrai et al. 2001, Kinnison et al. 2002). A first approach relies on demographic estimates and colonization scenario to show that, would sufficient time have elapsed, IBD should have been apparent (e.g. Leblois et al. 2000, Kinnison et al. 2002). A drawback of this approach is that it relies entirely on the precision of demographic estimates and often cannot be disentangled from statistical impediments to detect an IBD signal. Indeed, the absence of a clear pattern of isolation by distance in species with restricted dispersal is typically taken as an indication that populations depart from equilibrium conditions, even if a precise knowledge of recent demographic events is lacking (e.g. Hellberg 1995, Baer 1998, Hutchison and Templeton 1999, Ehrich and Stenseth 2001). Using a second approach, other studies have compared IBD patterns among sets of populations of different ages (Green et al. 1996, Barrai et al. 2001) and ascribed differences in IBD patterns to their temporal evolution. This comparative approach requires a large amount of data and thus typically confines the comparison to a limited number of discontinuous sets of populations within a small portion of the species' range (north *vs*. south of North America in Green et al. 1996, USA *vs.* Europe in Barrai et al. 2001). Furthermore, because habitat structure and migration patterns may eventually vary among sets of populations, it may also be difficult to control for several sources of additional variation when the number of samples is small. In sum, although empirical studies have provided important insights into the evolution of geographic patterns of genetic diversity, they have remained limited in scope by the number of populations surveyed, by the lack of knowledge on historical events and demography, and by uncertainties about the precise migration pattern of the species in a given habitat.

The present study is based on a nearly exhaustive sampling of all existing anadromous populations of the brook charr (*Salvelinus fontinalis* Mitchill), a salmonid fish inhabiting a linear coast associated with a temporal gradient of colonization. This gradient allowed a continuous investigation of the temporal evolution of IBD patterns over a homogeneous habitat in the native range of the brook charr. The brook charr is endemic to north-eastern North America, where the last Ice Age resulted in a 50 000-70 000 years long series of rapid northward and southward shifts of the whole biota (Hoccutt 1986, Pielou et al. 1991). These

dramatic climatic oscillations came to an end no earlier than 18,000 years ago and the last northward shift in distribution followed the retreat of the Wisconsinian Ice Sheet from eastern Canada (11,000 YBP, Dyke and Prest 1987). Brook charr probably reinvaded eastern Canada northward from the single "Atlantic" glacial refugium (Danzmann et al. 1998) located off the Atlantic coast of New-England (Schmidt 1986). No paleontological data are available on the dynamic of recolonization, but marine movements of brook charr appear to be strictly restricted to the coastal fringe, suggesting that colonists had to closely follow the coastline and colonize rivers they now inhabit. The Gulf of Maine (USA) was freed of ice 13,000 years ago (Borns et al. 1985) and the lower north shore of St-Lawrence River (Province of Québec, Canada) 10,000 years ago (Denton and Terence 1980), so the minimum time span between colonization of both areas was 3,000 years. Furthermore, because brook charr populations had to follow their invertebrate prey, which in turn had to follow vegetational range shifts (de Vernal et al. 1993), they could not establish instantaneously, and the date of ice retreat therefore provides a maximum time frame within which the last colonization must have occurred. For instance, palynological studies indicate that modern vegetation only developed in western Labrador around 3,770 years ago (de Vernal and Hillaire-Marcel 1987). The South-North gradient thus also corresponds to a time gradient, whereby northern charr populations, putatively younger, were founded at least 3,000 years later than southern populations, and possibly as much as 9,230 years later. Although there seem to be no major physiological constraints to rare long-distance migration events as long as salinity and temperature conditions remain tolerable (salinity 26.9 ± 3.1ppt, temperature 10.4 ± 2.5ºC degrees, van de Sande, Curry and Whoriskey, unpublished manuscript), distances covered over a season by brook charr in the coastal zone are typically short (< 0.5 km, van de Sande, Curry and Whoriskey, unpublished manuscript). Because tolerable temperature and salinity conditions for brook charr are only found in the coastal fringe, distances swum towards the ocean in large open water masses are probably even more limited (White 1942, Besner and Pelletier 1991).

Taken together, the one-dimensional nature of coastal areas and the restricted movements of anadromous brook charr in this habitat suggest that isolation by distance should be apparent if time was sufficient for an IBD pattern to establish. Therefore, we first tested the null hypothesis of no correlation between coastal distance and genetic distances. Second, if equilibrium was reached all along the 4992 kilometers of coast, then no variation in the slope

of the IBD relationship should occur along this south-north temporal gradient. Alternatively, if the effect of colonization was still perceptible, a lower IBD slope should be observed among the most recently settled populations. We thus tested the null hypothesis of no variations in the slope of IBD along the colonization gradient. Third, if colonization processes still prevail at the northern edge of the range, they should also translate into changes in the levels of genetic diversity and divergence. We thus also tested the null hypothesis of no spatial pattern in variation of intrapopulation genetic diversity and the extent of genetic divergence.

4.4. Materials and methods

4.4.1. Sampling design

Two thousand and eighty seven anadromous brook charr were collected from 52 rivers along the Canadian Atlantic coast and seven rivers from Anticosti Island, Québec, Canada (mean N= 35.4, Table 1, Fig. 1), a sampling covering nearly 75 % of all important rivers inhabited by anadromous brook charr in the region (Ryther 1997). The brook charr occurs in coastal habitats as far south as North Carolina, USA (McCrimmon and Campbell 1969), but no anadromous movements (seasonal movements of fish between freshwater used at reproduction and by juveniles until the age of one or two years, and saltwater used at feeding stages, Power 1980) are currently known to occur south of the gulf of Maine, USA (Bigelow & Schroeder 1953). Therefore, samples were collected from one of the southernmost rivers where anadromous movements currently occur (Hunters' Brook in Acadia National Park, Maine, USA, labeled kilometer zero) and spanned northward over 4992 km of coastline to the Lower North Shore of St-Lawrence River (Fig 1.). All fish were collected either in saltwater in river mouths, or in freshwater in the downstream section of the rivers, below any physical barrier to migration. Distances among river mouths were measured along the coastline on 1/250,000 topographic maps. No major stocking effort occurred for the species in coastal areas, such that all populations can be considered as native. Adipose fins were nonlethally removed and preserved in 95% ethanol for genetic analyses.

4.4.2. microsatellite polymorphism

Total DNA was isolated using a standard phenol-chloroform protocol (Sambruck et al. 1989), and individuals were genotyped at six microsatellite loci (SFO-12, SFO-18, SFO-23, SFO-8, SSA-197 and MST-85) as described in Castric et al. (2001).

The number of different alleles per locus (A) was standardized to the smallest sample size (N=13, i.e. 26 alleles sampled) using a rarefaction method (Petit et al. 1998). Although our mean sample size was much higher (N=35.4), Petit et al. (1998) showed that their method provides an efficient way to directly compare estimates of allelic richness among populations

with different sample sizes. Genetic diversity was quantified by the observed heterozygosity H_O and the unbiased estimate of heterozygosity corrected for the sampling bias (H_E, Nei 1987). Population means of genetic diversity in the present study were compared to those observed in Maine (USA) for populations strictly restricted to landlocked freshwater habitats (Castric et al. 2001) using the Student's t test in Statview v.5.01. (SAS Institute Inc. 1998).

Departures from Hardy-Weinberg (HW) proportions were tested in each sample using an approximation of an exact test based on a Markov chain iteration implemented in the Genepop software package version 3.1 (Raymond and Rousset 1995). Multilocus values of significance for HW tests were obtained following Fisher's method to combine probabilities of exact tests (Sokal and Rohlf 1995). Critical significance levels for multiple testing were corrected following the sequential Bonferroni procedure (α=0.05, k=59, Rice 1989). The extent of deviation from HW proportions was quantified by Weir and Cockerham's (1984) estimator of F_{IS} (*f*) at each locus in each river using Genetix 4.02 (Belkhir et al. 2000). We also tested whether the same loci consistently exhibited stronger deficits across all populations using Kendall's concordance method (Sokal and Rohlf 1995 pp. 593).

Heterogeneity of allele frequencies across samples was tested with Genetix's permutation procedure using 2 000 permutations in the global test and 30 000 permutations in the pairwise test to maintain the tablewide significance level at α=0.05 after sequential Bonferroni correction (k=1711 pairwise comparisons). Global population differentiation was estimated in Genetix by Weir & Cockerham's (1984) F_{ST} estimator θ. A neighbor-joining phenogram based on Cavalli-Sforza and Edwards (1967) chord distance was constructed using Phylip 3.57c (Felsenstein et al. 1993) to depict the pattern of genetic relationships among populations. Support for the topology was estimated using 1000 bootstrap replicates.

4.4.3. Isolation by distance

Isolation by distance patterns were analyzed under Rousset's (1997) regression-based framework. With finite variance of parental position relative to offspring position (σ^2), a linear relationship is expected between $F_{ST}/(1-F_{ST})$ and distance between populations pairs (j) in a

one-dimensional linear habitat: $F_{ST}/(1-F_{ST}) \approx A_1/(4N\sigma) + j/(4N\sigma^2\varepsilon)$, where N is effective subpopulation size, A_1 is a constant dependent on the shape of the dispersal distribution (constant C_0 in Sawyer 1977, equation 2.4) and ε is the distance among consecutive habitat patches. A permutation test implemented in Genetix 4.02 (2000 permutations) was used to test the significance of Mantel's correlation coefficient between coastal distance and $F_{ST}/(1-F_{ST})$. We then tested whether isolation by distance was constant over geographic scales by computing the regression slope of $F_{ST}/(1-F_{ST})$ over coastal distance, successively including pairwise comparisons of populations separated by increasingly large distances and. That is, the slope at 100 km was obtained by including pairs of populations separated by 100 km or less, while all pairs at 200 km or less were included for the 200 km slope. All following analyses were performed using the mathematics computer language Maple® 6 (Waterloo Inc. 1999).

4.4.4. isolation by distance on the way towards equilibrium

The evolution of isolation by distance patterns along the temporal colonization gradient was further investigated using a sliding window analysis based on Rousset's (1997) inference framework described above. Because northward colonization most likely followed the coastline, latitudinal distribution measured along the coast was used as a surrogate for age of populations. A constant width window was slid along the coast, successively including different sets of populations from the southernmost population (population #1 at coastal kilometer 0) to the northernmost population (population #52 at km 4992). Since they were geographically isolated, samples from Anticosti Island were excluded from this analysis. The width of the window (600 km) was chosen as a compromise so as to be as narrow as possible while constantly including at least four populations over the main part of the range. In order to consistently compare values across geographic areas, sampling density was kept constant by resampling all possible sets of four populations within each window if it included more than four populations (final density =1 sample every 150 km) and by removing the window from the analysis otherwise. The slope and intercept of the least-square regression line of all possible four-population subsamples were computed within each 600 km window, and their mean over all possible combinations were plotted against the location of the southern end of

the window (in kilometers). The window was then shifted by 10 km increment northward along the coast and computations of the mean slope and mean intercept were performed again with the populations now included in the new 600 km span. The slope provides an estimate of $N\sigma^2$ and should progressively increase in recent systems (more northern populations) evolving towards equilibrium (Slatkin 1993, see Rousset 1997 for the equivalence with Slatkin's notation system). The intercept provides an estimate of $A_1/(N\sigma)$ and is thus also dependent upon the shape of the distribution via the parameter A_1. Leptokurtic dispersal distributions tend to be characterized by large A_1, such that variations in the intercept can reveal variations in σ or variations in the shape of dispersal distances. The evolution of the slope and intercept along the coast was tested using a backward stepwise model simplification procedure available in Statview to determine whether a quadratic correlation explained significantly more variance than a linear correlation.

4.4.5. Joint evolution of IBD, F_{ST} and Allelic richness

If colonization processes still prevail at the northern edge of the range and can be detected on isolation by distance patterns, they may also have left their footprint on the level of intrapopulation genetic diversity and on the extent of genetic divergence. This was tested by comparing linear and quadratic correlations between the standardized number of alleles and latitude following the coastline using the backward stepwise model simplification procedure available in Statview. The evolution of F_{ST} along the colonization gradient was investigated using the sliding window analysis described above for isolation by distance, and the existence of either a linear or a quadratic variation pattern was tested similarly. Because geographic variations in genetic diversity may compromise the use of the fixation index F_{ST} as an indicator of population differentiation (Whitlock & McCauley 1999, Hedrick 1999), a second analysis was run by standardizing F_{ST} estimates by the maximal theoretical value they could reach at a given level of diversity in a window: $1-H_E$.

4.5. Results

4.5.1. microsatellite polymorphism

High levels of allelic richness and genetic diversity were found at all loci (Table 2, Fig. 2). Thus, consistently more alleles were found within the anadromous than within the landlocked populations from Maine (Castric et al. 2001, t=6.086, P<0.0001). A globally significant heterozygote deficit was observed over the whole data set (F_{IS}= 0.0817, P<0.0005). Kendall's rank test provided evidence that several loci were consistently more affected than others (P=0.0057), thus suggesting that technical artifacts such as non-amplifying alleles (Callen et al. 1993) or small allele dominance (Wattier et al. 1998) at specific loci (SFO-8 and MST-85) may have contributed to the deficit. The rank correlation was however very weak (Kendall's W= 0.05) and the deficit could be detected over all loci (P<0.0005 for all six loci, Table 2), suggesting that non-artifactual explanations had to be taken into account (Castric et al. 2002). Heterozygote deficits could also partly result from a Walhund effect in several rivers (e.g. Boula et al 2002), which would bias the estimation of genotype frequencies, but not that of alleles. Furthermore, because no spatial pattern was obvious in the distribution of deficits, the occurrence of heterozygote deficits in several samples is unlikely to affect any of our main interpretations and conclusions.

Significant heterogeneity of allele frequencies was observed among populations (P<0.0005). The global F_{ST} value was 0.1068, but this figure varied geographically (Fig. 3). Significant differences in allele frequencies were observed in 1695/1711 pairwise comparisons (99.1%) after sequential Bonferroni correction (final α=0.00323). As indicated by their clustering in the neighbor-joining phenogram (Fig. 4), geographically proximate populations tended to be genetically similar. With the exception of Anticosti Island populations, significant bootstrap values were restricted to the tip nodes, suggesting that no strong barrier to gene flow existed along the coast. In contrast, populations from Anticosti Island clustered together with strong statistical support (Bootstrap=86%), thus providing direct support to the hypothesis that the open waters act as a strong barrier to gene flow in anadromous brook charr. All further analyses were thus restricted to samples collected along the coast.

4.5.2. Isolation by distance pattern analysis.

The genetic similarity of geographically proximate populations was further confirmed by the strong and highly significant correlation observed over the whole dataset between distance and genetic divergence (Fig. 5, Mantel's test: $r=0.5675$, $P<0.0005$). The best-fit regression model had a slope of 3.37×10^{-5} km^{-1} and an intercept of 0.07743. The slope, however, varied as a function of the spatial scale at which the relationship was examined (Fig. 6). When considering only pairs of populations separated by less than 50 km, considerable variation in the value of the slope was found (range = -0.00111 to 0.00247). This was followed by a monotonous log-linear decrease of the slope with increasing spatial scale (Fig. 6).

4.5.3. Isolation by distance evolving towards equilibrium.

There was considerable geographic variation in the regression slope of the IBD pattern, especially at latitudes less than 1500 km, where negative as well as positive values were observed (Fig. 7). However, values were centered on zero, suggesting the absence of any significant trend in IBD pattern at latitudes less than 1500 km. When excluding southern populations below 1500 km from the analysis, IBD slopes followed a quadratic pattern of variation ($R^2=0.703$, $P<0.0001$) rather than the linear variation predicted if populations had been progressing monotonously towards equilibrium. The maximum slope was attained near population 30 at kilometer 3366. Similarly, geographic variation in the IBD intercept were quadratic rather than linear ($R^2=0.767$, $P<0.0001$), thus suggesting that a minimal value for parameter $A_1/(N\sigma)$ occurred at kilometer 2646 i.e. between populations 17 and 18 (Fig. 8). Commercial landings reveal no reduction in population size towards the north (Malouin 1996), such that increases in intercept may reveal higher A_1 (such as produced by more leptokurtic dispersal distributions) or lower σ (such as produced e.g. by lower migration rates).

4.5.4. Joint evolution of IBD, F_{ST} and allelic richness.

As for IBD slope and intercept, allelic richness and F_{ST} varied geographically, with a quadratic model capturing significantly more variance than a linear model (backward simplification procedure, Fig. 2, $P=0.0032$ and Fig. 3, $P<0.0001$ respectively). The number of alleles followed a bell-shaped pattern of geographic variation, with highest levels of diversity at intermediate latitude than either further north or further south. Thus, the least square

parabola showed a maximum allelic richness at km 2945, i.e. in the Chaleur's Bay near population 19 (Fig. 1, 2). The sliding window analysis revealed that F_{ST} also followed a quadratic pattern of variation, with lower values at intermediate latitudes (kilometer 2444, between populations 13 and 14) than either North or South (Fig. 4, backward simplification procedure, $P<0.0001$). Correcting for variation in intrapopulation diversity also provided a highly significant quadratic pattern of latitudinal variation ($P<0.0001$, data not shown), indicating that the different upper bounds possibly reached by F_{ST} with different levels of diversity were not responsible for this pattern.

4.6. Discussion

Overall, our results provided evidence for important variation in geographic patterns of genetic diversity and structuring among anadromous brook charr populations in eastern Canada. Isolation by distance appeared to be the basic process shaping population genetic structure in this species. Yet, the comparative analysis also showed that contemporary patterns of IBD, allelic richness and genetic divergence were different in areas colonized at different times. This suggests that the time scale required for equilibrium patterns to settle may be of the same order of magnitude as that of demographic disturbances experienced by brook charr over a large portion of its range during postglacial times. Contrary to the expectation under a simple "equilibration" model, however, spatial patterns did not maintain constant once they had emerged. Indeed, variation in latitudinal patterns of genetic diversity was also apparent at the southern end of the range, where populations have been present for a longer period of time. We propose that anadromy as a form of dispersal has declined in the region that was first colonized following deglaciation, leading to increased fragmentation, which is now blurring the patterns that were initially shaped by drift and migration. Our results therefore indicate that the temporal window within which latitudinal patterns of genetic diversity reflect the species' long-term interaction with its habitat may be narrow.

4.6.1. Biology of seawater migrations.

This study first provided insights into the biology of coastal migration of the brook charr. High levels of intrapopulation genetic diversity were also found compared to landlocked populations from Maine (Castric et al. 2001), indicating that the coastal habitat provides better opportunities for migration. Despite high connectivity in anadromous relative to freshwater populations, brook charr found in different rivers, even those separated by short distances, were genetically distinct, indicating that straying rates are low and/or homing is precise. This was most obvious in southern populations, where the regression curve predicted 24.8 alleles over the six microsatellite for the southernmost population (km 0). This low value was similar to levels found in lacustrine populations from Maine (Castric et al. 2001), thus suggesting that the loss of anadromy rendered populations as isolated as landlocked populations. The significant correlation observed between $F_{ST}/(1-F_{ST})$ and geographic distance together with the strong clustering of Anticosti populations also confirmed earlier direct observations of limited

movements of brook charr in high salinity waters (White 1942). Such limited movements may be explained by the species limited tolerance for high salinity water, but more elaborate mechanisms may be invoked as well. The observation of repeated incursions of fish into non-natal rivers before entering their "home" river (Smith and Saunders 1958) may suggest that the potential for straying is greater than shown by the genetic differentiation and that the homing behavior is active and strong. Direct observations and experimental data, however, remain elusive (but see Keefe and Winn 1990). Field observations of fish repeatedly returning to spawn in the same spawning ground within a river (S. Lenormand and J. J. Dodson, unpublished data) and evidence for genetic distinctiveness of fish spawning on different spawning grounds within a same river system (Boula et al. 2002) provide further support for the hypothesis that homing can be precise down to very fine geographic scales.

4.6.2. Initial formation of spatial patterns: "The rise…":

Had only the biology of seaward migration been taken into account and assuming equilibrium conditions, then no pronounced variation in the spatial patterns of either allelic richness, population similarity or isolation by distance patterns would be expected. Yet, each of these patterns decreased with increased latitude. Because northern latitudes are also the most recently colonized regions along the temporal gradient, our data supports the hypothesis that colonization processes are still prevailing in shaping spatial patterns of genetic diversity among northern populations. In phylogeographic studies, gradients of genetic diversity are commonly observed as the result of sampling processes during colonization from southern glacial refugia (Hewitt 1996, Avise 2000), thus suggesting that mutation rates and/or subsequent migration are usually too low for equilibrium levels of allelic richness to recover. The effect of colonization on population differentiation is less straightforward because it depends on the number and origin of colonists (Slatkin 1977, Le Corre and Kremer 1998). Assuming that the pattern of migration operating at earlier times of colonization was comparable to that observed among contemporary populations, colonists would have been successively drawn from the most recent populations at every step of the process. With numerous colonists, the sampling effect should have been negligible and lower levels of divergence among populations would have been expected in recent compared to older populations (Good's model of stepwise colonization in Slatkin 1993; Bernatchez and Wilson

1998). In contrast, with low number of colonists, a stepwise colonization would involve successive founder events and should thus lead to increased divergence in recently colonized populations (Le Corre and Kremer 1998). The general increase of divergence and decrease in allelic richness we observed in northern populations therefore suggests that founder effects may have prevailed at times of recolonization following deglaciation. Assuming constant N and σ across populations, the increased intercept of the IBD relationship (related to parameter $A_1/N\sigma$) in northern areas further indicates a leptokurtic distribution of dispersal distances during colonization (high A_1). If so, the early dynamic of colonization of new areas would have been very different from the contemporary dynamic of migration. Contrasts between early colonization and subsequent migration dynamics have been proposed in other studies, especially for plant species where colonization occurs through seeds while subsequent gene flow primarily occurs through pollen (Combs et al. 2001). In salmonids, exponential demographic growth of salmonid populations is frequently reported after removal of barriers to migration (e.g. Bryant et al. 1999, Tremblay et al. 2000). Competition may thus quickly intensify following population founding, decreasing fitness of subsequent migrants compared to colonists (Nichols and Hewitt 1994, Davis and Shaw 2001).

4.6.3. "… and fall.": disruption of spatial patterns and the evolution of dispersal.

Assuming that non-equilibrium dynamics had been the sole factor explaining the observed variation of latitudinal patterns of genetic diversity, then such patterns should have remained constant once established at equilibrium. Clearly, this was not the case, as all patterns were quadratic rather than linear. That is, following their initial increase allelic richness and the IBD slope decreased and the extent of population differentiation increased among southern populations. As the southernmost populations were progressing towards increased fixation, spatial patterns became blurred and varied randomly among them. Similar trends of decreased population connectivity at range margins have been observed in other taxa, including the green frog *Rana pretiosa* (Green et al. 1996) and the brown trout *Salmo trutta* (Bouza 1999) and have been interpreted as a lack of adaptation of the species to the marginal habitat. Why then have southern populations of anadromous brook charr evolved towards increased fragmentation? We propose two non-exclusive hypotheses for increased fragmentation among

southern populations that involve the evolution of anadromy. Because individual growth is increased in the marine environment due to higher food availability, payoffs for switching between habitats may outweight the costs of physiological acclimations to a hyper- and a hypo-osmotic environment (Boula et al. 2002). As such, anadromy may firstly be strictly viewed at as form of seasonal migration driven by the productivity gradient between fresh- and saltwater. Because this gradient declines in intensity at temperate latitudes (Gross et al. 1988), selective pressures for anadromous behavior become weaker and eventually disappear. Thus far, the evolution of anadromy has mainly been interpreted in that perspective. Yet, because anadromous behavior also provides the opportunity to reproduce in a different river, it is also subjected to the forces driving the evolution of dispersal (reviewed in Clobert et al. 2001). Namely, habitat instability ranks among the most powerful forces selecting for dispersal (Gandon & Michalakis 2001), while a costly dispersal form should decline in frequency in a stable environment (Van Valen 1971, Olivieri et al. 1995 Fig. 3, Cody & Overton 1996). Assuming that the more southern habitat occupied by the brook charr in postglacial times can be considered as stable, theory predicts that anadromy should decrease among southern (and therefore older) populations. The rate of decrease may be slow (Paradis 1998) and depends on several parameters, including the fitness cost of dispersing (Olivieri et al. 1995), mutation rate, and the level of habitat fragmentation (Paradis 1998). To summarize, whatever the exact causes for the loss of anadromy among southern populations, our results clearly indicate that brook charr populations inhabiting different rivers at southern latitudes are becoming increasingly isolated one from each other, which is leading to a independent drift and thus progressive disruption of geographic patterns of genetic diversity observed among more northern (and younger) populations.

4.6.4. Scale-dependence of IBD patterns.

As pointed by Rousset (1997, 2001) but seldom taken into account in empirical studies (but see Hellberg 1995, Ruckelshaus 1998, Ehrich and Stenseth 2001), the estimation of demographic parameters from the slope of the IBD relationship is strongly affected by the spatial scale of observation. Thus, our results showed that the IBD slope first varied randomly until scales of 50 km were considered, then decreased monotonously. Similar fading of IBD at larger geographic scales has been observed in several species (Hellberg 1995, Johnson and

Black 1998, Ehrich and Stenseth 2001) and has received various explanations. First, as genetic differences increased with geographic distances, F_{ST} may plateau if it reached its upper bound at large geographic distances. The mean expected heterozygosity was 0.72, such that the maximum theoretical F_{ST} value should be approximately 0.28 (Hedrick 1999). Because this value is much higher than the level of differentiation actually observed (F_{ST} = 0.11), a plateau seems unlikely to have been reached in this study. Second, the fading could reflect a non-equilibrium situation. The spatial scale over which isolation by distance signal should be apparent during the transitory period towards equilibrium in a one-dimensional array of populations depends upon the parameter $\sqrt{2Nm\tau}$ (Slatkin 1993). Thus, for recent systems (small τ values), IBD may be weak over large geographic scales and consequently remain undetected. Third, and non-exclusively, mutation may not remain negligible relative to migration when increasing geographic scales. Because mutations arise randomly in space, theory predicts that their effect should be similar to island migrations (Crow and Kimura 1970) and weakens the relationship between genetic and geographic distances. Regardless of the exact explanation for this scale-dependence, it is problematic since it is precisely the slope that is used in empirical studies to estimate $N\sigma^2$. Rousset (1997, 2001) advocates the use of prior independent estimates of σ to delimit the scale over which the linear relationship between $F_{ST}/(1-F_{ST})$ is expected to hold reasonably well. In cases where no such estimate is available and/or is difficult to obtain, we propose an investigation of the scale-dependence of the IBD slope as a possible alternative. We suggest that the maximum slope after random fluctuations at short distances have ceased (approximately 50 km in this study) would be most accurate and should be used to infer $N\sigma^2$ values because any bias would then be minimal.

In addition to scale-dependence, important latitudinal variation in IBD slope was observed even when controlling for scale of analysis and sampling density. As detailed above, those variations probably arise from spatial and temporal variations in migration parameters. New analytical methods, such as maximum likelihood frameworks (Beerli and Felsenstein 1999, Bahlo and Griffith 2000) may represent promising avenues to investigate the limitations imposed by spatial and temporal variations in migration parameters. The joint estimation of migration rates, speed of recolonization and decrease in the frequency of migrating

phenotypes that would maximize the likelihood of observing the data may thus become possible in the near future.

4.6.5. Conclusions

Processes underlying spatial patterns of genetic diversity must be correctly identified and accurately understood since they may impact a species' potential to respond to selection and to persist in the face of changing environments (Kirkpatrick and Barton 1997, Thomas et al. 2001). To that end, population genetics approaches have usually considered static systems, whereby spatial patterns of genetic diversity reflect a species' ecological characteristics with little regard for their evolution through time. Although mathematically simplifying, the assumption of temporal stability may prove especially unwieldy in evolutionarily young systems, because it fails to capture the dynamic essence of spatial patterns of genetic diversity, as was exemplified in this study. Clearly then, traditional population genetic models assuming equilibrium are not always adequate to characterize young populations. Most attempts to characterize the genetic impacts of habitat fluctuations have concentrated on smaller geographic scales in the framework of extinction-recolonization dynamic in metapopulations (e.g. Slatkin 1977, McCauley 1993). At a wider geographic and temporal scale however, the availability of suitable habitat has also constantly fluctuated due to climatic changes driven by the rotation axis of the earth (Pielou 1991). Our results reinforce the view that a biogeographic perspective is essential in order to fully understand the evolution of geographic patterns of genetic variation such as isolation by distance.

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Table 4-1 Anadromous brook charr samples collected. Geographic regions are based on coastal mophology.

Label	Sample location	Geographic region	Coastal distance from km 0	Latitude N	Longitude W	N
1	Hunter's brook	Gulf of Maine	0			40
2	Rivière Kennebecassis	Bay of Fundy	280	45° 19' 00"	66° 08' 00	41
3	Dolan Brook	Bay of Fundy	345	45° 21' 00"	65° 38' 00"	33
4	Cornwallis River	Bay of Fundy	530	45° 06' 00"	64° 21' 00"	40
5	Acacia Brook	Bay of Fundy	786	44° 35' 00"	65° 45' 00"	25
6	Jordan River N.S.	Bay of Fundy	1086	43° 46' 00"	65° 14' 00"	29
7	Petite Rivière	Atlantic Coast, N.-S.	1166	44° 14' 00"	64° 26' 00"	29
8	West River St-Mary	Atlantic Coast, N.-S.	1406	45° 15' 00"	62° 04' 00"	24
9	Baddeck River	Atlantic Coast, N.-S.	1806	46° 05' 00"	60° 52' 00	39
10	Clyburn Brook	Atlantic Coast, N.-S.	1886	46° 40' 00"	60° 24' 00"	30
11	McKenzies River	Magdalen Shelf	1956	46° 48' 25"	60° 49' 35"	30
12	South River	Magdalen Shelf	2126	45° 36' 00"	61° 55' 00"	38
13	Wallace River	Magdalen Shelf	2302	45° 49' 00"	63° 31' 00"	24
14	Black River	Magdalen Shelf	2522	47° 03' 00"	65° 13' 00"	15
15	Rivière Kouchibouguacis	Magdalen Shelf	2522	46° 47' 00"	64° 54' 00"	30
16	Cains Brook	Magdalen Shelf	2582	45° 41' 00"	65° 02' 00"	17
18	Rivière Tabusintac	Magdalen Shelf	2676	47° 20' 00"	64° 56' 00"	36
19	Rivière Jacquet	Chaleur's bay	2956	47° 55' 00"	66° 01' 00"	23
20	Rivière Matapedia	Chaleur's bay	2959	47° 58' 17"	66° 56' 32"	19
21	Rivière Patapedia	Chaleur's bay	2959	47° 51' 00"	67° 23' 00"	23
22	Rivière Restigouche	Chaleur's bay	2959	48° 04' 00"	66° 20' 00"	30
23	Rivière Nouvelle	Chaleur's bay	3019	48° 06' 14"	66° 16' 58"	30
24	Rivière Petite-Cascapedia	Chaleur's bay	3079	48° 09' 26"	65° 51' 14"	46
25	Rivière Bonaventure	Chaleur's bay	3110	48° 25' 16"	65° 30' 15"	50
26	Rivière Port Daniel	Chaleur's bay	3141	48° 10' 01"	64° 57' 45"	35
27	Rivière de l'A. à Beaufils	Chaleur's bay	3212	48° 28' 15"	64° 18' 33"	46
28	Ruisseau Murphy	Chaleur's bay	3251	48° 34' 19"	64° 17' 42"	31
29	Rivière St-Jean	Gaspésie	3286	48° 46' 08"	64° 26' 51"	35
30	Rivière York	Gaspésie	3301	48° 48' 57"	64° 33' 18"	19
31	Rivière de l'A. à Valleau	Gaspésie	3421	49° 05' 00"	64° 33' 00"	55

32	Rivière Grande Vallée	Gaspésie	3453	49° 14' 00"	65° 08' 00"	49
33	Ruisseau Manche d'Épée	Gaspésie	3476	49° 15' 00"	65° 26' 00"	57
34	Rivière Mont-Louis	Gaspésie	3499	49° 14' 00"	65° 44' 00"	42
35	Rivière Marsoui	Gaspésie	3525	49° 13' 00"	66° 04' 00"	21
36	Rivière Ste-Anne	Gaspésie	3558	49° 08' 00"	66° 30' 00"	15
37	Rivière Cap-Chat	Gaspésie	3578	49° 06' 00"	66° 40' 00"	28
38	Rivière Ste-Marguerite	North Shore	3958	48° 15' 49"	69° 56' 47"	50
39	Rivière des Escoumins	North Shore	3990	48° 20' 50"	69° 27' 00"	50
40	Rivière Laval	North Shore	4030	48° 46' 00"	69° 03' 00"	68
41	Rivière Godbout	North Shore	4158	49° 19‘ 00"	67° 35‘ 0O"	22
42	Rivière Trinité	North Shore	4188	49° 25' 05"	67° 18' 16"	50
43	Rivière du Calumet	North Shore	4214	49° 37' 00"	67° 13' 00"	48
44	Rivière Ile de Mai	North Shore	4264	49° 55' 38"	66° 57' 50"	50
45	Rivière Moisie	North Shore	4344	50° 16' 00"	65° 56' 00"	49
46	Rivière St-Jean	North Shore	4472	50° 17' 00"	64° 20' 00"	50
47	Baie-Johann-Beetz	Lower North Shore	4592	50° 17' 00"	62° 48' 00"	13
48	Rivière Washicoutai	Lower North Shore	4736	50° 13' 00"	60° 52' 00"	48
49	Rivière Watasheistic	Lower North Shore	4846	50° 24' 00"	59° 50' 00"	31
50	La Tabatière	Lower North Shore	4896	50° 50' 00"	58° 59' 00"	48
51	Rivière St-Augustin	Lower North Shore	4944	51° 12' 00"	58° 35' 00"	46
52	Rivière St-Paul	Lower North Shore	4992	51° 27' 00"	57° 42' 00"	41
A1	Rivère Bec-Scie	Anticosti Island	-	49° 43' 00"	64° 03' 20"	30
A2	Rivière à la Loutre	Anticosti Island	-	49° 37' 00"	63° 48' 00"	27
A3	Rivière Jupiter	Anticosti Island	-	49° 28' 34"	63° 35' 37"	26
A4	Rivière Ferrée	Anticosti Island	-	49° 09' 15"	62° 42' 55"	45
A5	Rivière Chaloupe	Anticosti Island	-	49° 08' 00"	62° 32' 00"	32
A6	Rivière Patate	Anticosti Island	-	49° 43' 00"	62° 55' 00"	24
A7	Rivière McDonald	Anticosti Island	-	49° 45' 27"	63° 03' 10"	15

Table 4-2 Number of alleles (A) standardized to 26 alleles, expected (H_E) and observed heterozygosity (H_O), F_{IS} estimate (*f*) and significance of the test for Hardy-Weinberg equilibrium (P_{HW}). Overall significant P-values following Bonferroni correction are indicated in bold. 0 stands for P_{HW} <0.0005

	Sample	1	2	3	4	5	6
SFO-12	A	4.99	5.52	4.50	3.83	4.36	2.96
	H_E	0.646	0.671	0.704	0.692	0.642	0.423
	Ho	0.600	0.725	0.645	0.590	0.792	0.310
	f	0.072	-0.082	0.085	0.149	-0.24	0.27
	P_{HW}	0.4428	0.7701	0.0095	0.1223	0.959	0.0098
SFO-18	A	3.97	6.11	3.98	5.17	3.55	4.92
	H_E	0.622	0.790	0.464	0.727	0.292	0.763
	Ho	0.486	0.778	0.375	0.775	0.320	0.464
	f	0.222	0.015	0.195	-0.067	-0.097	0.396
	P_{HW}	0.1313	0.5593	0.0069	0.8595	1	0.0007
SFO-23	A	6.33	10.47	9.21	12.41	6.34	9.54
	H_E	0.702	0.898	0.864	0.913	0.771	0.883
	Ho	0.649	0.925	0.633	0.947	0.640	0.607
	f	0.077	-0.03	0.271	-0.038	0.173	0.316
	P_{HW}	0.3356	0.7886	0	0.3634	0.0231	0
SFO-8	A	6.79	14.27	7.74	8.57	6.11	12.28
	H_E	0.688	0.942	0.790	0.796	0.779	0.917
	Ho	0.737	0.868	0.471	0.686	0.840	0.846
	f	-0.071	0.079	0.411	0.141	-0.08	0.079
	P_{HW}	0.7698	0.0468	0	0.006	0.857	0.0409
SSA-197	A	1.99	3.35	3.88	2.40	3.34	2.00
	H_E	0.258	0.302	0.334	0.192	0.570	0.503
	Ho	0.300	0.290	0.375	0.207	0.625	0.393
	f	-0.164	0.042	-0.126	-0.08	-0.099	0.223
	P_{HW}	1	0.411	1	1	0.6749	0.21
MST-85	A	5.52	8.02	6.70	8.68	3.05	6.18
	H_E	0.668	0.817	0.838	0.883	0.329	0.821
	Ho	0.649	0.800	0.720	0.821	0.333	0.667
	f	0.029	0.02	0.143	0.071	-0.014	0.191
	P_{HW}	0.5976	0.1338	0.0821	0.0807	0.6008	0.0316
All	A	4.93	7.96	6.00	6.84	4.46	6.31
	He	0.598	0.737	0.666	0.700	0.564	0.718
	Ho	0.570	0.731	0.537	0.671	0.592	0.548
	f	0.05151	0.0235	0.20416	0.02844	-0.00707	0.26281

	P_{HW}	0.4812	0.0993	***0***	0.0241	0.7134	***0***

7	8	9	10	11	12	13
2.04	3.00	4.48	4.64	5.76	6.89	5.91
0.086	0.568	0.652	0.734	0.762	0.820	0.806
0.087	0.708	0.737	0.724	0.897	0.694	0.739
-0.011	-0.253	-0.132	0.014	-0.18	0.155	0.084
1	0.9836	0.5569	0.3935	0.9387	0.0387	0.2262
5.71	5.68	4.04	4.99	6.73	5.31	4.32
0.729	0.757	0.318	0.617	0.684	0.673	0.624
0.640	0.739	0.351	0.524	0.546	0.600	0.650
0.124	0.023	-0.105	0.154	0.206	0.11	-0.042
0.1667	0.563	1	0.2101	0.0034	0.1567	0.7182
9.20	10.45	12.25	7.89	10.49	11.76	11.70
0.884	0.902	0.917	0.796	0.911	0.925	0.916
0.889	0.864	0.889	0.750	0.846	0.865	0.750
-0.006	0.043	0.031	0.059	0.073	0.065	0.184
0.3721	0.3401	0.179	0.4825	0.1794	0.092	0
8.38	8.93	12.89	10.47	13.75	12.54	12.99
0.767	0.866	0.924	0.847	0.925	0.890	0.918
0.727	0.682	0.970	0.778	0.750	0.886	0.833
0.054	0.216	-0.051	0.083	0.192	0.005	0.094
0.3999	0.0023	0.8883	0.0158	0.1213	0.3899	0.0573
3.18	4.05	4.55	3.43	3.50	4.20	3.78
0.541	0.579	0.682	0.624	0.554	0.651	0.618
0.643	0.625	0.622	0.600	0.333	0.714	0.542
-0.193	-0.082	0.09	0.04	0.404	-0.098	0.126
0.873	0.7188	0.4227	0.3927	0.0061	0.8752	0.3536
7.00	6.41	7.02	5.93	7.94	9.37	7.55
0.863	0.813	0.809	0.620	0.825	0.900	0.749
0.300	0.696	0.737	0.552	0.800	0.886	0.583
0.665	0.147	0.09	0.111	0.031	0.016	0.225
0	0.1745	0.1189	0.2709	0.2325	0.4715	0.0251
5.92	6.42	7.54	6.23	8.03	8.35	7.71
0.645	0.747	0.717	0.706	0.777	0.810	0.772
0.548	0.719	0.718	0.655	0.695	0.774	0.683
0.16843	0.05972	0.045	0.08965	0.16691	0.02638	0.14362
0.0154	0.1052	0.3734	0.0157	0.0036	0.0052	***0***

14	15	16	17	18	19	20	21
5.77	4.84	4.69	5.03	4.81	4.25	5.55	6.31
0.775	0.748	0.731	0.725	0.678	0.590	0.772	0.792
0.867	0.800	0.824	0.851	0.694	0.522	0.737	0.714
-0.123	-0.071	-0.131	-0.176	-0.024	0.119	0.047	0.1
0.6674	0.7708	0.7885	0.0421	0.4665	0.0787	0.3758	0.2314
4.70	5.09	4.57	5.13	7.02	5.76	3.32	6.51
0.484	0.607	0.514	0.652	0.819	0.620	0.259	0.749
0.429	0.586	0.563	0.745	0.743	0.667	0.278	0.783
0.119	0.034	-0.098	-0.144	0.094	-0.077	-0.076	-0.046
0.0718	0.0395	0.8751	0.9586	0.2266	0.5344	1	0.1137
8.33	13.48	11.48	11.71	12.07	12.06	10.91	10.93
0.837	0.938	0.893	0.914	0.916	0.853	0.794	0.872
0.600	0.767	0.824	0.918	0.829	0.909	0.833	0.909
0.29	0.185	0.08	-0.005	0.097	-0.067	-0.052	-0.043
0.0586	0.034	0.3078	0.275	0.0251	0.9506	0.919	0.504
8.55	11.40	13.70	10.92	12.51	14.34	16.80	14.78
0.881	0.921	0.921	0.906	0.913	0.932	0.969	0.951
0.786	0.800	1.000	0.860	0.778	0.895	0.895	0.850
0.112	0.134	-0.088	0.051	0.15	0.041	0.078	0.109
0.2169	0.1234	1	0.0148	0.0945	0.4466	0.0466	0.0013
3.00	3.39	3.81	3.70	3.80	3.48	3.94	4.77
0.569	0.586	0.673	0.618	0.618	0.556	0.597	0.681
0.429	0.429	0.688	0.680	0.515	0.476	0.500	0.727
0.254	0.273	-0.022	-0.102	0.168	0.147	0.167	-0.07
0.2749	0.1049	0.5105	0.9061	0.2609	0.0139	0.2872	0.531
6.19	6.32	7.18	9.05	6.65	6.52	6.61	9.11
0.786	0.742	0.832	0.879	0.827	0.821	0.794	0.865
0.800	0.800	0.647	0.840	0.778	0.682	0.750	0.619
-0.018	-0.08	0.228	0.044	0.06	0.173	0.058	0.29
0.5514	0.8542	0.0421	0.3859	0.2797	0.0739	0.4718	0
6.09	7.42	7.57	7.59	7.81	7.73	7.85	8.74
0.722	0.757	0.761	0.782	0.795	0.729	0.697	0.818
0.652	0.697	0.757	0.816	0.723	0.692	0.665	0.767
0.12329	0.0941	0.01473	-0.01827	0.11018	0.05182	0.06702	0.04964
0.0637	***0.0005***	0.3152	0.0438	0.0032	0.0172	0.1373	***0.0001***

22	23	24	25	26	27	28	29
7.09	6.30	4.72	5.32	3.96	5.31	5.18	4.53
0.842	0.760	0.693	0.720	0.720	0.763	0.739	0.685
0.643	0.690	0.783	0.694	0.941	0.848	0.484	0.743
0.239	0.095	-0.132	0.036	-0.313	-0.113	0.349	-0.087
0.0201	0.1216	0.1094	0.345	0.9991	0.8492	0.0013	0.8549
4.93	6.09	5.38	4.21	3.47	3.54	5.08	3.97
0.652	0.726	0.659	0.731	0.407	0.562	0.776	0.706
0.552	0.607	0.581	0.674	0.429	0.578	0.548	0.833
0.156	0.166	0.119	0.079	-0.055	-0.028	0.297	-0.185
0.3384	0.1508	0.1417	0.1345	0.7746	0.5952	0.0006	0.9563
10.22	5.30	7.62	9.08	11.34	8.16	11.42	10.39
0.884	0.632	0.672	0.790	0.898	0.839	0.899	0.756
0.857	0.679	0.630	0.816	0.800	0.767	0.871	0.818
0.031	-0.075	0.062	-0.033	0.11	0.086	0.032	-0.084
0.2334	0.8785	0.0131	0.5844	0.156	0.1462	0.0282	0.9267
16.21	11.89	13.41	14.40	15.42	16.50	13.17	14.39
0.959	0.908	0.919	0.932	0.939	0.965	0.935	0.927
0.966	0.714	0.744	0.917	0.807	0.800	0.909	0.794
-0.007	0.217	0.193	0.017	0.143	0.173	0.028	0.145
0.553	0.0163	0	0.423	0	0	0.2058	0
3.44	4.20	3.62	3.90	4.74	4.26	5.17	3.38
0.635	0.630	0.581	0.665	0.733	0.735	0.766	0.602
0.517	0.846	0.552	0.617	0.686	0.733	0.821	0.727
0.188	-0.353	0.051	0.073	0.065	0.002	-0.074	-0.212
0.1102	0.9947	0.4426	0.2314	0.3791	0.5877	0.8562	0.9416
7.78	7.21	7.02	8.15	6.41	4.67	7.19	5.19
0.852	0.801	0.814	0.858	0.637	0.453	0.708	0.703
0.621	0.346	0.816	0.820	0.618	0.489	0.444	0.485
0.275	0.573	-0.003	0.045	0.031	-0.081	0.377	0.314
0	0	0.2773	0.1594	0.197	0.9118	0.0017	0.0055
8.28	6.83	6.96	7.51	7.56	7.07	7.87	6.97
0.804	0.743	0.723	0.783	0.722	0.720	0.804	0.730
0.693	0.647	0.684	0.756	0.713	0.703	0.680	0.733
0.14752	0.11761	0.0792	0.03715	0.04866	0.00505	0.147	0.00874
0.0021	***0***	***0***	0.3452	0.0613	0.1002	***0***	0.036

30	31	32	33	34	35	36	37
5.85	5.86	4.49	5.11	4.91	5.89	4.98	5.47
0.733	0.779	0.690	0.629	0.707	0.733	0.743	0.805
0.684	0.836	0.714	0.625	0.800	0.778	0.857	0.750
0.068	-0.074	-0.036	0.007	-0.134	-0.063	-0.16	0.07
0.2746	0.0534	0.525	0.5131	0.9518	0.1802	0.5862	0.3573
3.84	3.88	4.44	3.67	3.99	4.28	3.99	6.31
0.527	0.484	0.603	0.577	0.520	0.532	0.712	0.795
0.333	0.415	0.551	0.509	0.378	0.438	0.500	1.000
0.374	0.143	0.087	0.118	0.275	0.183	0.305	-0.267
0.0027	0	0.0061	0.1633	0.0207	0.58	0.0603	1
7.39	10.37	10.43	7.51	10.97	11.32	8.13	8.87
0.623	0.786	0.868	0.827	0.890	0.897	0.733	0.790
0.526	0.836	0.878	0.768	0.857	0.778	0.533	0.700
0.159	-0.065	-0.011	0.072	0.037	0.136	0.28	0.116
0.0151	0.8769	0.2113	0.1876	0.0802	0.0168	0.0146	0.1944
11.91	15.95	15.96	13.65	14.57	13.37	16.14	12.83
0.933	0.954	0.945	0.936	0.946	0.927	0.960	0.930
0.790	0.902	0.978	0.755	0.850	0.813	1.000	0.842
0.158	0.055	-0.036	0.195	0.102	0.128	-0.043	0.097
0.0371	0.1493	0.944	0.0063	0.0152	0.0192	1	0.1247
4.99	5.63	4.19	3.39	3.79	5.93	2.87	3.88
0.755	0.724	0.625	0.484	0.590	0.772	0.297	0.487
0.421	0.611	0.532	0.453	0.675	0.529	0.200	0.520
0.449	0.157	0.15	0.064	-0.146	0.321	0.333	-0.068
0.0042	0	0.1007	0.357	0.7823	0.0013	0.2031	0.7967
6.57	6.11	3.34	5.00	5.15	5.77	6.50	4.05
0.818	0.585	0.235	0.513	0.527	0.642	0.812	0.411
0.611	0.500	0.250	0.500	0.568	0.632	0.867	0.316
0.258	0.146	-0.066	0.026	-0.079	0.016	-0.071	0.237
0.0145	0.0369	1	0.3712	0.0738	0.6162	0.3844	0.0277
6.76	7.97	7.14	6.39	7.23	7.76	7.10	6.90
0.731	0.719	0.661	0.661	0.697	0.751	0.709	0.703
0.561	0.684	0.650	0.602	0.688	0.661	0.660	0.688
0.26095	0.05675	0.02777	0.07936	0.02493	0.10908	0.15339	0.00388
0	***0***	0.0241	0.0118	***0.0002***	***0***	0.051	0.1311

38	39	40	41	42	43	44	45
5.59	5.70	4.80	4.64	4.18	4.35	3.32	3.05
0.768	0.699	0.672	0.660	0.429	0.490	0.302	0.524
0.720	0.674	0.569	0.667	0.429	0.479	0.200	0.366
0.063	0.037	0.153	-0.011	0.001	0.021	0.341	0.304
0.2583	0.4502	0.0474	0.6579	0.717	0.2613	0.0003	0.0001
5.41	6.56	3.26	3.55	5.98	6.00	2.93	3.27
0.523	0.774	0.380	0.583	0.720	0.727	0.186	0.617
0.500	0.739	0.302	0.550	0.698	0.600	0.109	0.625
0.045	0.046	0.206	0.059	0.032	0.177	0.419	-0.013
0.4395	0.4304	0.002	0.3324	0.5638	0.0012	0.0004	0.5345
8.57	12.13	8.43	10.80	12.82	11.85	9.27	9.41
0.847	0.908	0.748	0.887	0.912	0.900	0.853	0.866
0.820	0.796	0.655	0.800	0.867	0.821	0.857	0.778
0.032	0.125	0.125	0.101	0.05	0.089	-0.004	0.103
0.0077	0.0099	0.0509	0.0415	0	0	0.4026	0.0891
12.70	11.45	9.37	10.14	12.42	9.96	9.53	12.13
0.927	0.890	0.856	0.800	0.922	0.881	0.859	0.920
0.917	0.694	0.746	0.667	0.875	0.544	0.696	0.889
0.011	0.222	0.129	0.17	0.051	0.386	0.192	0.035
0.3595	0.0134	0.0328	0.011	0	0	0.0059	0.2841
4.22	4.98	3.96	5.76	4.75	5.07	3.74	3.87
0.550	0.577	0.682	0.771	0.729	0.747	0.582	0.680
0.600	0.408	0.603	0.700	0.721	0.587	0.478	0.475
-0.093	0.295	0.116	0.094	0.011	0.216	0.18	0.305
0.7013	0.0615	0.129	0.0041	0.4076	0.0052	0.0386	0.0012
6.41	8.47	7.07	8.32	7.30	8.33	8.49	7.20
0.784	0.830	0.784	0.779	0.853	0.875	0.818	0.749
0.720	0.551	0.758	0.778	0.820	0.761	0.744	0.745
0.082	0.339	0.034	0.002	0.039	0.132	0.091	0.006
0.008	0	0.3934	0.6336	0.0092	0.0281	0.0073	0.2208
7.15	8.21	6.15	7.20	7.91	7.59	6.21	6.49
0.733	0.780	0.687	0.747	0.761	0.770	0.600	0.726
0.713	0.644	0.606	0.694	0.735	0.632	0.514	0.646
0.03091	0.1873	0.11356	0.08841	0.02703	0.19947	0.11476	0.0927
0.0075	***0***	***0***	***0.0009***	***0***	***0***	***0***	***0***

46	47	48	49	50	51	52	A1
3.57	5.00	3.52	5.13	5.44	6.17	5.92	4.44
0.306	0.652	0.551	0.610	0.640	0.783	0.772	0.797
0.220	0.833	0.354	0.600	0.553	0.773	0.718	0.750
0.282	-0.294	0.36	0.016	0.136	0.013	0.07	0.060
0.0014	0.9877	0	0.0118	0.1057	0.5616	0.1892	0.210
4.24	4.98	2.65	3.15	5.16	3.85	6.40	2.46
0.683	0.735	0.544	0.315	0.590	0.483	0.788	0.592
0.612	0.846	0.521	0.323	0.438	0.422	0.692	0.500
0.105	-0.158	0.043	-0.024	0.261	0.127	0.123	0.157
0.0558	0.9437	0.4534	0.6588	0.018	0.0887	0.0089	0.073
11.33	7.83	5.63	12.13	10.25	10.86	9.68	10.03
0.887	0.739	0.750	0.857	0.858	0.896	0.842	0.893
0.884	0.539	0.773	0.714	0.745	0.932	0.805	0.655
0.004	0.279	-0.031	0.169	0.133	-0.041	0.045	0.270
0.3647	0.1423	0.3822	0.1048	0.1481	0.7014	0.2975	0.000
11.48	7.00	9.79	11.24	14.26	12.84	14.99	6.06
0.897	0.855	0.827	0.877	0.940	0.907	0.937	0.793
0.723	1.000	0.750	0.567	0.875	0.810	0.731	0.759
0.195	-0.179	0.094	0.358	0.07	0.109	0.223	0.043
0	1	0.1294	0	0.0325	0	0.0019	0.213
4.22	3.00	2.54	2.42	4.15	3.90	3.03	1.26
0.694	0.582	0.301	0.502	0.607	0.495	0.220	0.128
0.714	0.692	0.313	0.484	0.646	0.476	0.158	0.133
-0.029	-0.2	-0.038	0.036	-0.064	0.038	0.285	-0.040
0.7141	0.7278	0.7261	0.5047	0.2001	0.5114	0.0559	0.101
7.07	2.83	5.39	6.70	6.66	6.99	6.74	6.54
0.820	0.301	0.741	0.812	0.767	0.811	0.804	0.814
0.698	0.083	0.792	0.690	0.583	0.850	0.677	0.897
0.15	0.732	-0.069	0.153	0.242	-0.048	0.161	-0.104
0.0139	0.0062	0.7912	0.1529	0.0072	0.7052	0.0014	0.830
6.98	5.11	4.92	6.80	7.65	7.44	7.79	5.13
0.714	0.644	0.619	0.662	0.734	0.729	0.727	0.669
0.642	0.666	0.584	0.563	0.640	0.710	0.630	0.616
0.05784	0.00236	-0.01189	0.15968	0.13693	0.00727	0.12247	0.082
0	0.6866	0.0672	***0***	***0***	0.085	***0***	0.020

A2	A3	A4	A5	A6	A7	Overall
3.37	3.14	4.76	3.87	3.00	3.00	4.76
0.786	0.719	0.639	0.696	0.747	0.646	0.672
0.630	0.480	0.691	0.688	0.583	0.667	0.657
0.201	0.337	-0.081	0.013	0.223	-0.033	0.028
0.013	0	0.713	0.373	0.022	0.422	***0***
3.49	2.94	3.72	3.80	3.71	3.64	4.56
0.606	0.340	0.420	0.438	0.370	0.361	0.585
0.680	0.208	0.409	0.452	0.250	0.333	0.539
-0.126	0.392	0.026	-0.031	0.328	0.079	0.084
0.736	0	0.281	0.412	0.002	0.125	***0***
10.57	12.72	10.97	10.88	13.49	11.44	10.15
0.857	0.854	0.908	0.897	0.880	0.897	0.848
0.769	0.720	0.929	0.875	0.875	0.800	0.786
0.104	0.160	-0.023	0.025	0.006	0.111	0.074
0.031	0	0.548	0.208	0.307	0.033	***0***
13.51	12.56	12.09	7.23	8.64	7.84	11.96
0.611	0.888	0.861	0.922	0.858	0.828	0.890
0.480	0.720	0.923	0.852	0.792	0.786	0.802
0.217	0.193	-0.073	0.078	0.079	0.053	0.101
0.004	0	0.879	0.045	0.095	0.185	***0***
3.19	2.86	3.15	1.60	2.73	1.54	3.68
0.175	0.425	0.427	0.613	0.290	0.395	0.552
0.185	0.364	0.356	0.563	0.333	0.333	0.517
-0.057	0.147	0.168	0.083	-0.154	0.162	0.057
0.183	0	0.026	0.183	0.525	0.108	***0***
7.14	8.02	7.04	6.64	6.85	6.59	6.71
0.804	0.822	0.854	0.695	0.828	0.810	0.746
0.600	0.560	0.850	0.630	0.609	0.714	0.652
0.258	0.323	0.004	0.095	0.269	0.122	0.127
0.003	0	0.374	0.083	0.000	0.070	***0***
6.88	7.04	6.96	5.67	6.40	5.67	6.97
0.640	0.675	0.685	0.710	0.662	0.656	0.715
0.557	0.509	0.693	0.676	0.574	0.606	0.659
0.131	0.250	-0.012	0.049	0.136	0.080	0.087
0.001	***0***	0.653	0.083	***0.001***	0.059	***0***

Figure 1

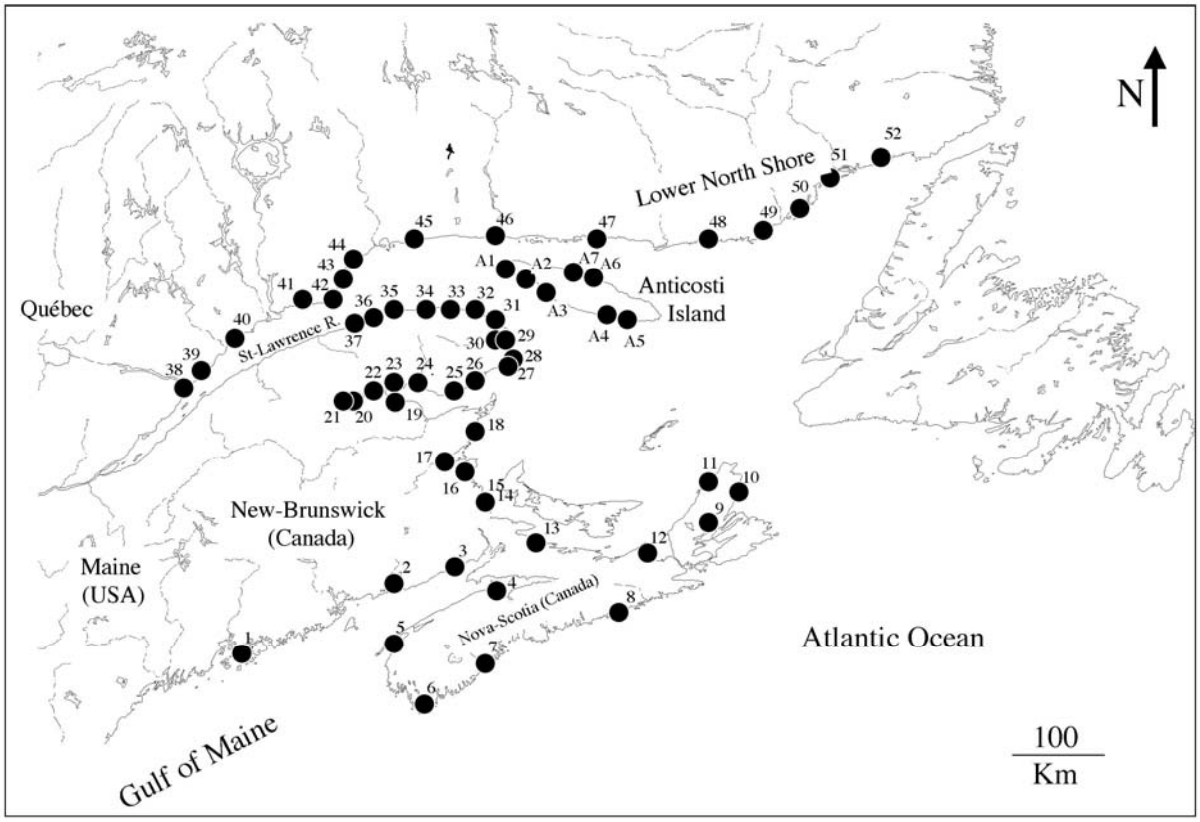

Figure 4-1Location of brook charr samples. Numbers refer to locations in Table 1. The southernmost population is labeled km 0 and is close to the southern limit of anadromous brook charr distribution. Distances were linearly measured along the coast in a northward direction to kilometer 4992.

Figure 2

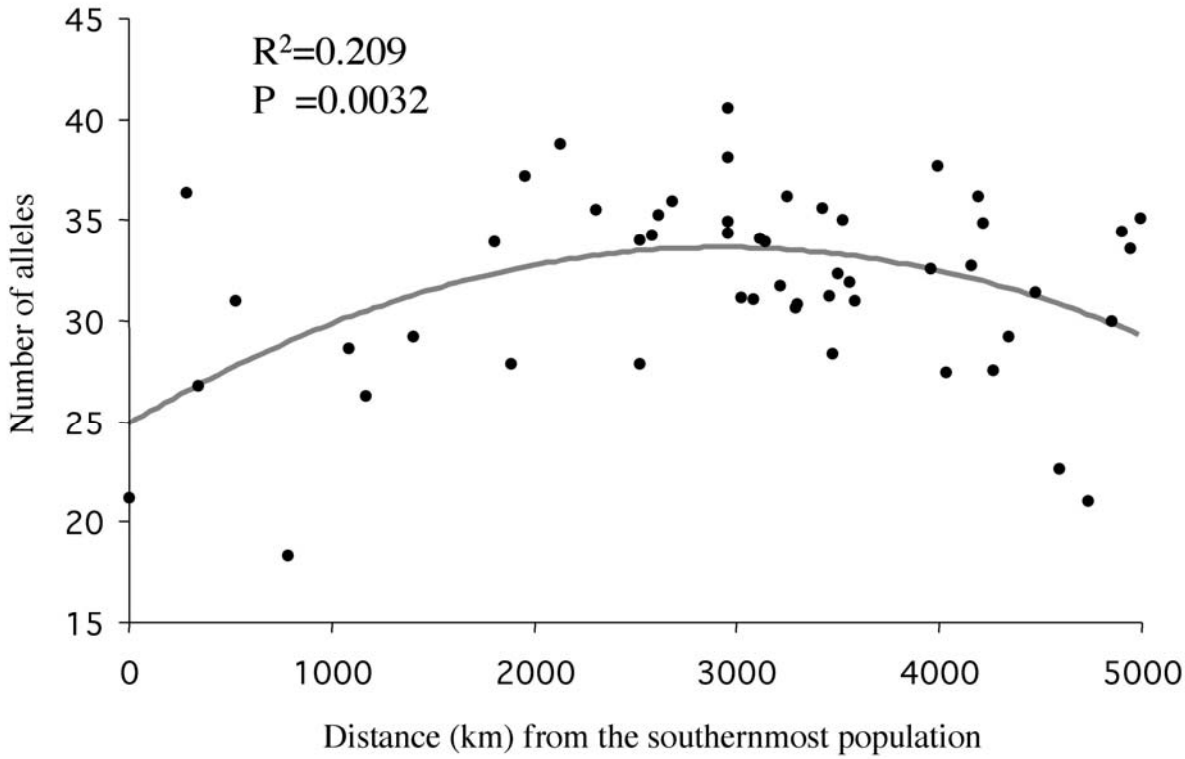

Figure 4-2. Geographic variation in allelic richness (A) along the coast. Allelic richness was estimated at a constant population size (N=26 alleles) using a rarefaction method. A parabola best fitted the observed distribution.

Figure 3

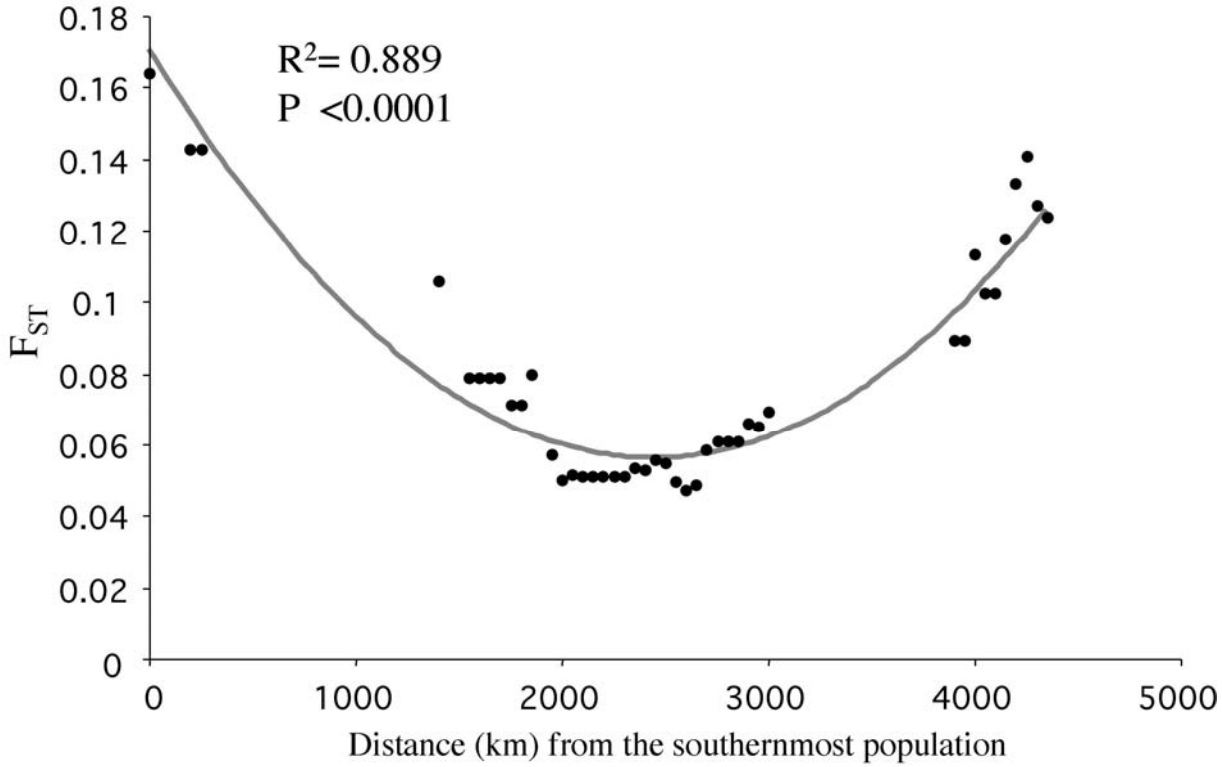

Figure 4-3 Geographic variation in F_{ST} depicted using a sliding window analysis. A 600 km-wide window was shifted along the coast by 10 km increment. Each data point refers to the mean F_{ST} over all possible combinations of four populations within each window. Windows including less than four populations were discarded.

Figure 4

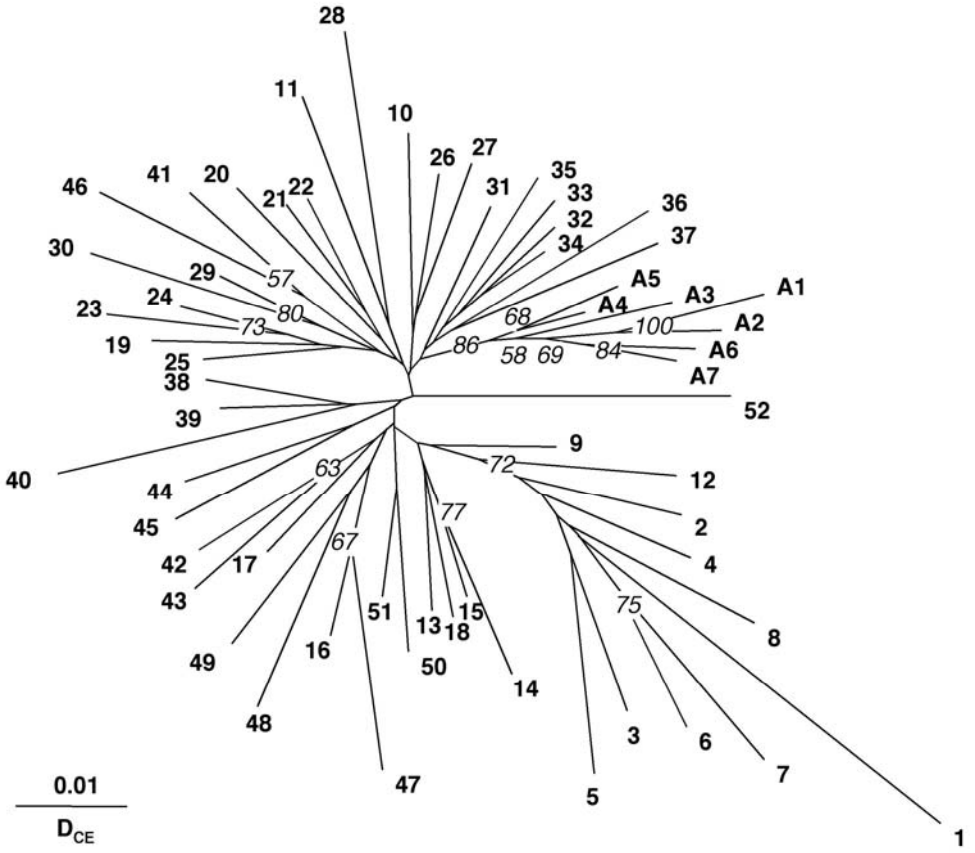

Figure 4-4. Neighbor-joining phenogram based on D_{CE} distances depicting genetic similarities among populations. Population numbers refer to table 1. Nodes confidence values are percentage values over 1000 bootstrap replicates. Note the tight clustering with a high bootstrap value of 86% of Anticosti Island populations. Only bootstrap values over 50% are shown.

Figure 5

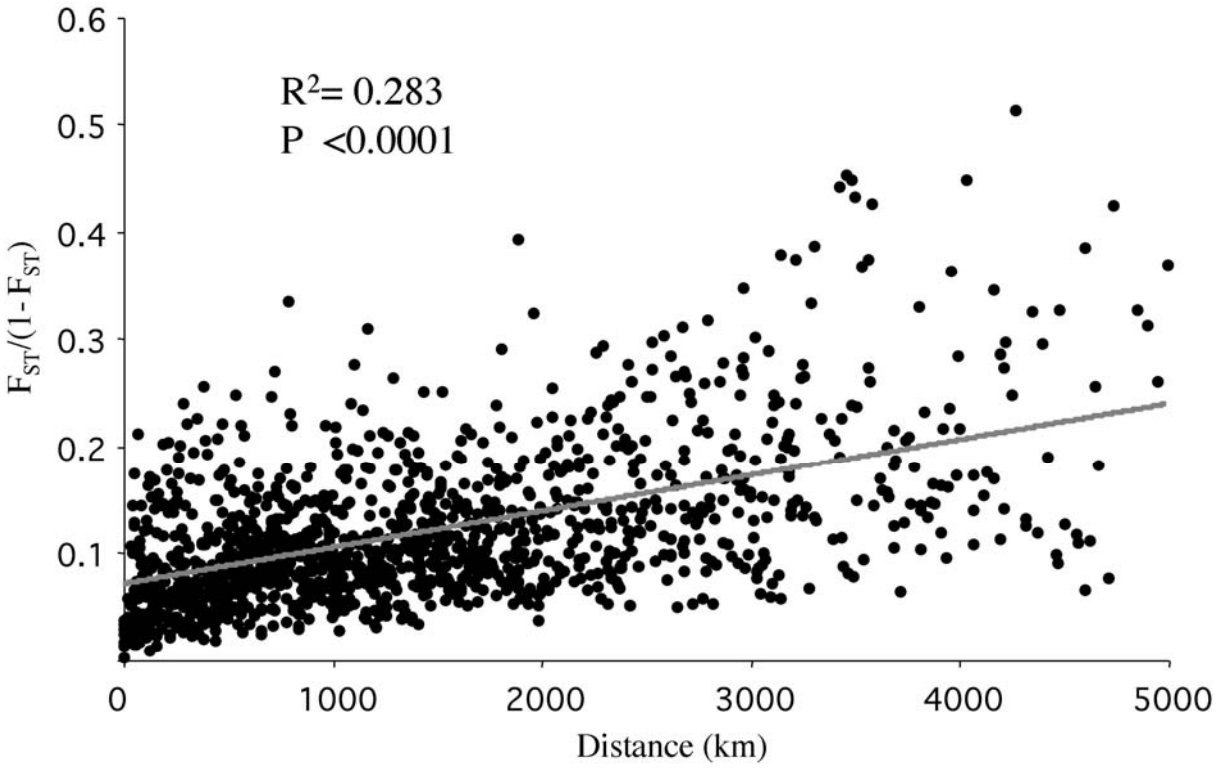

Figure 4-5. Isolation by distance relationship, where $F_{ST}/(1- F_{ST})$ was regressed over coastal distances.

Figure 6

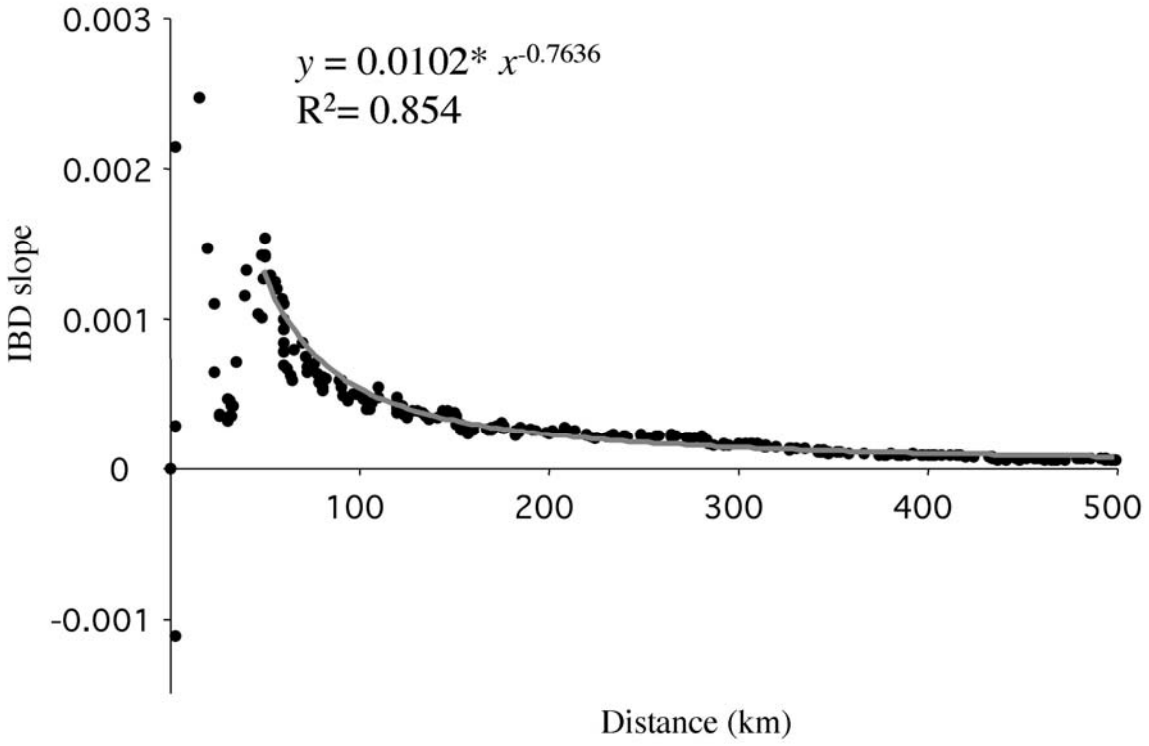

Figure 4-6. Variation of the slope of the isolation by distance regression as a function of the spatial scale of observation. Slopes were computed by progressively including population pairs at increasing geographic distances. To better show initial fluctuations, only the 500 first km are shown.

Figure 7

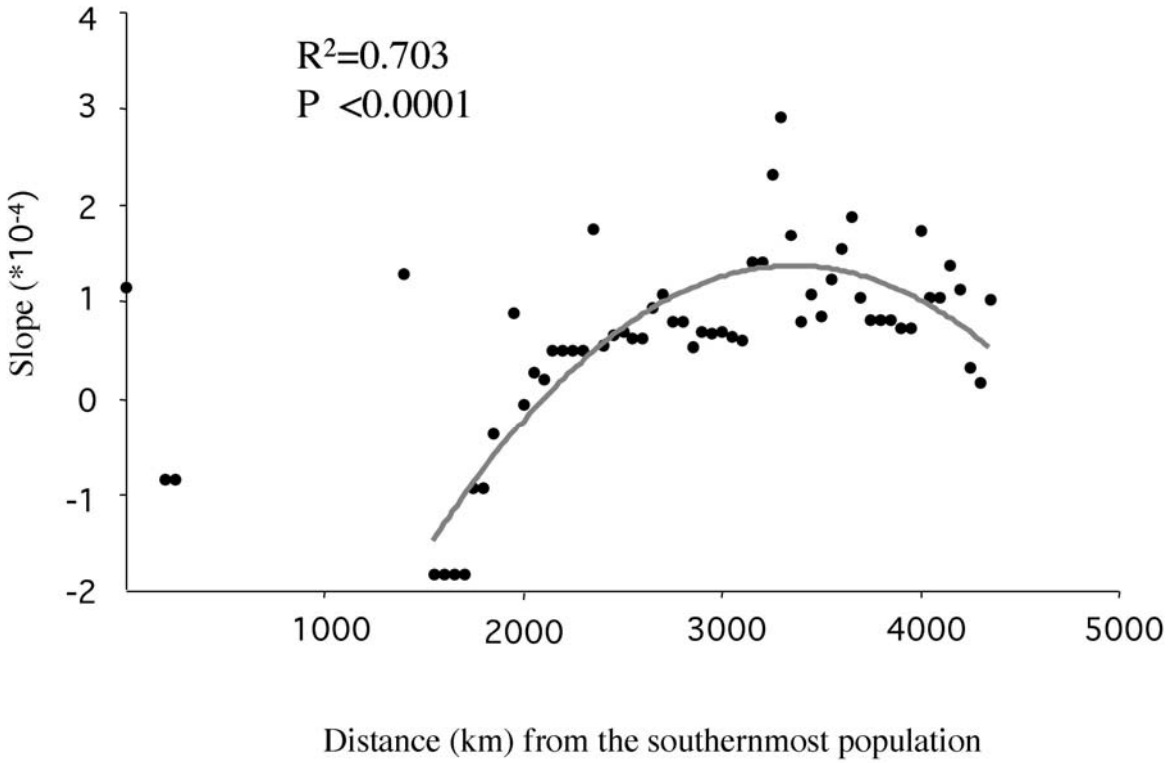

Figure 4-7. Variation in the slope of the isolation by distance regression. A 600 km-wide window was shifted along the coast by 10 km increment. Each data point refers to the mean slope over all possible combinations of four populations within each window. Windows including less than four populations were discarded.

Figure 8

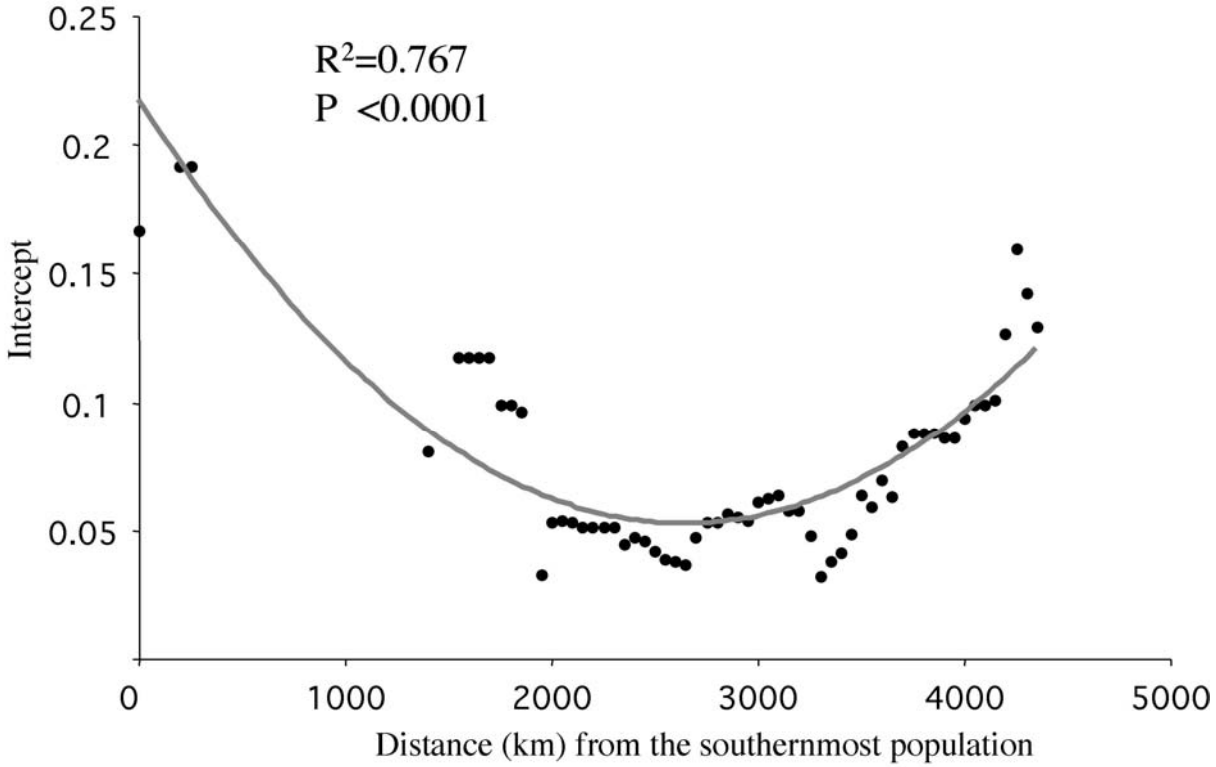

Figure 4-8. Geographic variation in the intercept of the isolation by distance regression revealed by the sliding window analysis.

5. Should I stay or should I go ? Individual inbreeding as a determinant of anadromy in coastal populations of *Salvelinus fontinalis*.

5.1. Résumé

Chez certaines populations de salmonidés côtiers, la fraction des individus anadromes exprime par définition une tolérance à l'eau salée et migre vers l'eau salée. Cette tolérance s'accompagne de modifications majeures de plusieurs traits d'histoire de vie (incluant taille corporelle, fécondité, survie, longévité). Chez plusieurs espèces, la croissance juvénile semble impliquée dans la décision d'initier ou non la migration anadrome. Lorsque les deux phénotypes anadrome et résident sont exprimés au sein d'un même ensemble de gènes, l'anadromie peut être considérée comme la forme de dispersion de l'espèce car l'accès à l'eau salée confère, en milieu côtier, une probabilité non-nulle de dispersion entre rivières. Les modèles théoriques ont montré qu'une forme de dispersion pouvait évoluer sous l'effet de la dépression de consanguinité. Comme celle-ci peut avoir des conséquences délétères sur la croissance juvénile, et peut donc interférer avec la décision d'initier la migration, nous avons cherché à déterminer si les niveaux individuels de consanguinité différaient entre individus anadromes et résidents. Globalement, nos résultats indiquent que les individus anadromes et résidents d'une même rivière appartiennent bien à un même ensemble de gènes. Ils démontrent de plus que dans deux des quatre rivières étudiées, les individus anadromes ont des niveaux de consanguinité individuelle supérieurs aux individus résidents. Dans ces deux rivières, qui sont aussi les deux situées le plus au nord et les plus récentes le long d'un gradient de colonisation post-glaciaire, la décision d'initier la migration anadrome semble donc liée au niveau de consanguinité individuelle. Ces résultats suggèrent que le potentiel de dispersion chez l'omble de fontaine est influencé par la dynamique de la dépression de consanguinité.

5.2. Abstract

In some populations of coastal salmonids, the fraction of anadromous individuals expresses by definition a tolerance to saltwater and migrates to the ocean. In several species, the decision to initiate the anadromous migration seems to be related to juvenile growth and has major consequences on several life-history traits such as body size, fecundity, survival and longevity. When both anadromous and resident phenotypes are expressed within a single gene pool, anadromy can also be considered as a form of dispersal because access to saltwater provides a non-null probability of dispersing to a neighbouring river. Theoretical models have shown that dispersal could evolve in response to inbreeding depression. Yet, because inbreeding depression can have deleterious consequences on juvenile growth, it may potentially interfere with the decision to initiate migration. We used microsatellite markers to compare individual inbreeding in anadromous and resident individuals from four rivers in the native range of the brook charr *Salvelinus fontinalis*. Our results indicate that anadromous and resident individuals belong to a single gene pool. Furthermore, in the two most recently recolonized rivers, anadromous brook charr had significantly higher levels of inbreeding than resident fish, which supports the hypothesis that the decision to disperse is inbreeding-dependant in these two rivers. These findings suggest that dispersal in the brook charr is at least partially driven by the evolution of inbreeding depression.

5.3. Introduction

Dispersal is one of the most ubiquitous natural processes in plant and animal taxa. Indeed, examples of species in which all offspring reproduce exclusively where their parents did are very scarce (Dingle 1996, Clobert et al. 2001). Theoretical models have shown that dispersal could evolve in response to a variety of ultimate factors, including (1) temporal variability in local carrying capacity, (2) spatial heterogeneity in the distribution of resources if dispersal is conditioned on habitat quality (Holt & McPeek 1992) or if dispersal rates vary across life history stages (Greenwood-Lee and Taylor 2001), (3) kin competition (Hamilton and May 1977) and (4) inbreeding depression (Motro 1991). Accordingly, dispersal traits typically show high levels of variation between species and populations which can provide insight into the underlying evolutionary factors selecting for dispersal (Ronce et al. 2001).

Different individuals within a population often show unequal propensity for dispersal. In such cases, dispersal can be conditional, that is, individuals may adjust their dispersal decision by matching their phenotype against prevailing environmental conditions in terms of fitness prospects (Ims and Hjermann 2001). The decision can be modulated by numerous proximate factors, including additive genetic determinism (Roff and Fairbairn 2001), maternal effects (Venable and Burquez 1989, Massot and Clobert 1995), population density (Wolff 1997), sex (Greenwood and Harvey 1982) and life-history stage (Greenwood-Lee and Taylor 2001). Although proximate behavioural mechanisms are subjected to natural selection, they need not be the same as ultimate factors (Stamps et al. 2001). One reason for this difference is that dispersal is seldom free to evolve independently from other life history traits and reproductive characters (Olivieri and Berger 1985, Roff and Fairbairn 2001). Thus, selection on other traits can influence an individual's probability to disperse.

Anadromous salmonid species provide useful model systems to investigate the relationship between ultimate and proximate factors in the evolution of dispersal. Anadromous salmonids spawn in freshwater, where eggs hatch and juveniles spend the first part of their life. In several species such as the brook charr (*Salvelinus fontinalis*), Atlantic salmon (*Salmo salar*), brown trout (*S. trutta*), the fraction of anadromous individuals experience major physiological rearrangements that allow them to tolerate saltwater. Anadromous individuals may gain access

to the highly productive oceanic environment, thus experiencing increased growth. They also have the potential to reproduce in a different river from the one they originate from, although such "capability of migration does not mean that it will be exercised" (Roff and Fairbairn 2001). In contrast, resident individuals complete their whole life cycle in freshwater, reach a smaller body size and have a null probability to reproduce in a different river. Thus, anadromous salmonids exhibit a polymorphism of dispersal capability.

Individuals initiating anadromous migration (and thus potential dispersers) are not a random subset of the individuals found in a population. Thus, the decision to initiate or not anadromous migration seems to be conditioned during juvenile growth in several species, whereby slower growing individuals have a higher propensity to perform anadromous migrations than fast growing individuals **(**Thorpe 1986, Rowe and Thorpe 1990**).** Consequently, juvenile growth negatively affects the potential for dispersal through its effect on the propensity to perform anadromous migrations. Therefore, any factor modifying juvenile growth may also affect the potential for dispersal. Inbreeding depression may be one such factor.

Because inbreeding depression can affect many morphological and life-history traits, and particularly juvenile growth, it may also interact with traits involved in conditional dispersal. In this study, we tested whether the relationship between juvenile growth and the expression of anadromy could be associated with levels of inbreeding in anadromous and resident individuals in brook charr populations. To that end, we genetically compared anadromous and non-anadromous brook charr from four different rivers using microsatellite loci. We first tested the null hypothesis of no reproductive segregation between andromous and resident fish from a same river. Secondly, we tested whether both anadromous and resident phenotypes had identical individual levels of inbreeding. Because inbreeding depression is a dynamic variable in natural populations (Keller and Waller 2002 and references therein), we also tested whether the observed inbreeding-conditioned expression of anadromy remained constant through time by comparing populations from different areas that were most likely recolonized at different times in postglacial times.

5.4. Material and methods

Whole cell DNA was extracted from 394 anadromous and 224 resident individual brook charr *Salvelinus fontinalis* Mitchill identified as detailed in Boula et al. (2002). Fish were collected in four rivers from eastern Canada (Fig. 5-1., Table 5-1.) chosen so as to represent different stages of a postglacial colonization gradient. Brook charr survived the last glaciation in southern refugia and therefore most likely recolonized coastal areas of eastern Canada northward (Danzman et al. 1998). Southern populations may therefore have existed for a longer period of time than more northern ones, thus creating a colonization gradient along the eastern coast of Canada. Accordingly, the Laval and Ste-Marguerite Rivers represented the two most recently settled populations, the Petite-Cascapedia was intermediate, and the Kennebecasis River located near the southern end of anadromous brook charr's native range (See Table 1 in chapter 3, Ryther 1997) was considered as the oldest population in this study. To avoid any spatial effect due to geographic genetic differentiation within a river basin (Boula et al. 2002), fish were either directly collected in the main stem of the river for the Laval**,** Petite-Cascapédia and Kennebecasis River or in a single tributary (Allaire Creek) where both anadromous and resident brook charr reproduce in the Ste-Marguerite River. Anadromous fish from the Sainte-Marguerite River was also collected at two locations within the main branch of the river (Big Pool; N=30, and Anse à Pierrot; N=50). All fish were genotyped at six microsatellite loci as detailed in Chapter 2.

We first tested whether anadromous and resident brook charr belonged to a single pool of genes. Allele frequencies in anadromous and resident samples were compared using the genotypic exact test for population differentiation in Genepop v.3.1. (Raymond and Rousset 1995). Significance level was adjusted to account for multiple testing using Bonferroni sequential procedure (k_i=6 for single-locus comparisons, $P_{\alpha=0.05}$=0.0083 Rice 1989). Differentiation between anadromous and resident fish within each river was quantified by F_{ST} estimated by θ (Weir and Cockerham 1984) using Genetix 4.02 (Belkhir et al. 2000). Significance level for multilocus F_{ST} was tested by 5000 random permutations and corrected for multiple testing using Bonferroni correction (k_i=4, $P_{\alpha=0.05}$=0.05). In the Ste-Marguerite River, the test for population differentiation between anadromous and resident fish was restricted to samples from Allaire Creek where both anadromous and resident samples were

collected at the same site. The extent of within-river spatial differentiation was then quantified in that river using a hierarchical analysis of molecular variance (AMOVA) performed in Arlequin v2.000 (Schneider et al. 2000) by grouping samples according to three geographic locations: Anse à Pierrot, Big Pool, Allaire Creek.

We then compared inbreeding levels between anadromous and resident brook charr in each river. In the absence of a complete pedigree for the populations, individual multilocus genotypes were used to compute compare individual inbreeding coefficients. By definition, inbred individuals have genetically related parents, such that the two alleles they carry at any locus have a greater probability of being identical by descent than if their parents had been unrelated. Thus, the level of homozygosity at molecualr markers was used to estimate individual's inbreeding coefficient in each population. We used a Maple® 6 (Waterloo Inc. 1999) spreadsheet to program Ritland's (1996) method-of-moments estimator weighting homozygosity at a given allele by the frequency of that allele in the population. Individual inbreeding was averaged over all anadromous and resident fish within each river and the 95% confidence intervals around average values were generated by 5000 bootstrap replicates over loci. The significance of the observed difference was then tested using a permutation test to rule out the hypothesis that the difference could be due to chance alone. To that end, individuals from each river were randomly grouped 5000 times in two groups: one of the size of the resident sample and one of the size of the anadromous sample. The difference in the mean inbreeding between the two groups was computed for each of these random configurations and used to generate the null distribution of differences in inbreeding levels under the assumption of random difference.

We then determined whether this difference was due to anadromous fish being more inbred or to resident fish being more outbred than expected at random, or both. We tested this hypothesis by generating the expected distribution of individual inbreeding coefficients in a randomly mating population with genotypic frequencies identical to that observed for the anadromous or resident samples in a population. This null distribution was obtained by randomly permuting 5000 times the single-locus genotypes in each sample and was compared to the observed average of individual inbreeding coefficients in the sample. The sample was considered as departing from random expectations whenever the probability of the observed

average value of individual inbreeding coefficients fell outside the 95% interval of all permutations. Maple spreadsheets for the preceding tests of significance are available upon request from the authors.

5.5. Results

5.5.1. Genetic segregation

Globally, only weak evidence was found for population differentiation between anadromous and resident brook charr, although results differed among the four rivers. No evidence for differentiation was found in the Laval river (Table 2, F_{ST}= 0.0034, P=0.151), with none of the six loci showing significant allele frequency differences among samples. Random mating between anadromous an resident charr could be ruled out for the Petite Cascapedia and Kennebecasis Rivers. However, F_{ST} values for these two rivers were very weak (Table 2, F_{ST}= 0.0042, P=0.018; F_{ST}= 0.0064 P=0.013), and differed greatly among loci. In the Kennebecasis River, for example, three of the six loci analyzed had positive F_{ST} values and three of them had negative values. In those two rivers, the significance of the differentiation was entirely due to a single locus (Table 2, SFO-8 for the Petite Cascapedia, SFO-12 for the Kennebecasis). In the Ste-Marguerite River, the multilocus F_{ST} between andromous and resident fish from Allaire Creek was significantly higher than observed in the other rivers (Table 2, F_{ST}= 0.0160, P=0.0008). Yet again, only one locus (SFO-23) showed significant differences in genotype frequencies. Furthermore, the proportion of genetic variance imputable to differences between anadromous and resident fish within Allaire Creek ($9.67x10^{-3}$) was much weaker than that imputable to differences among samples collected in the main stem of the Ste-Marguerite river ($2.24x10^{-2}$) among fish

5.5.2. Inbreeding-conditioned migration in brook charr

Overall, the mean level of individual inbreeding significantly differed between anadromous and resident brook charr collected within a river (Table 1, Fig 2, Fisher's method to combine probabilities for overall significance P=0.033). Within a river, individual inbreeding coefficients for anadromous individuals were on average 1.43 fold higher than those of resident ones. Yet, all rivers did not contribute equally to this pattern. The difference in individual inbreeding coefficients was strong in the two northernmost rivers, the St-Marguerite River (mean inbreeding coefficient of anadromous individuals 2.02 times higher than residents, P = 0.016) and the Laval River (2.07 times higher, P=0.066). In contrast, this pattern was reversed in the two southern rivers where the average values of inbreeding coefficient

were smaller, albeit not significantly, for anadromous than for resident fish (Petite Cascapedia; ratio = 0.75, P = 0.376, Kennebecasis; ratio = 0.89, P =0.594).

This overall difference in individual inbreeding between anadromous and resident fish within each river was due to anadromous fish being drawn from the upper end of the population distribution of inbreeding coefficient values. Thus, anadromous individuals were significantly more inbred than expected if they had been randomly drawn from a randomly mating population (Table 1, Fisher's method across anadromous samples, P=0.0210). In contrast, no departure from random expectation was found in samples of resident individuals (P=0.7326). Yet again, all rivers did not contribute equally to this result. Anadromous individuals were significantly more inbred than expected for the Ste-Marguerite River (P=0.013), and the probability value was smaller for the Laval River (P = 0.234) than the for the Petite Cascapédia (P = 0,264) and the Kennebecasis River (P = 0,307).

5.6. Discussion

The main objective of this study was to test whether the relationship between juvenile growth and the expression of anadromy could be associated with different levels of inbreeding between anadromous and resident individuals in the brook charr. Our results showed that anadromous brook charr had significantly higher levels of inbreeding than resident fish in the two northernmost rivers, which supports the hypothesis that the decision to disperse is inbreeding-dependant in these two rivers. These findings therefore suggest that dispersal in the brook charr is at least partially driven by the evolution of inbreeding depression.

Two explanations can account for the observed differences in inbreeding levels between anadromous and resident fish within the same river. First, anadromous and resident individuals may belong to two genetically distinct populations. Population segregation between resident and anadromous fish has previously been reported in several salmonid species *Salmo salar* (Vuorinen and Berg 1989, Birt et al. 1991), *Onchorhynchus nerka* (Foote et al. 1989), and *Salmo trutta* (Skaala and Naevdal 1989, but see Hindar et al. 1991, Cross et al. 1992). When gene pools are isolated, the genealogy of their alleles can vary independently and may differ as a function of several factors. Thus, individuals from a small, isolated, population could show higher inbreeding than those from a large population connected to a set of populations. In the same manner, a population with matings biased toward genetically related individuals would show higher inbreeding than one experiencing random mating (Castric et al. 2002). Hence, the distribution of individual inbreeding coefficients can differ between isolated gene pools. We found no or very weak evidence for genotype frequency differences between andromous and resident charr in three of the four rivers investigated (Laval, Petite-Cascapedia and Kennebecasis Rivers). There, significant differentiation was restricted to a single locus, while all others showed no evidence for differentiation. This indicates that that genetic drift that could cause an apparent pattern of differential inbreeding between andromous and resident fish was probably limited in those three rivers. In the Ste-Marguerite River, however, the level of differentiation among migratory phenotypes was higher and significant. Yet, the extent of differentiation between them was nearly ten times weaker than the geographical component of genetic variance. Moreover, anadromous individuals experience a higher potential for dispersal and for connectivity to a much larger set of populations. Therefore, anadromous fish

should exhibit lower values of inbreeding those observed for residents, should they comprise genetically distinct populations. However, the opposite pattern was observed in the Ste-Marguerite River, and consequently, genetic segregation is very unlikely to explain the observed difference in inbreeding observed in that river. Alternatively, direct count census size estimates suggest that the number of anadromous spawner using Allaire Creek is low (<20 individuals, Lenormand and Dodson pers. comm.). Because anadromous males and females have much higher fecundity than resident individuals (>10:1, Lenormand and Dodson pers. comm.), a large proportion of the individuals may actually be derived from a small number of families. Thus, genotype frequency differences may actually reflect differences among families, as theoretically demonstrated by Allendorf and Phelps (1981) and empirically examplified by Hansen et al. (1997). In such a case, differences in inbreeding between samples would translate into differences between families. That is, inbred families would be over-represented in the anadromous samples. Thus, even if the differentiation observed in the Ste-Marguerite River is due to inbreeding differences among families, the conclusion remains unchanged : inbred families produce more anadromous individuals than outbred families, which further argues for a role of individual inbreeding in triggering anadromous migration.

The second explanation that may account for the observed differences in inbreeding levels between anadromous and resident fish within the same river is that the initiation of anadromous migration may be triggered by an individual's level of inbreeding. As a consequence, the potential for dispersal would be conditioned by inbreeding, such that potential dispersers would be among the most inbred individuals in a population. The relationship between inbreeding and dispersal has been most studied in plants, where greater dispersal potential is typically reported for seeds derived from cleistogamous, potentially outcrossed, than from chasmogamous flowers, potentially selfed (the extreme case of inbreeding) (Olivieri and Berger 1985, but see Cheptou et al. 2000, Berg 2000). This pattern is usually explained under the hypothesis of local adaptation (Schmitt and Gamble 1990) stating that selfed progenies should inherit locally adapted sets of genes complexes and have therefore more to gain from not dispersing. Why then do brook charr follow the reversed pattern? In other words, when should dispersal evolve conditionally to inbreeding? We propose three hypothetical explanations for this.

First, inbred individuals that successfully disperse can outcross and therefore reduce the probability of producing inbred progenies. Yet, because the effects of inbreeding are not transmitted to the progeny and can be offset by a single generation of outcrossing, dispersal would be equally beneficial for every individual in a population, regardless of its level of inbreeding. Thus, although inbreeding depression can select for the evolution of dispersal in a population (Motro 1991), it cannot explain inbreeding-conditioned dispersal.

Secondly, as shown by McPeek and Holt (1992), spatial variations in habitat quality can select for dispersal if dispersal is conditioned by habitat quality. Under the hypothesis that populations from different rivers vary in levels of inbreeding depression and load of deleterious mutations, anadromy could confer the potential of escaping rivers with high probability of mating with relatives. The level of inbreeding depression would thus be used to assess habitat "quality" defined as the probability to incur inbreeding depression in a population. The recent postglacial colonization of eastern Canada was associated with severe and repeated demographic bottlenecks (Chapter 3), and may have contributed to generate spatial variation in the genetic load (Kirkpatrick and Jarne 2000). In such case, the absence of inbreeding-conditioned dispersal observed for the two southern populations in this study could stem from a more homogeneous genetic load in older populations. Older populations along the colonisation gradient are also more divergent one from each other (Chapter 3), such that the efficacy of selection is theoretically expected to be higher (Whitlock 2002). Thus, the greater population fragmentation may possibly result in lower and more homogeneous levels of inbreeding depression in older, more fragmented populations. We are however unaware of any empirical quantification of spatial variations in the load of deleterious mutations in natural brook charr populations, such that it remains difficult to further assess the likelihood of this explanation.

A third hypothesis explaining why dispersal through anadromy evolved conditionally to inbreeding could be by an effect on body growth. Since slow-growing juvenile salmonids have a higher probability of initiating migration (Fleming 1996, Therriault 2001), inbreeding depression could incidentally increase the probability of migrating if it negatively effect growth. That is, inbreeding-conditioned dispersal would be an indirect result of the conditional strategy based on growth. In such a case, the dispersal potential provided by the expression of

anadromy would not be driving the evolution of anadromy. Yet, the picture would then be incomplete since inbreeding depression is a dynamic variable in natural populations, especially for species made of relatively isolated populations with limited dispersal such as the brook charr (Keller & Waller 2002). Thus, it has been theoretically demonstrated that inbreeding depression is decreased by population structure (Whitlock 2002), which in turn is reduced by the expression of anadromy. Thus, by expressing anadromy, individuals may contribute to weaken population structure, further increasing the intensity of inbreeding depression, which in turn leads to increased expression of anadromy. The absence of difference in inbreeding between andromous and resident brook charr in older populations could thus be associated to weaker inbreeding depression in older populations. Thus, following the purge of deleterious mutations over time, inbred individuals would suffer no growth handicap compared to non-inbred individuals, therefore eliminating the potential selective benefit of dispersing.

5.7. Conclusion

The relationship between inbreeding and anadromy led us to suggest that inbreeding depression may be a major proximate factor driving the evolution of anadromy in the brook charr. Yet, the relationship may be indirect : inbreeding depression triggers dispersal *via* its effects on juvenile growth that is involved in the expression of anadromy. Thus, inbreeding depression needs not be the ultimate factor driving the evolution of anadromy in the brook charr : other factors including the increased productivity of the oceans compared to freshater environments are clearly involved. Yet anadromy interferes with population structure (Whitlock 2002), which can regulate the level of inbreeding depression in a species. Therefore, our results suggest that even indirectly, the evolution of anadromy cannot be considered without consideration for its dispersal consequences. Properly evaluating this hypothesis will now require a quantification of inbreeding depression in different rivers. Moreover, because currently existing models for the evolution of dispersal under inbreeding depression do not allow the genetic load to evolve with dispersal (Gandon and Michalakis 2001, Perrin and Goudet 2001), further modelling efforts are clearly required.

5.8. Acknowledgments

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Table 5-1. Mean individual inbreeding coefficients in anadromous and resident brook charr. P_1 is the probability of observing a higher *f*-value in a population with identical genotypic frequencies (anadromous and resident samples considered separately) and $P_{A=R}$ is the significance of the difference between the two samples.

River	Migratory Phenotype	Sample Size	Mean *f*	P_1	$P_{A=R}$
1. Laval	Anadromous	80	0.1837	*0.234*	*0.066*
	Resident	39	0.0888	*0.204*	
2. Ste-Marguerite (Allaire Creek)	Anadromous	41	0.0668	*0.013*	*0.016*
	Resident	38	0.0331	*0.886*	
3. Petite-Cascapedia	Anadromous	109	0.0922	*0.264*	*0.376*
	Resident	94	0.1236	*0.873*	
4. Kennebecassis	Anadromous	84	0.0689	*0.307*	*0.594*
	Resident	53	0.0778	*0.416*	
Combined	Anadromous	394	-	*0.021*	*0.033*
	Resident	224	-	*0.733*	

Table 5-2. Genetic differentiation between anadromous and resident individuals within the four studied rivers. F_{ST} is Weir and Cockerham's (1984) θ estimator and P is the exact P-value estimated using a Markov chain in Genepop. Significance level for F_{ST} combined over loci is obtained using 2000 permutations in Genetix 4.02. Significant F_{ST} following sequential Bonferroni correction are figured in bold.

		SFO-12	SFO-18	SFO-23	SFO-8	SSA-197	MST-85	Combined
1. Laval	F_{ST}	0.0109	0.0150	0.0003	0.0110	-0.0080	-0.0050	0.0034
	P	0.108	0.096	0.3505	0.054	0.789	0.7915	0.151
2. St-Marguerite (Allaire Creek)	F_{ST}	0.0050	0.0048	**0.0292**	0.0059	0.0212	0.0203	**0.0160**
	P	0.241	0.23	<0.005	0.134	0.074	0.0425	0.001
3. Petite-Cascapedia	F_{ST}	0.0028	-0.0012	0.0008	**0.0157**	0.0002	0.0022	**0.0042**
	P	0.186	0.448	0.269	<0.005	0.330	0.197	0.018
4. Kennebecasis	F_{ST}	**0.0425**	-0.0050	0.0048	0.0005	-0.0011	-0.0019	**0.0064**
	P	0.002	0.777	0.095	0.374	0.399	0.573	0.013

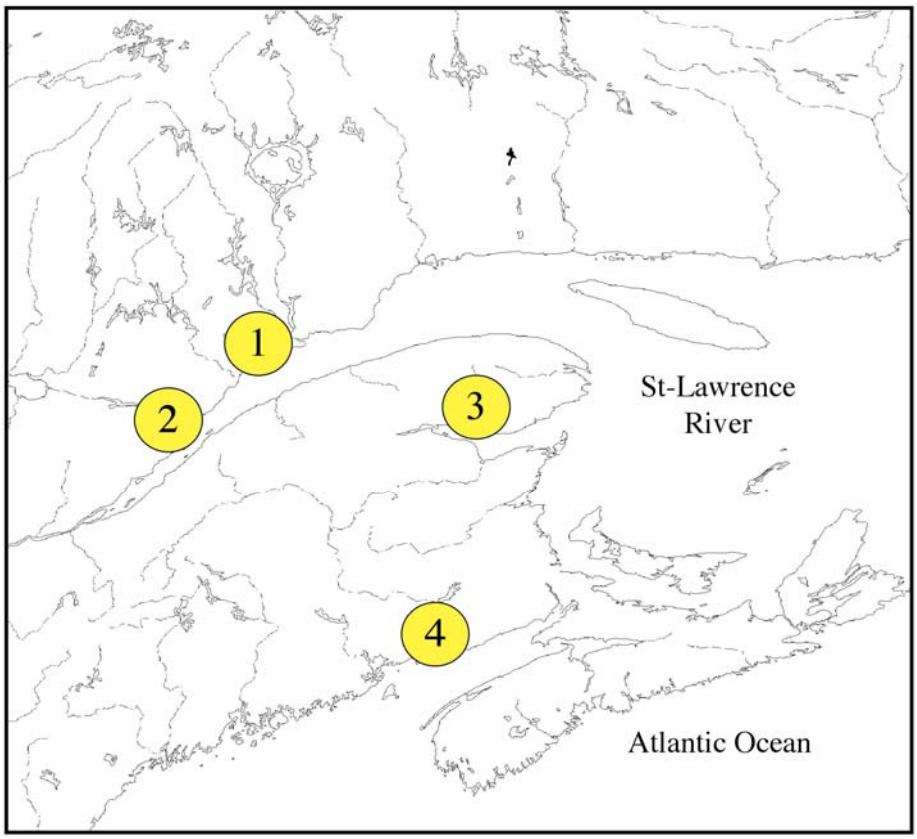

Figure 5-1. Sampling locations of anadromous and resident brook charr along the Canadian Atlantic coast. 1. Laval River (samples included in Boula et al. 2002, excluding fish from Adam River but including 46 anadromous individuals sampled in 1999) 2. Ste-Marguerite River. 3. Petite-Cascapédia River. 4. Kennebecasis River.

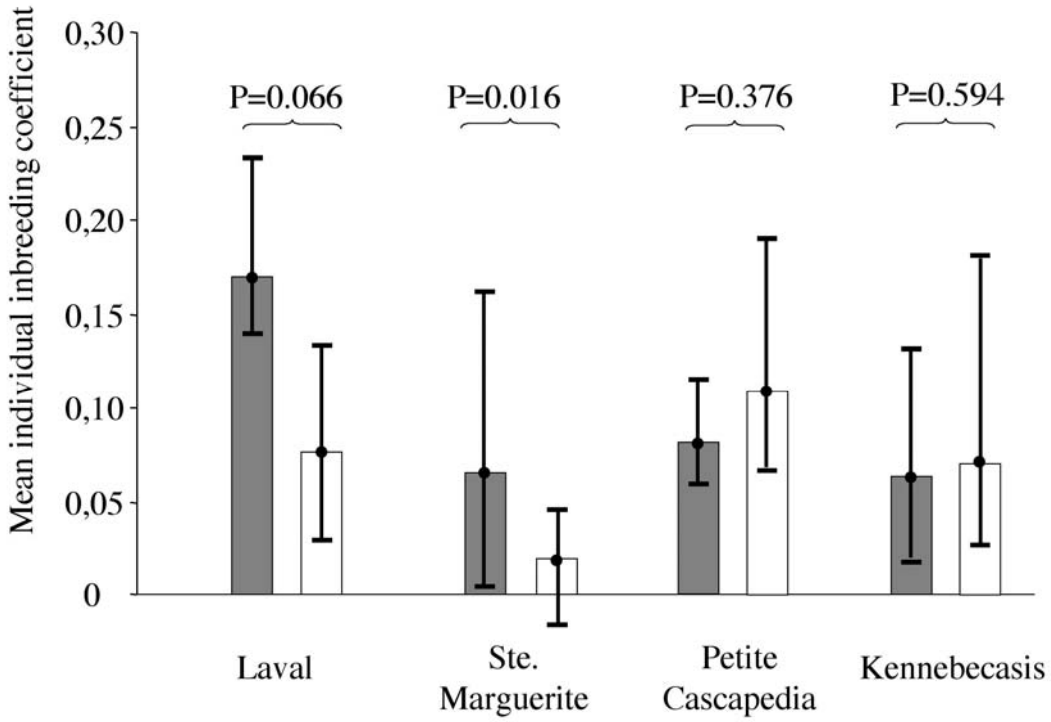

Figure 5-2 Mean individual inbreeding coefficient for anadromous (grey bars) and resident brook charr (open bars). The 95% confidence intervals were generated by 5000 bootstrap iterations over loci. Values above bars indicate $P_{A=R}$, the probability of identical inbreeding coefficient between anadromous and resident fish in each river.

6. Isolation by distance in Atlantic salmon *Salmo salar* L. and brook charr *Salvelinus fontinalis* Mitchill: a comparative analysis.

6.1. Résumé

Des différences marquées, parfois clinales, peuvent être observées entre les populations de saumon Atlantique de différentes rivières et sont généralement interprétées comme l'illustration de forts niveaux d'adaptation locale par l'action de la sélection naturelle. Les migrations océaniques du saumon Atlantique se font cependant sur de grandes distances géographiques qui rendent possible un égarement à longue distance et oblitérerait la possibilité d'une exposition répétée des mêmes génotypes à un même environnement, donc l'évolution clinale des patrons d'adaptation locale. Nous procédons ici à une analyse des patrons d'isolement par la distance chez le saumon Atlantique pour déterminer l'échelle spatiale de l'égarement. Une forte variation étant généralement associée à ce type d'analyses, nous utilisons ici une approche strictement comparative en utilisant l'omble de fontaine anadrome comme espèce de référence. Les niveaux de diversité génétique des deux espèces dans une même rivière n'étaient pas corrélés et étaient plus homogènes entre rivières chez *S. salar* que chez *S. fontinalis.* En accord avec les différences de leurs patrons de migration, les populations de *S. salar* étaient plus faiblement différenciées les unes des autres et cette différenciation s'accroissait plus faiblement avec la distance qu'entre les populations de *S. fontinalis*. De plus, si cette accroissement n'etait pas significatif à l'échelle globale chez *S. salar*, il ne l'était pas non plus à cette échelle chez *S. fontinalis* dont la dispersion est pourtant géographiquement limitée par des contraintes physiologiques. La décroisssance plus rapide du signal d'isolement par la distance avec l'échelle géographique chez *S. salar* que *S. fontinalis* suggère que les égarements chez le saumon se produisent principalement à petite échelle mais également à grande échelle avec une fréquences plus élevée que chez *S. fontinalis*. Ces observations illustrent l'intérêt de l'approche comparative employée par rapport à une méthode d'inférence absolue.

6.2. Abstract

Wild populations of Atlantic salmon exhibit marked, sometimes clinal, differences in a number of biochemical, morphological and life-history traits in various parts of their distribution range. These differences are usually interpreted as indications that populations have become locally adapted by natural selection. Yet, oceanic migrations in Atlantic salmon involve large-scale movements, therefore providing potential for straying at long distances. With frequent long-distance straying, genotypes would not be repeatedly exposed to constant selective pressures, such that populations could not become adapted to their local environment. In the present study, we thus analyse isolation by distance patterns in Atlantic salmon in order to assess the spatial scale of straying. We then compared the observed patterns with that of the brook charr (*Salvelinus fontinalis*), an anadromous species inhabiting the same rivers than salmon, but exhibiting more restricted coastal movements. No correlation was found between the levels of genetic diversity of both species sampled in the same rivers, although genetic diversity was more homogeneous among *S. salar* than *S. fontinalis* populations. *S. salar* populations were also less differentiated from one another, and the increase of differences with geographic distance was weaker than for *S. fontinalis* populations. Moreover, at the widest geographic, the increase was significant neither in *S. salar* nor in *S. fontinalis*, although dispersal is geographically restricted by physiological constraints in the latter. The faster decrease of the isolation by distance signal with increasing geographic scale in *S. salar* compared to *S. fontinalis* thus suggests that straying in *S. salar* occurs mostly at short distances, but that large scale straying is more frequent in *S. salar* than in *S. fontinalis*. Together, these observations support the hypothesis that differences in straying behaviour of both species have led to contrasted spatial patterns of genetic diversity. They also illustrate the benefits of using a comparative approach rather than a strictly model-based inference method in situations where homogeneity and stability of demographic parameters cannot be assumed.

6.3. Introduction

Salmonid populations inhabiting different rivers commonly differ in morphology and life history traits (Thorpe et al. 1998 and references therein). Some of this variation may be due to additive genetic variation (Saunders 1981), and consequently, phenotypic variation among salmon populations is believed to reflect local adaptation, and therefore enhance population persistence (Power 1981, Taylor 1991, Verspoor 1997). The consideration of such variation is therefore considered central in the design of management and conservation plans in salmonid species (Dodson et al. 1998). In the Atlantic salmon (*Salmo salar* L.) the strongest case for the adaptive value of phenotypic variation has been inferred from clinal variation (Schaffer and Elson 1975, reviewed in Taylor 1991). For instance, a positive relationship has been reported between water temperature and the initiation of spawning date (Heggberget 1988) as well as the proportions of precocious males in a population (Myers 1986). The most compelling evidence for local adaptation stemmed from biochemical studies consistently reporting an association between allele frequencies at the NADP-dependent malic enzyme-2 locus ($_{m}$MEP-2*) and summer freshwater temperature at both a local (among sections within a stream) and a regional scale (parallel north-south clines in North America and Europe, Verspoor and Jordan 1989). Furthermore, differences in growth between $_{m}$MEP-2* homozygote genotypes have been experimentally demonstrated (Jordan and Youngson 1991), thus providing strong evidence that this cline has been shaped by natural selection. Cumulatively, such clines suggest that Atlantic salmon populations are adapted to their local environment because repeated associations of genetic and environmental variation remain inconsistent with neutral genetic variation hypotheses.

Whether populations can adapt to local conditions depends essentially on the relative rates of gene flow and selection. If genes diffuse across a continuous habitat, then an allele can become established provided that it is favoured in a region larger than a critical distance set by the characteristic scale $l=\sigma/\sqrt{2s}$ (Slatkin 1973, Nagylaki 1975), where σ is the standard deviation of distance between parent and offspring and s is the selective advantage of an allele. Thus, unless clinal patterns are regenerated each generation, the potential for local adaptation depends on the spatial scale of dispersal. For a given intensity of selection (*s*), local adaptation is more likely to evolve when dispersal is unfrequent and geographically restricted than under

an island model of population structure. In contrast, intense migration and/or long-distance migration both contribute to increase σ, thus increasing the selective intensity required for local adaptation to evolve. Thus, an evaluation of the potential for local adaptation in an anadromous salmonid species would involve a quantification of parameters *s* and σ. The parameter *s* has been estimated experimentally (Jordan and Youngson 1991) only for mMEP-2* alleles in the Atlantic salmon. Data about the dispersal parameter σ are also scarce for this species

Reproduction in Atlantic salmon is strictly restricted to freshwater. Following an initial period of juvenile growth, individuals (all females and a fraction of males) may express a tolerance to saltwater and run downstream to the marine environment where they undergo large-scale seasonal migrations to foraging grounds in the Atlantic Ocean. Mark-recapture studies, indicate that most fish not homing to their river of origin stray into neighbouring rivers in proportion to the distance between rivers (Potter & Russel 1994, Hvidsen, Heggberget and Hansen 1994, Mills 1994). Yet, relevant studies (tags on downstream migrating juveniles) are rare and most of them involve populations from the European part of the range and/or hatchery-reared individuals. Furthermore, because foraging journeys occur over long distances, individuals have the potential to reproduce in a river very distant from the one they originate from. Such long distance dispersal represent a major logistic difficulties associated with surveying dispersing individuals among populations covering a large geographic area. "Direct" studies therefore run the risk of underestimating long-distance dispersal. This is problematic in the framework of studying local adaptation, since the parameter of central σ, is strongly influenced by the tail of the dispersal distances distribution.

Analysis of the correlation between genetic and geographic distances can provide indirect insight into the pattern and intensity of genetic exchange among rivers. As shown by Wright (1943), geographically restricted dispersal results in an increase of genetic divergence with geographic distance which can be used to infer the intensity of dispersal via the parameter $N\sigma^2$ (Rousset 1997). Thus, population genetic approaches can be used to infer directly the parameter of interest σ. Population genetic studies in Atlantic salmon published to date have remained equivocal. Fontaine et al. (1997) reported no correlation between genetic and geographic distances. In contrast, McConnell (1997), Bourke et al. 1997 and King et al. (2001)

reported some level of association, although most of the isolation by distance signal in those studies was due to the inclusion of a very remote sample (Newfoundland) in McConnell (1997) or landlocked samples from Maine (USA) in King et al (2001). Thus, previous studies have remained limited by a patchy distribution of sample collection, a small number of populations collected, and/or an either very small (within rivers) or very large (range-wide) sampling scale. Consequently, little is currently known of the spatial scale over which straying may occur in Atlantic salmon.

In the present study, we used spatial patterns of genetic diversity to compare $N\sigma^2$ values in Atlantic salmon and the andromous brook charr (*Salvelinus fontinalis)*. The contrast between the dispersal distances distributions of the two species allowed us to investigate the sensitivity of the methodology used. The brook charr is a salmonid whose marine incursions are limited to short distances (typically <500 m, van de Sande and Curry, unpublished manuscript). Consequently, a one-dimensional stepping-stone model of population structure has been shown to apply in that species (chapter 4). If identical processes are shaping spatial patterns of genetic diversity in salmon and charr, then concordant patterns of isolation by distance should be apparent because samples of both species were collected in the same geographic area including some of the same locations. Thus, any observed difference would be due to contrasts in their migratory behaviour. Thus, we first tested for isolation by distance in *S. salar* and *S. fontinalis*. Including *S. fontinalis* in this analysis allowed us to assess whether our sampling design was adequate for the detection of isolation by distance at this spatial scale. We then tested for geographic variation in the level of genetic differentiation and isolation by distance signal using a sliding window analysis.

6.4. Materials and methods

6.4.1. Samples collection

Four hundred and thirty three adult anadromous Atlantic salmon (including grilses and multi sea winter fish) were collected from ten rivers on the north shore of the Gulf of St-Lawrence River in Québec, Canada. (mean N=43.3, Table 6-1., Fig. 6-1.). A subset of fifteen anadromous populations of *S. fontinalis* analyzed in chapter 4 and including six populations collected in the same rivers than salmon was analysed along the same coast (664 individuals, mean N=44.3, Table 6-1., Fig. 6-1). Total DNA was isolated using a standard phenol-chloroform protocol (Sambrook et al. 1989), and individuals were genotyped at six microsatellite loci (SSA-85, SSA-171, SSA-197, SSA-202, SSOSL-85 and μ3) as described in Garant et al. (2000).

6.4.2. Genetic diversity within and among populations

Intrapopulation genetic diversity was estimated as the number of different alleles per locus, expected and observed heterozygosity (H_E and H_O). The number of different alleles per locus (A) was standardized to the smallest sample size (N=21 for *S. salar* and N=13 for *S. fontinalis*) using a rarefaction method (Petit et al. 1998). Gradients of allelic richness along the coast were tested for each locus independently in Statview 5.01 (SAS Institute 1998) and the overall significance level was combined over loci using Fisher's method (Sokal and Rohlf 1995). Although the same number of loci was used for both species, the loci were not the same, such that genetic diversity could not be compared directly. Hence, the variance ratio F-test available in Statview was applied to multilocus estimates of allelic richness to determine whether allelic richness was equally variable among *S. fontinalis* and *S. salar* populations.

Heterogeneity of allele frequencies among samples was tested using the permutation test (5000 iterations) in Genetix 4.02 (Belkhir et al. 2000). Pairwise comparisons were also performed using 30000 permutations and the critical significance threshold maintained at 5% using Bonferroni sequential adjustment for multiple tests (Rice 1989). Genetic differentiation was then quantified by F_{ST} as estimated by θ (Weir and Cockerham) and the 95% confidence intervals generated by 1000 bootstrap iterations over loci as implemented in Genetix.

Because latitudinal variation in the level of differentiation were revealed in chapter 4, a sliding window analysis was used to investigate variation along the coast. The same procedure was used as in chapter 4, except that the window was shifted by 5 km increment. The null hypothesis of no variation in F_{ST} along the coast was tested using the a Kendall's non-parametric rank correlation in Statview.

6.4.3. Spatial patterns of genetic diversity

Because reproduction in anadromous salmonids is strictly restricted to freshwater, populations are discrete and linearly organized in one dimension. Assuming that dispersal is geographically restricted, anadromous salmonids therefore closely match the assumptions of a one-dimensional stepping-stone model of population structure (Kimura and Weiss 1964). Theoretical predictions for this model were provided by Rousset's (1997) regression-based framework. With finite variance of parental position relative to offspring position (σ^2), a linear relationship is expected between $F_{ST}/(1-F_{ST})$ and distance between populations pairs (j) in a one-dimensional linear habitat: $F_{ST}/(1-F_{ST}) \approx A_1/(4N\sigma) + j/(4N\sigma^2\varepsilon)$, where N is effective subpopulation size, A_1 is a constant dependent on the shape of the dispersal distribution (constant C_0 in Sawyer 1977, equation 2.4) and ε is the distance among consecutive habitat patches. A permutation test implemented in Genetix 4.02 (1000 permutations) was used to test the significance of Mantel's correlation coefficient between coastal distance and $F_{ST}/(1-F_{ST})$. Mantel's test relies on the computation of a correlation coefficient while the quantity of interest in Rousset's (1997) inference procedure is the slope of the isolation by distance relationship. We thus directly tested the significance of the slope by randomly permuting 1000 times populations along the coast. A slope value was computed for each random configuration and the resulting distribution was compared to the observed slope. As revealed in chapter 4, patterns of isolation by distance can vary in space. We thus investigated variation in the slope of isolation by distance along the coast using the sliding window analysis. As in chapter 4, sampling density was kept constant by resampling all possible sets of four populations within each window. The null distribution of the slope was generated within each window containing more than four populations and used to generate the 95% confidence intervals. The null hypothesis of no variation in the slope of the isolation by distance relationship along the coast was tested using Kendall's non-parametric rank correlation in Statview.

Because spatial patterns are also sensitive to scaling effects and may fade at larger geographic scales (chapter 4), we then tested whether the isolation by distance slope remained constant over increasing geographic scales by computing the regression slope of $F_{ST}/(1-F_{ST})$ over coastal distance, successively including pairwise comparisons of populations separated by increasingly large distances. The variation pattern was depicted using a log-log graph in which the steepness of the regression illustrates the rate of decrease of the isolation by distance slope with geographic scale.

6.5. Results

6.5.1. Genetic diversity within and among populations

High levels of polymorphism were found for both species in all populations (Table 4.2., Table 6.2). The mean expected heterozygosity (H_E) over six microsatellite loci was higher for *S. salar* (H_E=0.8230) than for *S. fontinalis* (0.7088). No geographic variation in allelic richness was apparent among *S. salar* populations (Fig 6.2., combined probability over individual loci P=0.523). However, there was a marginally significant trend of decreasing allelic richness towards the east among *S. fontinalis* populations (Fig 6.2., P= 0.05735). The lower variance of multilocus estimates of allelic richness in *S. salar* than in *S. fontinalis* (F= 4.146, P= 0.0277, two tailed) further illustrated that genetic diversity was more evenly distributed across *S. salar* populations than across *S. fontinalis*, Highly significant overall heterogeneity in allele frequencies was observed in both salmon and charr (P<0.0005). In both species, each population was clearly differentiated from all others. Following Bonferroni correction, all pairwise comparisons were significant for *S. fontinalis* (Table 6.3., final P=0.0014) and all but one in *S. salar* (Table 6.4., final P=0.0023). *S. fontinalis* populations were genetically more differentiated that *S. salar*. (F_{ST}= 0.1070 vs F_{ST}= 0.0445), with non-overlapping 95% IC ([0.0833-0.1300] vs [0.0310-0.0597]. In both species, the extent of differentiation significantly increased from west to east, as revealed by the sliding window analysis (Fig 6.3., P=0.0039 for *S. fontinalis*, P=0.0058 for *S. salar*). In the case of salmon however, this pattern became marginally significant when the two most western populations (rivière St-Marguerite and rivière des Escoumins) were removed from the analysis (P=0.0854).

6.5.2. Spatial patterns

Mantel tests revealed no globally significant association between geographic and genetic distances as measured by $F_{ST}/(1-F_{ST})$ for either *S. salar* (Fig 6.4., r = 0.010, P=0.4556) or *S. fontinalis* (Fig 6.4., r = 0.081, P = 0.2208) at the spatial scale of this study . However, contrasting signals of isolation by distance signal were revealed by focusing on smaller geographic scales using the sliding window analysis. In *S. salar*, this analysis further confirmed that geographic and genetic distances were unrelated. Thus, none of the slopes computed from the sliding window analysis differed significantly from their expected null

distribution (Fig. 6.5.) when restricting the analysis to the 600 km windows. In *S. fontinalis*, however, the slope varied along the coast, and departed from the 95% CI for random values in the westernmost windows, while no such departure was apparent in the eastern part of the coast (Fig 6.6.). Thus, despite the non-significant overall Mantel test including all samples, the sliding window analysis revealed a signal of isolation by distance signal at smaller geographic scales (600 km) in *S. fontinalis,* but no signal in *S. salar*.

Though weak and statistically non-significant in both species, the slope of isolation by distance was approximately an order of magnitude larger for *S. fontinalis* (Fig 6.4., 1.34×10^{-5}) than for *S. salar* (Fig 6.4., 1.12×10^{-6}), further indicating that isolation by distance was stronger in *S. fontinalis*. The investigation of variation in the slope with geographic scale revealed that this difference was not constant over all geographic scales (Fig 6.7.). When including only populations separated by the shortest distances, the isolation by distance slope was similar for both species or even higher for *S. salar* than for *S. fontinalis*. For example, the slope computed from populations separated by 60 km or less was 0.0033 for *S. salar* and 0.0021 for *S. fontinalis*. When including populations at wider geographic scales, however, there was a more rapid decay of the slope along geographic scales for *S. salar* than for *S. fontinalis*, ultimately leading to the lower overall slope when considering all samples. Accordingly, the regression line of the log-log graph showed a steeper decline in slope for *S. salar* (Fig 6.7., $y = -2.23 x + 1.1799$) than for *S. fontinalis* (Fig 6.7., $y = -1.52 x + 0.0242$). Thus, the globally lower slope of isolation by distance in *S. salar* was only apparent at large geographic scales.

6.6. Discussion

Overall, our results indicated that isolation by distance is weak among north-american populations of Atlantic salmon *Salmo salar* and brook charr *Salvelinus fontinalis* at the global geographic scale investigated in this study . Yet, a finer comparison that considered variation of geographic scales revealed that isolation by distance was apparent in *S. fontinalis* but not in *S. salar*. Contrasts in the distribution of dispersal distances between both species may thus be sufficient to affect the correlation between geographic and genetic distances. For a given spatial scale and selective pressure then, the differential pattern of isolation by distance suggests that local adaptation is therefore more likely to evolve in *S. fontinalis* than in *S. salar*.

6.6.1. Comparative spatial patterns of *S. salar* and *S. fontinalis*

6.6.1.1.Allelic diversity

Contrary to *S. fontinalis*, no decrease in allelic richness toward the east was observed in *S. salar*. As discussed in chapter 3, a decrease of allelic richness can result from recolonization by a subset of populations issued from a larger glacial refugia, as reported in phylogeographic studies (Hewitt 1996). Although brook charr and Atlantic salmon are now found in rivers from eastern Canada, they may have differed in their pattern of colonisation. Namely, the north-south coastal colonization gradient inferred for the brook charr in Chapter 4 may not apply to *S. salar*. Alternatively, the more homogeneous distribution of genetic diversity among populations of Atlantic salmon can stem from a higher probability of island migration in *S. salar* than in *S. fontinalis*. That is, long-distance dispersal could have led to a quick replenishment of allelic richness within recently settled populations.

6.6.1.2.Genetic differentiation

The higher F_{ST} observed among *S. fontinalis* than *S. salar* populations fits the expectation of increased differentiation in a stepping-stone model relative to an island model of population structure (Crow and Kimura 1970). This supports the view that *S. fontinalis* and *S. salar* may be characterized by different ditributions of dispersal distances. Yet, the increase of differentiation towards the east for both species is surprising. In fact, if island migrations occur frequently enough, the extent of genetic differentiation should be the same whatever the

location on the coast. One possible explanation may be that the increase of differentiation observed in salmon may be related to the high occurrence of males developping as grilse in this region (Tremblay 2000). Grilse are fish that return to spawn after a single season of growth in the marine environment and undergo shorter marine migrations, such that they may have lower potential for long-distance straying than multi sea-winter salmon. Consequently, rivers with a greater fraction of males developing as grilse (such as the eastern end of the coast) may be characterized by lower σ and increased differentiation. Yet, we are not aware of any empirical data comparing grilse and multi sea-winter salmon straying distance and rate, such that further assessing this explanation currently remains difficult. Alternatively, this increase could also be related to a historical "stocking" gradient, whereby western populations may have been stocked with a greater intensity than populations from eastern rivers (Fontaine et al. 1997). The fact that the significance of the geographical variation in the extent of differentiation was removed for *S. salar* when removing the two westernmost populations from the analysi supports this possibility.

6.6.1.3.Isolation by distance

Isolation by distance was apparent in *S. fontinalis* when restricting the analysis to geographic scales of 600 km. In contrast, no evidence for isolation by distance was apparent in *S. salar* at either spatial scale. Because long-distance straying is predicted to increase the variance of the position of an offspring relative to its parent and thus decrease the slope of isolation by distance (Rousset 1997), the weaker isolation by distance pattern in *S. salar* compared to *S. fontinalis* (a 10-fold decrease in the slope) may be related to more frequent long-distance straying in *S. salar* compared to *S. fontinalis*. Yet, the rate of decrease of the isolation by distance relationship with geographic scale revealed that the slope of both regressions was similar when restricting the analysis to pairs of populations at small geographical distances. This suggested that the isolation by distance patterns were similar at short distances in both species. We thus propose that most strays actually stray at short distances, closely matching the migration pattern of anadromous *S. fontinalis* at this geographic scale. When further increasing the geographic window however, the slopes for *S. salar* decreased quicker than those for *S. fontinalis,*as a consequence of more frequent long-

distance straying that thus progressively contributed to disrupt the relationship between geographic and genetic distances in salmon realtive to brook charr.

6.6.2. Conclusions. Statistical issues for a comparative analysis

The Mantel test detected no association between geographic and genetic distances in either *S. fontinalis* or *S. salar*. Yet, isolation by distance slopes departed from random expectation in the western part of the coast for *S. fontinalis,* therefore indicating that a significant pattern of isolation by distance applied to that species. The discrepancy between the results observed here and those reported in Chapter 4 may result from the different spatial scales considered in both chapters, as exemplified by the variation of the slope of isolation by distance as a function of geographic distance. The lack of significance of the Mantel test for *S. fontinalis* also suggest that the variance around the expected relationship given our sampling scheme (15 populations, randomly distributed along the coast as opposed to an ideal constant spacing) may be too large for detection by a Mantel test, especially as the system may still be on the way to reach migration-drift equilibrium (Chapitre 4).

6.7. Ackowledgements

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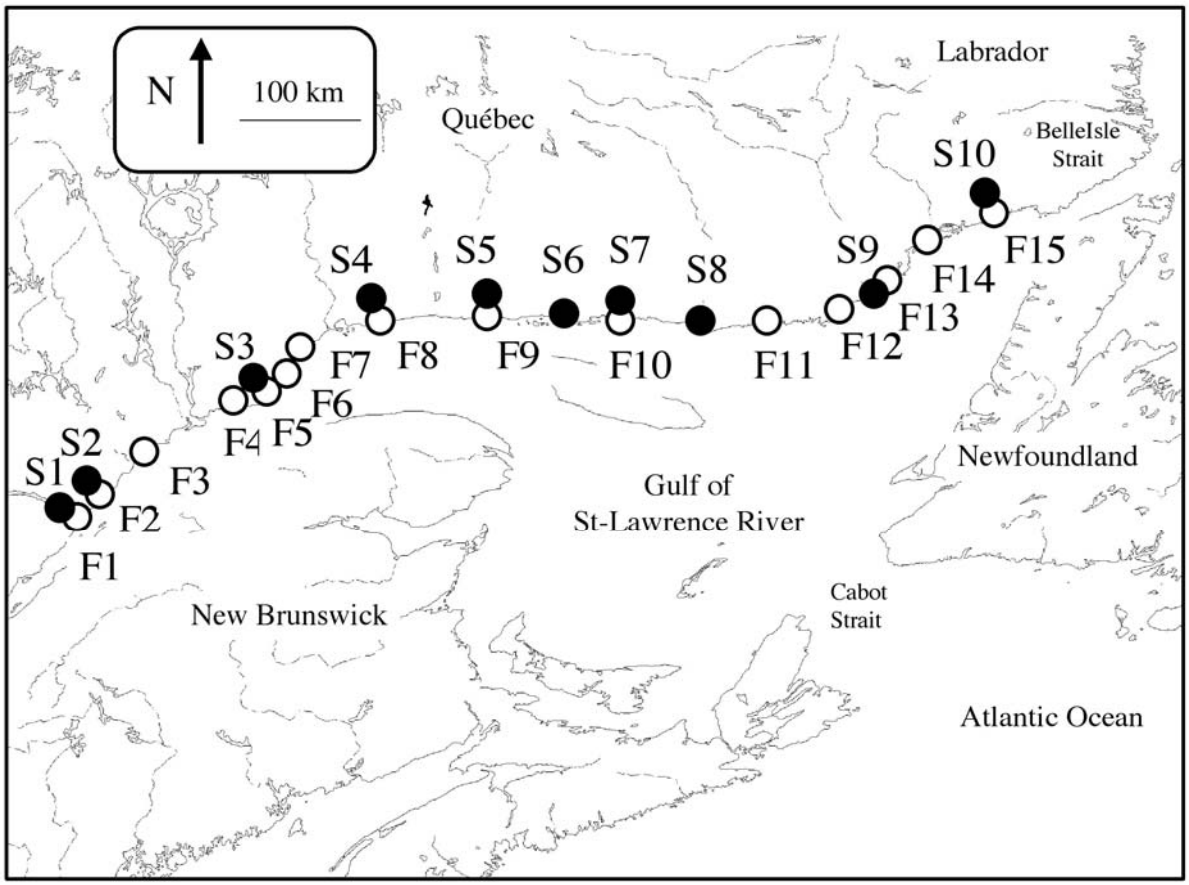

Figure 6-1 Location of *S. salar* (black circles) and *S. fontinalis* samples. Codes refer to locations in table 1.

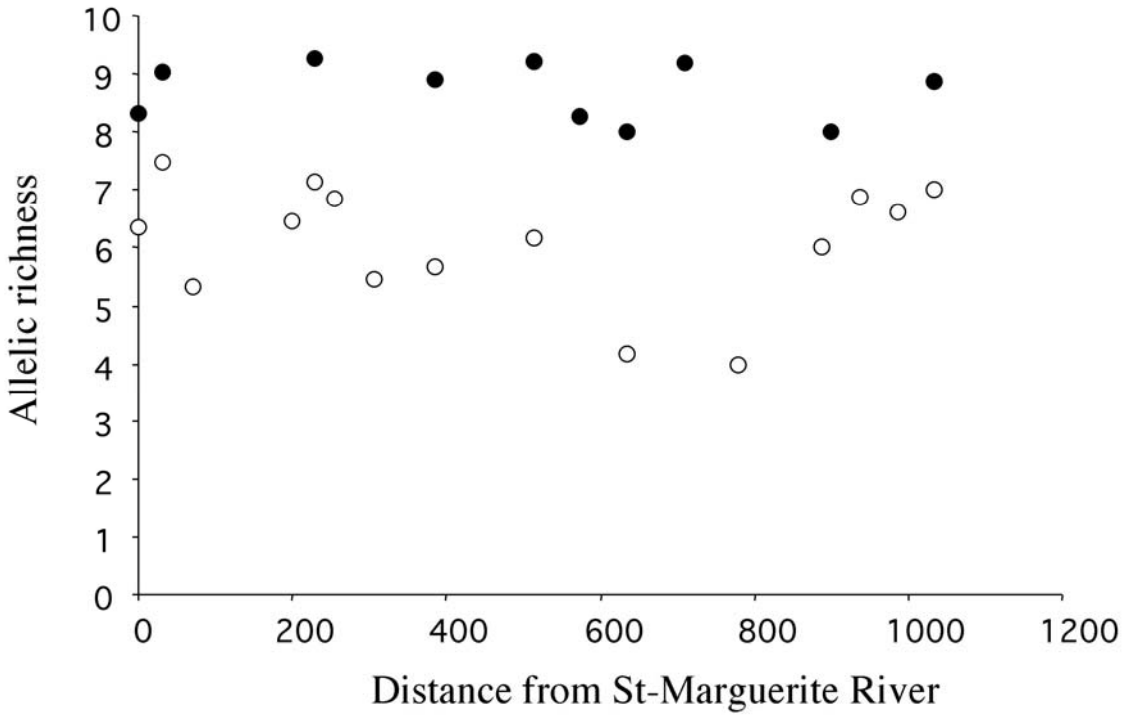

Figure 6-2 Geographic variation in mean allelic richness along the coast across loci. Distances are measured along the coast from the westernmost river. Allelic richness was estimated at a constant population size (N=21 for *S. salar*, black dots; N=13 for *S. fontinalis,* open dots) using a rarefaction méthode.

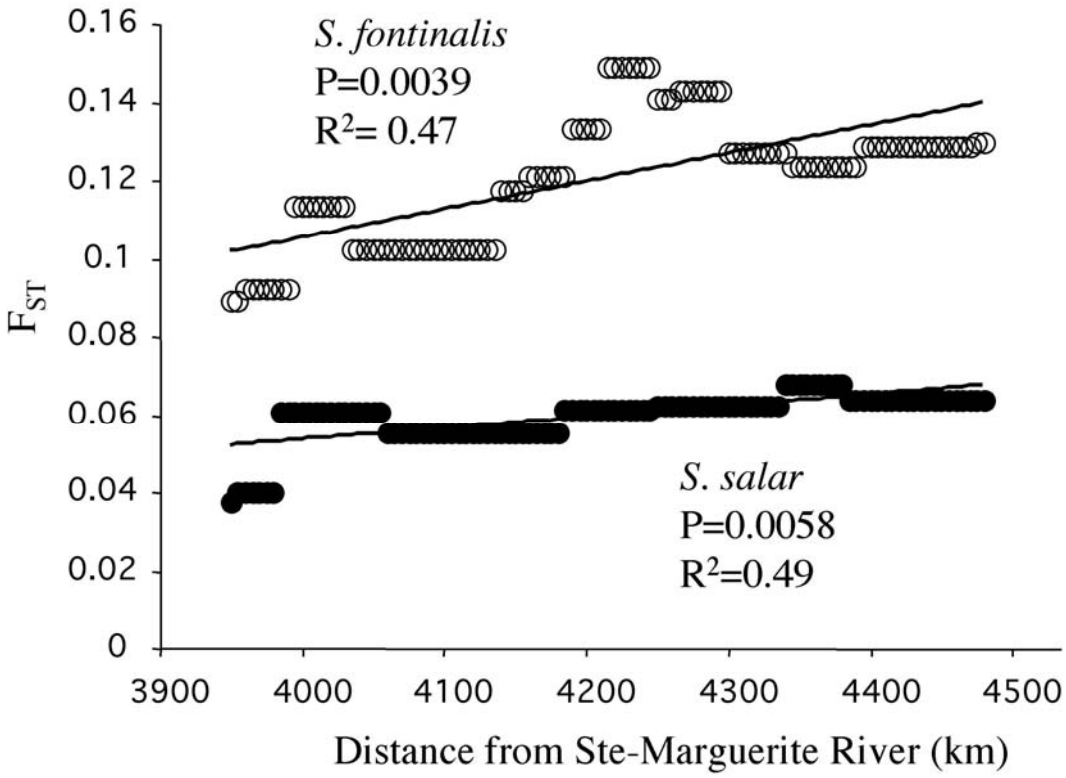

Figure 6-3 Geographic variation in F_{ST} depicted using a sliding window analysis. See chapter 3 for details. Black dots stand for *S. salar* and open dots for *S. fontinalis*

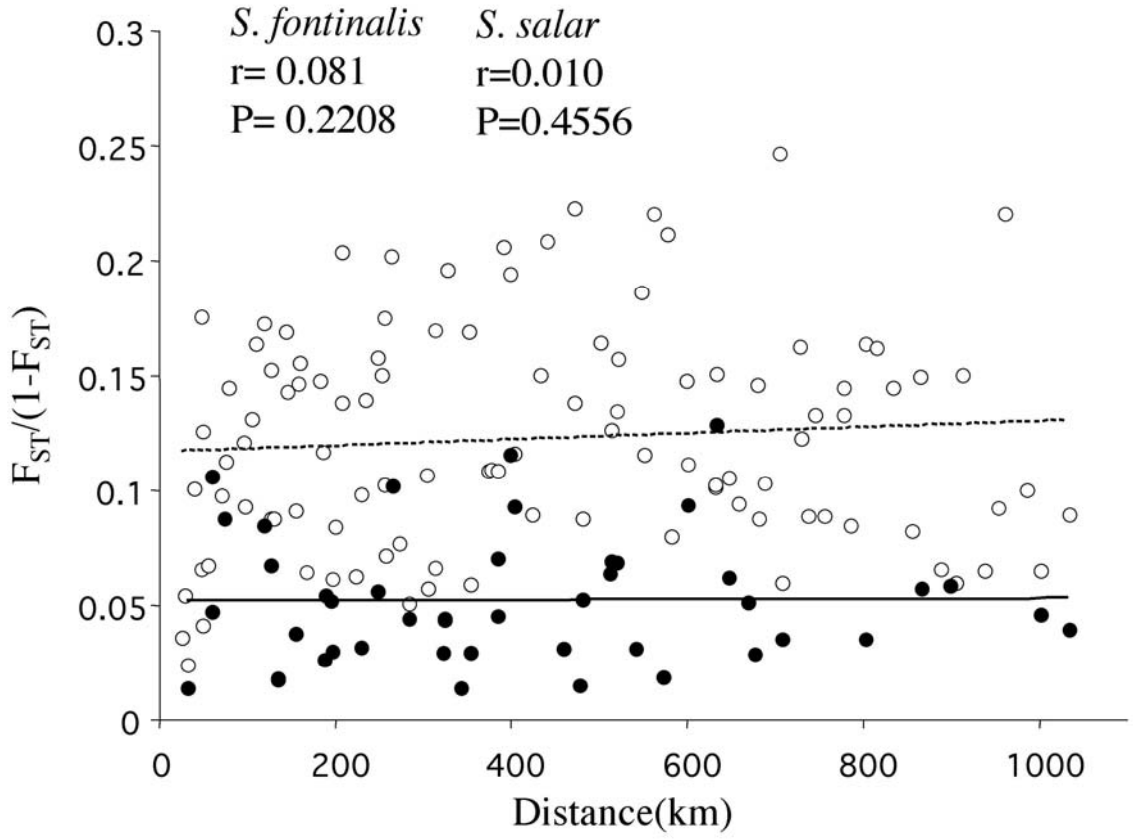

Figure 6-4 Isolation by distance relationship in *S. salar* (black dots, solid line) and *S. fontinalis* (open dots, dotted line). r and P-values are spearman's correlation and the probability of observing as strong a correlation in the absence of any true association.

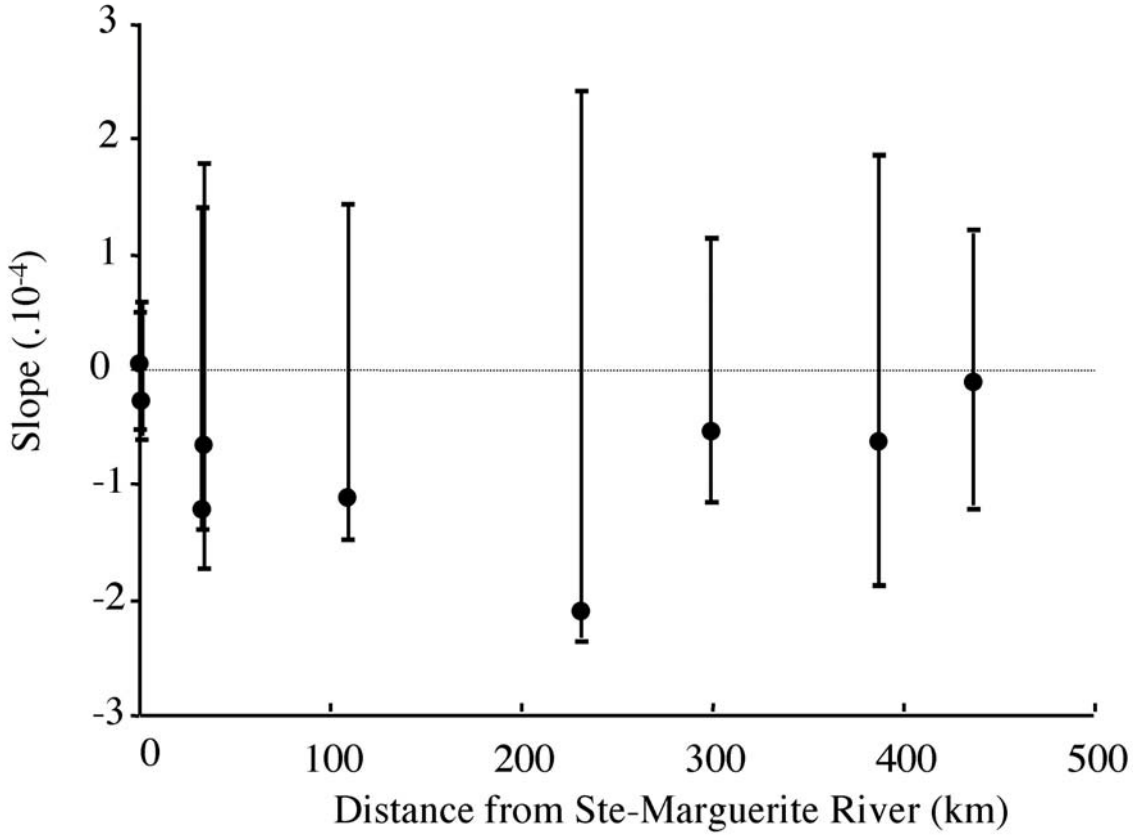

Figure 6-5 Variation in the slope of the isolation by distance relationship along the coast for *S. salar*. Bars represent 95% CI under the assumption of no association between geographic and genetic distances.

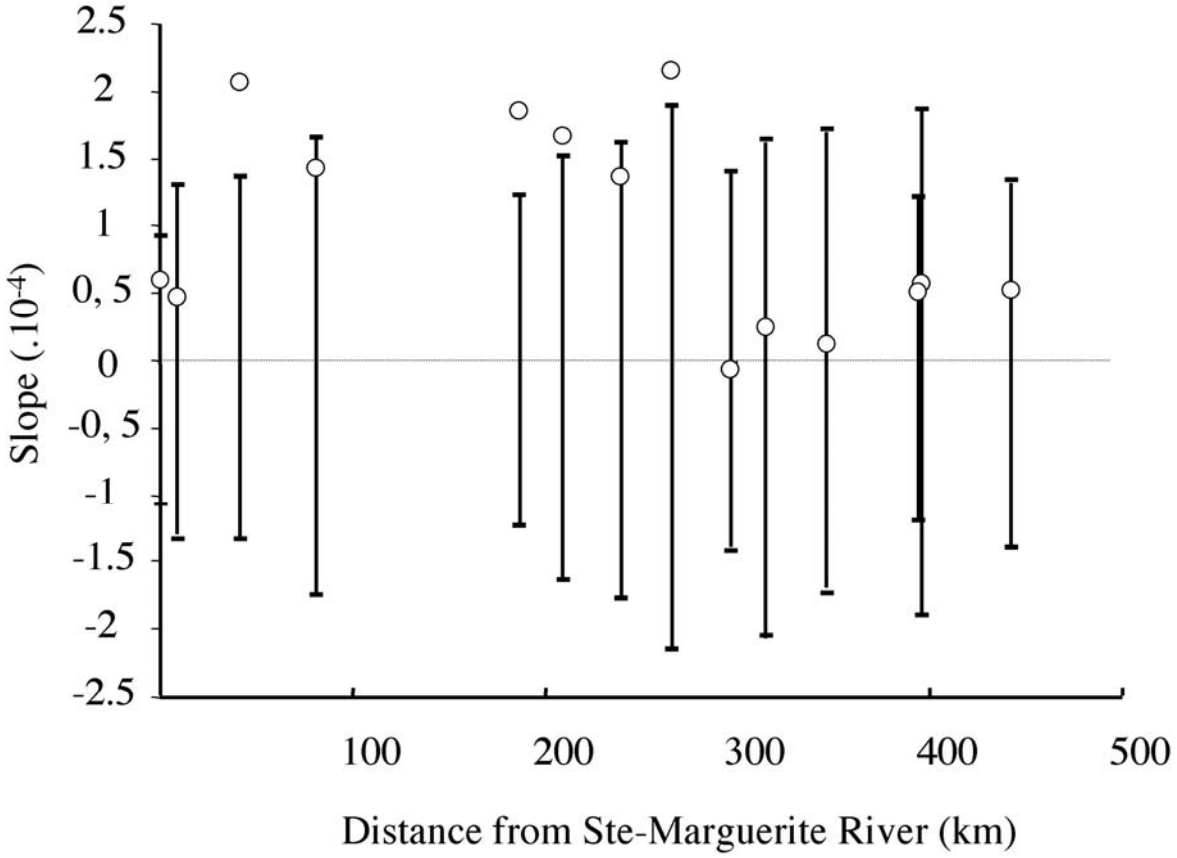

Figure 6-6. Variation in the slope of the isolation by distance relationship along the coast for *S. fontinalis*. Bars represent 95% CI under the assumption of no association between geographic and genetic distances.

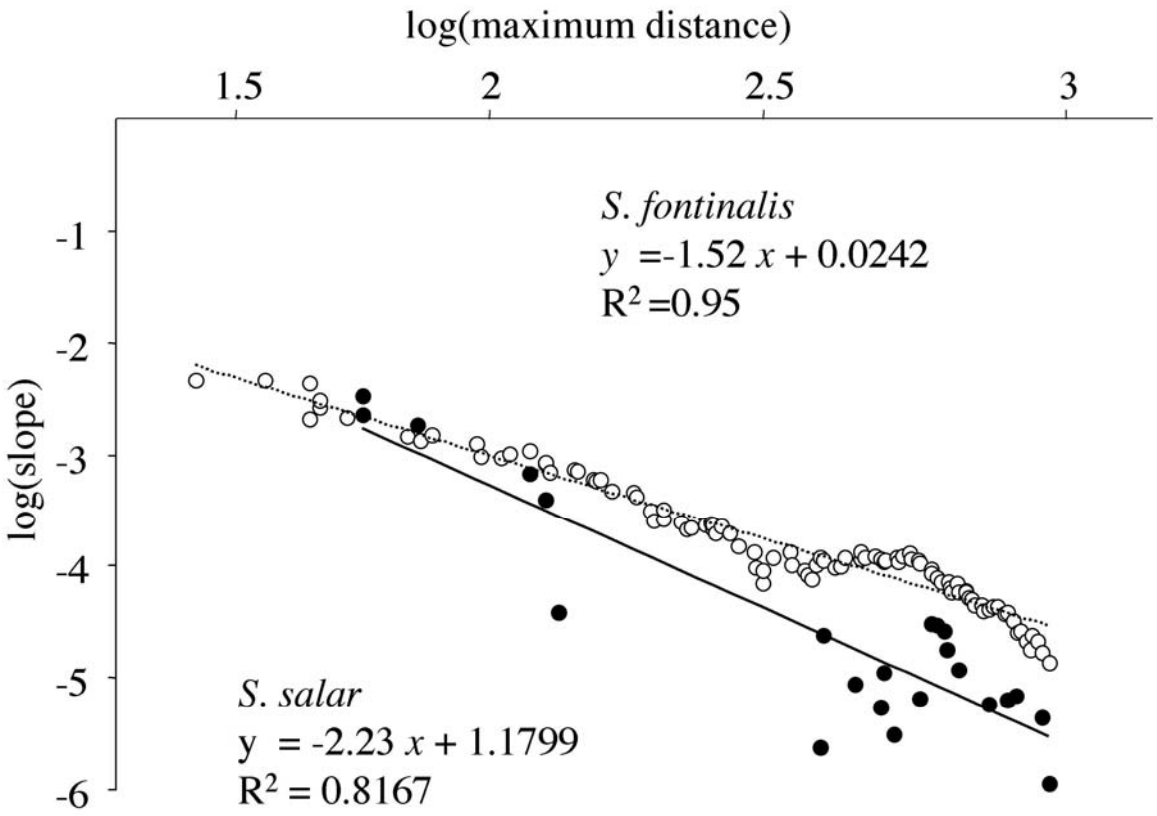

Figure 6-7 Variation of the slope of the isolation by distance relationship in *S. salar* (black dots, solid line) and *S. fontinalis* (open dots, dotted line) as a function of the geographic scale of observation. Note the steeper decline for *S. salar* than for *S. fontinalis*.

Table 6-1 Atlantic salmon and anadromous brook charr samples collected in eastern Canadian rivers. N is the number of individuals analyzed. Kilometer zero is set at Rivière Ste-Marguerite and coastal distances are measured along the coastline.

	Label	Location	N	coastal distance from km 0	latitude	longitude
S. salar	S1	Rivière Ste-Marguerite	76	0	48° 15' 49"	69° 56' 47"
	S2	Rivières des Escoumins	43	32	48° 20' 50"	69° 27' 00"
	S3	Rivière Trinité	50	230	49° 25' 05"	67° 18' 16"
	S4	Rivière Moisie	32	386	50° 16' 00"	65° 56' 00"
	S5	Rivière St-Jean	40	514	50° 17' 00"	64° 20' 00"
	S6	Rivière Mingan	29	574	50° 18' 00"	63° 59' 00"
	S7	Rivière Piashti	21	634	50° 17' 00"	62° 48' 00"
	S8	Rivière Natashquan	50	709	50° 07' 00"	61° 48' 00"
	S9	Rivière du Gros Mécatina	50	899	50° 46' 06"	59° 05' 40"
	S10	Rivière St-Paul	42	1034	51° 27' 00"	57° 42' 00"
S. fontinalis	F1	Rivière Ste-Marguerite	50	0	48° 15' 49"	69° 56' 47"
	F2	Rivière des Escoumins	50	32	48° 20' 50"	69° 27' 00"
	F3	Rivière Laval	68	72	48° 46' 00"	69° 03' 00"
	F4	Rivière Godbout	22	200	49° 19‘ 00"	67° 35‘ 0O"
	F5	Rivière Trinité	50	230	49° 25' 05"	67° 18' 16"
	F6	Rivière du Calumet	48	256	49° 37' 00"	67° 13' 00"
	F7	Rivière Ile de Mai	50	306	49° 55' 38"	66° 57' 50"
	F8	Rivière Moisie	49	386	50° 16' 00"	65° 56' 00"
	F9	Rivière St-Jean	50	514	50° 17' 00"	64° 20' 00"
	F10	Rivière Piashti	13	634	50° 17' 00"	62° 48' 00"
	F11	Rivière Washicoutai	48	778	50° 13' 00"	60° 52' 00"
	F12	Rivière Watasheistic	31	888	50° 24' 00"	59° 50' 00"
	F13	La Tabatière	48	938	50° 50' 00"	58° 59' 00"
	F14	Rivière St-Augustin	46	986	51° 12' 00"	58° 35' 00"
	F15	Rivière St-Paul	41	1034	51° 27' 00"	57° 42' 00"

Table 6-2. Microsatellite polymorphism in *S. salar* populations. Population codes refer to Table 1. He and Ho are expected and observed heterozygosities, respectivement. *f* is Weir & Cockerham's (1984) F_{IS} estimator and P_{HW} is the associated p-value generated from 2000 permutations. Significant multilocus p-values following sequential Bonferroni correction ($P_{\alpha=0.05}$=0.0083, k_i=10) are indicated in bold. 0 stands for P_{HW}<1/2000.

		S1	S2	S3	S4	S5	S6
SSA-171	**He**	0.9211	0.8848	0.9104	0.8724	0.9215	0.9080
	Ho	0.9474	0.8182	0.6818	0.8966	0.8667	0.9091
	f	-0.0290	0.0760	0.2530	-0.0280	0.0600	-0.0010
	P_{HW}	0.7096	0.0104	0.0009	0.7870	0.0200	0.4198
SSA-197	**He**	0.8855	0.8687	0.8974	0.8969	0.8693	0.8708
	Ho	0.9474	0.8000	0.8125	0.9032	0.7750	0.9286
	F	-0.0700	0.0800	0.0950	-0.0070	0.1100	-0.0680
	P_{HW}	0.9213	0.1351	0.0232	0.5013	0.1097	0.4168
SSA-202	**He**	0.8380	0.8881	0.9054	0.8367	0.6870	0.8856
	Ho	0.8421	0.8718	0.7556	0.6087	0.4615	0.6667
	f	-0.0050	0.0190	0.1670	0.2770	0.3310	0.2510
	P_{HW}	0.6813	0	0.0014	0.0420	0.0562	0.0011
SSA-85	**He**	0.6504	0.7547	0.8483	0.8414	0.9021	0.7669
	Ho	0.6842	0.6667	0.8723	0.8065	0.8421	0.6786
	f	-0.0520	0.1180	-0.0290	0.0420	0.0670	0.1170
	P_{HW}	0.7327	0.0033	0.6494	0.4358	0.0537	0.0201
SSOSL-85	**He**	0.8696	0.8576	0.8322	0.8633	0.8632	0.8672
	Ho	0.8947	0.7667	0.7500	0.6667	0.7632	0.8148
	f	-0.0290	0.1080	0.1000	0.2310	0.1170	0.0620
	P_{HW}	0.7874	0.0061	0.3639	0	0.0537	0.1539
mu3	**He**	0.7482	0.7691	0.6604	0.6499	0.7349	0.7459
	Ho	0.7895	0.6429	0.6600	0.6774	0.7353	0.6522
	f	-0.0560	0.1660	0.0010	-0.0430	-0.0010	0.1280
	P_{HW}	0.8308	0.0012	0.5803	0.5345	0.3921	0.0354
Multilocus	**He**	0.8188	0.8372	0.8423	0.8267	0.8296	0.8407
	Ho	0.8509	0.7610	0.7554	0.7598	0.7406	0.7750
	f	-0.0500	0.1160	0.0912	0.0441	0.0689	0.0456
	P_{HW}	0.9830	**0**	**0**	0.0995	0.0175	0.1225

Table 6-2. continued

		S7	S8	S9	S10
SSA-171	**He**	0.9349	0.8981	0.9176	0.9179
	Ho	0.7778	0.7250	0.8222	0.7826
	f	0.1720	0.1950	0.1050	0.1500
	P_{HW}	0.0166	0.0037	0.0333	0.0402
SSA-197	**He**	0.8048	0.8361	0.8402	0.8424
	Ho	0.7778	0.7551	0.7400	0.7500
	F	0.0340	0.0980	0.1200	0.1110
	P_{HW}	0.3810	0.0020	0.1936	0.1355
SSA-202	**He**	0.8943	0.8942	0.9194	0.8948
	Ho	0.6190	0.5000	0.8000	0.7778
	f	0.3130	0.4440	0.1310	0.1320
	P_{HW}	0.0125	0	0.0118	0.0043
SSA-85	**He**	0.7974	0.8731	0.7577	0.7479
	Ho	0.6500	0.7600	0.7500	0.6410
	f	0.1890	0.1310	0.0100	0.1450
	P_{HW}	0.0869	0.0209	0.4785	0.3394
SSOSL-85	**He**	0.7897	0.8765	0.8279	0.8782
	Ho	0.7500	0.6563	0.7381	1.0000
	f	0.0520	0.2540	0.1100	-0.1410
	P_{HW}	0.3461	0.0018	0.1282	1
mu3	**He**	0.4476	0.7574	0.5067	0.5558
	Ho	0.4375	0.7000	0.4800	0.6765
	f	0.0230	0.0760	0.0530	-0.2210
	P_{HW}	0.5649	0.3199	0.0936	0.9920
Multilocus	**He**	0.7781	0.8559	0.7949	0.8061
	Ho	0.6687	0.6827	0.7217	0.7713
	f	0.0916	0.1582	0.0820	0.0237
	P_{HW}	0.0410	**0**	**0.0025**	0.2280

Table 6-3. Pairwise F_{ST} (above diagonale) and associated P-values (below diagonale) among 15 populations of *S. fontinalis*. All pairwise comparisons are significant following Bonferroni correction

	F1	F2	F3	F4	F5	F6	F7	F8	F9	F10	F11	F12	F13	F14	F15
F1	-	0	0	0	0	0	0	0	0	0	0	0	0	0	0
F2	0,0233	-	0	0	0	0	0	0	0	0	0	0	0	0	0
F3	0,0890	0,0915	-	0	0	0	0	0	0	0	0	0	0	0	0
F4	0,0773	0,0605	0,1320	-	0	0	0	0	0	0	0	0	0	0	0
F5	0,0894	0,0574	0,1277	0,0512	-	0	0	0	0	0	0	0	0	0	0
F6	0,0928	0,0589	0,1282	0,0631	0,0342	-	0	0	0	0,0001	0	0	0	0	0
F7	0,0540	0,0711	0,1219	0,1156	0,1010	0,1115	-	0	0	0	0	0	0	0	0
F8	0,0975	0,0557	0,1448	0,1044	0,0832	0,0805	0,1262	-	0	0	0	0	0	0	0
F9	0,1119	0,0802	0,1724	0,0621	0,0483	0,0664	0,1213	0,0801	-	0	0	0	0	0	0
F10	0,1308	0,1002	0,1806	0,1303	0,1041	0,0981	0,1638	0,1362	0,1468	-	0	0	0	0	0
F11	0,1263	0,1170	0,1978	0,1744	0,1567	0,1356	0,1822	0,1710	0,1679	0,1445	-	0	0	0	0
F12	0,0613	0,0760	0,1390	0,0930	0,0859	0,0926	0,0738	0,1408	0,0978	0,1300	0,1406	-	0	0	0
F13	0,0610	0,0560	0,1300	0,0815	0,0559	0,0805	0,0918	0,1035	0,0820	0,0962	0,1343	0,0393	-	0	0
F14	0,0907	0,0843	0,1301	0,0777	0,0815	0,1089	0,1269	0,1284	0,1212	0,1443	0,1694	0,0850	0,0615	-	0
F15	0,0816	0,0607	0,1806	0,1263	0,1406	0,1172	0,1394	0,0951	0,1183	0,1625	0,1487	0,1246	0,1075	0,1490	-

Table 6-4. Pairwise F_{ST} (above diagonale) and associated P-values (below diagonale) among 10 populations of *S. salar*. Significantl pairwise comparisons following Bonferroni corrections areindicated in bold.

	S1	S2	S3	S4	S5	S6	S7	S8	S9	S10
S1	-	0	0	0	0	0	0	0	0	0
S2	**0.01329**	-	0	0	0	0	0	0	0	0
S3	**0.03047**	**0.02869**	-	0	0	0.003	0	0.001	0	0
S4	**0.04335**	**0.02833**	**0.03607**	-	0	0	0	0	0	0
S5	**0.06469**	**0.04993**	**0.04226**	**0.06276**	-	0	0	0	0	0
S6	**0.01811**	**0.03022**	0.01342	**0.02522**	**0.04498**	-	0	0.0005	0	0
S7	**0.11368**	**0.08507**	**0.08488**	**0.0528**	**0.07757**	**0.09574**	-	0	0	0
S8	**0.03405**	**0.028**	**0.01469**	**0.02841**	**0.04935**	**0.01731**	**0.08051**	-	0	0
S9	**0.05508**	**0.05393**	**0.04849**	**0.05959**	**0.06536**	**0.04198**	**0.09212**	**0.05133**	-	0
S10	**0.03766**	**0.04365**	**0.03387**	**0.05799**	**0.06405**	**0.02985**	**0.10342**	**0.04153**	**0.01704**	-

Conclusion

Ce travail est une tentative d'appréhender de façon aussi large que possible l'ensemble des facteurs responsables de l'organisation géographique de la diversité génétique chez l'omble de fontaine *Salvelinus fontinalis*. L'approche employée, résolument empirique, s'est appuyée sur une méthode comparative entre populations confrontées à des paysages de structure différente, entre populations d'age différent le long d'un gradient de colonisation, entre phénotypes migratoires au sein d'une même rivière et entre espèces (saumon et omble de fontaine) dans un même habitat. De l'ensemble des résultats produits, quatre aspects majeurs me semblent émerger qui permettent de détailler quelques aspects de la dynamique de la diversité génétique chez l'omble de fontaine. (1) l'impact du paysage semble n'être sensible qu'à long terme et aux petites échelles spatiales, (2) les variations du patron d'isolement par la distance le long du gradient de colonisation postglaciaire nous indiquent l'échelle temporelle de sa mise en place, (3) l'évolution de la forme de dispersion qu'est l'anadromie a un impact mesurable sur la structure génétique des populations et (4) je propose un mécanisme liant évolution de l'anadromie, évolution de la dépression de consanguinité et évolution de la structure génétique des populations.

Nous avons montré que l'effet du paysage pouvait être difficile à mettre en évidence, particulièrement à de grandes échelles géographiques. Ceci était vrai lors de l'analyse des populations du Maine (chapitre 2) que lors de l'analyse comparative des populations de saumon et de truite le long de la côte Nord du Golfe du St-Laurent (chapitre 6). L'échantillonnage réalisé nous ayant permis de couvrir de façon détaillée une vaste gamme d'échelles géographiques, à quels facteurs peut-on attribuer cette difficulté ? La permanence de l'effet des perturbations récentes peut d'une part être invoquée. La non-stabilité observée du patron d'isolement par la distance le long du gradient de colonisation post-glaciaire suggère en effet que la structure des populations n'en est qu'aux étapes initiales de sa convergence vers celle du paysage. Mais, cette faible concordance peut d'autre part provenir de la stochasticité inhérente au processus de coalescence. Si le fort polymorphisme des locus microsatellites utilisés permet bien de minimiser la variance de l'estimation des paramètres de la structure des populations tels F_{ST} (voir p. e. Estoup et Angers 1999), la variance due à la

stochasticité du processus de coalescence ne peut être minimisée qu'en augmentant le nombre de locus analysés car les allèles à un même locus ont une histoire commune. Le faible nombre de locus utilisé ici pour représenter l'histoire de coalescence de l'ensemble du génome (six), peut être à l'origine d'une partie de nos difficulté à mettre en évidence des corrélations claires. Des marqueurs moins polymorphes mais plus nombreux comme par exemple le polymorphisme de longueur de fragments amplifiés (AFLP) ou les polymorphismes nucléotidiques (SNPs) représentent de ce point de vue une perspective attrayante. Devant les limites des données générées, l'approche strictement comparative utilisée dans le cas de la truite et du saumon (chapitre 6) propose une perspective différente qui permet de s'affranchir des limitations dues aux caractéristiques de l'échantillonnage utilisé et du nombre de marqueurs analysés. Une prochaine étape -actuellement en cours- pourrait inclure le développement d'outils de simulation pour déterminer la sensibilité de la méthode comparative. Pour cela, l'évolution de deux espèces pourrait être simulée au sein de l'habitat réel, les deux espèces différant par exemple par leur patron de migration. Les différences dans la structure de la diversité qui en résulterait au bout d'un certain nombre de génération pourraient alors être comparées aux différences observées pour en évaluer la significativité.

Nous avons par ailleurs documenté l'évolution des patrons d'isolement par la distance le long du gradient de colonisation post-glaciaire. Ces résultats permettent de préciser la vitesse de mise en place des patrons d'isolement par la distance et d'avancer l'idée que l'échelle de temps de la stabilisation de ce patron spatial est du même ordre de grandeur que celle des perturbations glaciaires. Il est donc permis de penser que l'organisation géographique de la diversité génétique est en constante évolution, le paysage pouvant être perturbé avant même que le patron d'organisation n'ait terminé de se mettre en place (voir figure 2.2). Or ces patrons sont couramment utilisés dans le cadre de méthodes d'inférences démographiques, qui font l'hypothèse que la structure des populations n'évolue plus (encadré 2). Nos résultats mettent en évidence une situation dans laquelle l'histoire des populations ne peut pas être négligée. Bien sûr, une telle analyse n'est pas envisageable dans toutes les situations empiriques. Mais dans le cas où on choisit de négliger l'histoire des systèmes considérés, nos résultats contribuent à démontrer qu'il convient au minimum de justifier cette approximation. Il s'agit là d'un sujet de préoccupation très actuel, un nombre croissant d'études empiriques faisant mention de cette limitation (par exemple Bohonak 1999), et on peut espérer que des

études telles que celle-ci mèneront à une meilleure compréhension du phénomène. Si le développement théorique des conséquences génétiques du fonctionnement en métapopulation (voir p. e. Whitlock 2001) permet de réconcilier une approche de type « génétique des populations » dont la majeure partie des prémisses reposent sur un habitat homogène et des pressions de sélections constantes, et une approche à sensibilité plus écologique, qui place la dynamique du paysage au cœur du fonctionnement des écosystèmes, peu de systèmes ont été empiriquement décrits qui permettent d'examiner en détail les conséquences d'un événement de colonisation sur la dynamique de la diversité génétique (Giles et Goudet 1997, Clegg et coll. 2002). Peu de systèmes sans doute se prêtent aussi bien que l'omble de fontaine anadrome à une analyse détaillée, les patrons de migration de l'espèce et l'histoire démographique récente restant souvent mal connus. Lorsque le cadre temporel de la dynamique de colonisation n'est pas aussi bien connu que dans le cas présent (par exemple lorsqu'il n'existe pas de données extérieures permettant de fournir un cadre temporel maximum), et / ou lorsque les patrons de migration sont plus équivoques, un cadre d'inférence par maximum de vraisemblance (Bahlo et Griffith 2000, Beerli et Felsenstein 1999) pourrait permettre d'estimer conjointement les paramètres démographiques des populations (par exemple $N\sigma^2$) et le temps depuis colonisation. L'application de ces méthodes d'analyse à des jeux de données comme ceux produits pour le chapitre 4 de cette thèse pourrait contribuer à en estimer la puissance et la pertinence.

À la dynamique temporelle des patrons d'organisation de la diversité s'ajoute une dimension de variation spatiale des paramètres démographiques. Par exemple, les bassins versants des rivières St-John et Penobscot du Maine (chapitre 2) se caractérisent par des effets contrastés de l'altitude et de la distance. De même, la connectivité des populations côtières du golfe du Maine, de la baie de Fundy et de Nouvelle-Écosse semble réduite par rapport aux populations plus nordique (qui se traduit par une fixation accrue et une désorganisation des patrons d'isolement par la distance, chapitre 3). Si la limite sud de la répartition de la forme anadrome était connue, aucun gradient évident n'avait été décrit chez l'omble de fontaine qui permettait de prédire cette diminution de la connectivité. Ce gradient se confondant avec le gradient d'age des populations (voir ci-dessous), on peut avancer l'idée que cette diminution de la connectivité résulte de l'évolution temporelle de la forme anadrome. Dans ce cas, nos résultats indiqueraient que l'évolution de l'anadromie chez l'omble de fontaine se produit à la

même échelle de temps que les perturbations glaciaires. Comme la mise en place du patron d'isolement par la distance peut également s'observer à cette échelle de temps, les résultats de cette thèse suggèrent que l'équilibre migration-dérive aboutissant à une stabilisation des patrons spatiaux de diversité génétique ne sera jamais atteint. D'une part parce que l'habitat est trop jeune pour qu'ils aient eu le temps de se stabiliser. D'autre part parce que la forme anadrome, responsable de la connectivité des populations, donc des taux de migrations entre rivières, a déjà eu le temps de diminuer en fréquence le long du gradient de colonisation à l'extrémité sud de l'aire de répartition.

Nous avons de plus mis en évidence que l'expression de l'anadromie était liée au niveau de consanguinité individuelle, au moins dans les populations les plus récentes. L'anadromie a, sauf exception (Kaitala 1990), été strictement considéré d'un point de vue écologique comme une forme de migration saisonnière. Suite aux résultats du chapitre 4, un système à seuil semble adapté à la description de l'évolution de la forme anadrome : l'anadromie s'exprime au-delà d'un certain seuil de consanguinité. L'explication la plus parcimonieuse semble être qu'il s'agit d'un effet indirect, la consanguinité modifiant la probabilité d'initier la migration anadrome à travers ses effets délétères sur la croissance, qui est liée à chez plusieurs salmonidés dont l'omble de fontaine (Thériault 2001). Le niveau de consanguinité ne serait alors considéré que comme une des composantes de la condition sur laquelle un individu base sa décision de migrer ou non, qui lui permet d'évaluer la fitness qu'il peut attendre s'il adopte l'une ou l'autre stratégie (au même titre que la taille ou la croissance juvénile, Thorpe et al. 1998). Selon cette explication, il ne serait pas nécessaire de faire appel aux modèles d'évolution de la dispersion, et il serait possible de ne considérer l'anadromie qu'à une échelle locale. Un modèle à seuil basé sur les niveaux de consanguinité fait cependant l'hypothèse implicite qu'il existe des effets délétères aux croisements consanguins. Or ces effets délétères ne peuvent être considérés indépendamment de la connectivité entre les populations, étant donné que l'intensité du fardeau de mutations délétères est modulée par l'intensité de la différenciation entre populations (Whitlock 2002). L'anadromie, par son impact direct sur la connectivité des populations (voir l'augmentation des niveaux de différenciation dans la partie sud de l'aire de répartition où l'anadromie n'est exprimée que de façon sporadique), peut donc moduler l'intensité de la dépression de consanguinité. Cette dépression de consanguinité étant à son tour impliquée dans l'expression de l'anadromie, il se crée une boucle de rétroaction

(Figure 6-8). L'anadromie doit donc être comprise comme une forme de dispersion de l'espèce, même si le mécanisme proximal qui détermine l'expression du phénotype anadrome n'est pas lié à la dispersion. En effet, si un poisson anadrome ne cherche pas nécessairement à disperser, il peut contribuer à amoindrir la structure génétique des populations, donc à augmenter l'intensité de la dépression de consanguinité. En augmentant l'intensité de la dépression de consanguinité, il favorise l'expression de plus nombreux phénotypes anadromes à la génération suivante. En d'autres termes, si la dispersion n'est pas la cause proximale de l'expression de l'anadromie, l'évolution de l'anadromie est influencée par son impact sur les possibilités de dispersion.

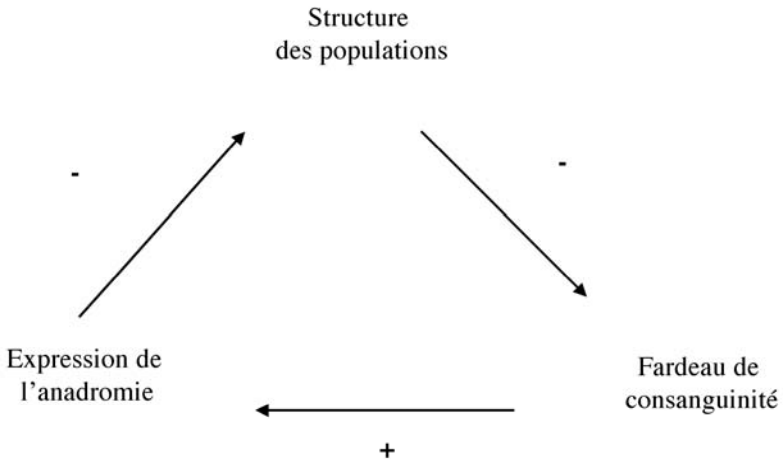

Figure 6-8 Représentation schématique de l'ensemble des interactions proposées impliquées dans la dynamique de l'anadromie chez l'omble de fontaine

Cet ensemble d'interactions peut être perturbé par plusieurs facteurs extérieurs. D'une part, la structure des populations est soumise à une dynamique historique, liée à celle de l'habitat. D'autre part, les coûts et bénéfices associés à l'expression de l'anadromie peuvent varier dans le temps et dans l'espace (McDowall 1997). Enfin, le fardeau de consanguinité dépend de paramètres historiques, démographiques (Whitlock 2002) et environnementaux (Keller et coll. 2002).

Plus généralement, le mécanisme proposé peut se replacer dans le cadre de l'évolution des aires de répartition (Brown et al. 1996, Kirkpatrick et Barton 1997) et de ses conséquences génétiques. On peut en effet s'interroger sur le lien entre la dynamique de la dépression de consanguinité et la répartition de la forme anadrome le long de l'aire de répartition. Chez la plusieurs salmonidés, la forme anadrome est restreinte à l'extrémité nordique de l'aire de répartition (McDowall 1987). Cette répartition est généralement expliquée par le plus fort différentiel de productivité entre eaux douces et eaux salées dans le nord que dans le sud, qui rend la migration marine plus payante dans le nord que dans le sud (Gross et al. 1987). Mais ce gradient se confond avec le gradient d'age des populations, l'ensemble de l'écosystème ayant été confronté à l'avancée des glaciers. Si le décalage de la distribution vers le nord suite au retrait du glacier a profondément perturbé l'organisation géographique de la diversité, il a également fait plus. En rendant disponibles de nouveaux habitats, il a également permis l'expansion de l'espèce par la forme de dispersion. Ce faisant, les nouveaux colonisateurs ont été confrontés à un habitat au sein duquel l'intensité de la compétition était réduite et l'efficacité de la sélection diminuée. Bien que sur un temps relativement court, les mutations délétère ont alors pu s'accumuler plus facilement que dans les populations plus anciennes, accentuant ainsi l'intensité de la dépression de consanguinité, donc l'expression de l'anadromie. Avec le temps, la purge du fardeau de mutations délétères progressant, les effets délétères des croisements consanguins ont pu s'estomper, un nombre croissant d'individus se développant au-dessus du seuil déterminant l'expression de l'anadromie (et demeurant donc résidents). Si le scénario qui précède -et qui, bien sûr, reste spéculatif- se révèlait exact, et si le lien entre l'expression de la migration anadrome et la dynamique de la dépression de consanguinité se confirmait chez d'autres espèces, il serait alors possible d'avancer l'idée que c'est la dynamique de la dépression de consanguinité qui détermine la répartition spatiale de la forme anadrome chez les salmonidés. L'importance de variations spatiales de la dépression de consanguinité commence à être prise en compte, tant par des études théoriques (Cheptou et Mathias 2001) qu'empiriques (Dole et Ritland 1993, Cheptou et al. 2000). Étayer cet argument encore spéculatif nécessitera la collecte de données sur l'intensité de la dépression dans les populations naturelles ainsi qu'un aperçu de sa variation géographique. Il manque également une formalisation analytique complète du résultat des interactions entre évolution de la dispersion, structure des populations et dépression de consanguinité (dont une ébauche est

proposée dans la figure 6-9). Les travaux de Gandon et Michalakis (2001) paraissent de ce point de vue un point de départ prometteur auquel il faudrait intégrer un modèle génétique de dépression de consanguinité. Comme la forme anadrome est responsable des bonnes capacités de colonisation de nouveaux habitats par les salmonidés, il est permis de penser que ce mécanisme serait également impliqué dans l'évolution de leurs aires de répartition. De ce point de vue, les descriptions existantes des caractéristiques écologiques et d'histoire de vie des formes anadromes et résidentes sont des données qui, bien que produites dans une perspective légèrement différentes, peuvent être très utiles à la compréhension de la dispersion chez les salmonidés côtiers. Les travaux en cours visant à déterminer l'héritabilité des phénotypes migratoires sauront à coup sûr apporter une grande partie de l'information manquante à ce chapitre.

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