

The Rise and Fall of Isolation by Distance in the Anadromous Brook Charr (*Salvelinus fontinalis* Mitchell)

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ABSTRACT

Geographic patterns of genetic diversity depend on a species' demographic properties in a given habitat, which may change over time. The rates at which patterns of diversity respond to changes in demographic properties and approach equilibrium are therefore pivotal in our understanding of spatial patterns of diversity. The brook charr *Salvelinus fontinalis* is a coastal fish exhibiting limited marine movements, such that a stable one-dimensional isolation-by-distance (IBD) pattern should be observed over the whole range. Its range, however, recently shifted northward such that northern populations may still be in the process of reaching equilibrium. We investigated variation in IBD patterns, genetic divergence, and allelic richness at six microsatellite markers in 2087 anadromous brook charr from 59 rivers along the most likely postglacial colonization route. We observed a decrease in allelic richness, together with an increase in differentiation and a decrease in IBD in the most recently colonized northern populations, as expected following recent colonization. Contrary to expectation, however, similar patterns were also observed at the southernmost part of the range, despite the fact that these populations are not considered to be newly colonized. We propose that the loss of dispersal capabilities associated with anadromy may have caused the southernmost populations to evolve relatively independently of one another. This study thus demonstrated that changes in a species' geographic range and dispersal capabilities may contribute to shaping geographic patterns of genetic diversity.

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 in which it reproduces. Theoretical results have been obtained for increasingly realistic models of populations, among which isolation-by-distance (IBD) models are widely used because they account for the common observation that dispersal capabilities of many species are limited in most habitats. Obviously, such models predict an 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). Equilibrium should be more 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 the fraction of

a population replaced by migrants each generation m (SLATKIN 1993). These methods are commonly used in the empirical literature of both plant and animal species (*e.g.*, NEIGEL 1997; BOHONAK 1999; POGSON *et al.* 2001 and references therein).

Such inferences, however, neglect to consider 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 quaternary period 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 limit, successively advancing and retreating, such that one may question the assumption that the timescale of these fluctuations was very large relative to the time required for equilibrium patterns to establish. Indeed, although that time 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

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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) showed theoretically that in a species expanding its range instantaneously to a new habitat, the correlation between genetic and geographic distances should 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 is evident should increase with the parameter $\sqrt{2 Nm\tau}$, 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) and 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; BERNATCHEZ and WILSON 1998; WILCOCK *et al.* 2001) or increased (BERLOCHER 1984; JOHNSON 1988; WHITLOCK 1992; McCAULEY *et al.* 1995; INGVARSSON and GILES 1999; COMPS *et al.* 2001), depending on the dynamic of colonization (SLATKIN 1977; IBRAHIM *et al.* 1996; AUSTERLITZ *et al.* 1997, 2000; LE CORRE and KREMER 1998). Empirical data on the evolution of IBD patterns during the early settlement of a species in a new habitat remain even scarcer (but see LEBLOIS *et al.* 2000; BARRAI *et al.* 2001; KINNISON *et al.* 2002). A first approach relies on demographic estimates and a colonization scenario showing that IBD should have been apparent if sufficient time had elapsed (*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 IBD 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 in North America, GREEN *et al.* 1996; United States *vs.* Europe, 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 of historical events and demography, and by uncertainties about the precise migration pattern of the species in a given habitat.

This study is based on a nearly exhaustive sampling of brook charr (*Salvelinus fontinalis* Mitchell) populations exhibiting anadromy (seasonal migrations between fresh- and saltwater used for reproduction and feeding, respectively) along a linear coast associated with a temporal gradient of colonization. This gradient allowed us to infer the temporal evolution of IBD patterns from their spatial variation along the linear coast. The brook charr is endemic to northeastern North America (POWER 1980), where the quaternary period resulted in a series of rapid northward and southward shifts of the whole biota (HOCUTT and WILEY 1986; PIELOU 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). Because the ice cap retreated from south to north, the brook charr 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 restricted to the coastal fringe, suggesting that colonists had to follow the coastline to colonize rivers they now inhabit. The Gulf of Maine was freed of ice 13,000 years ago (BORNS *et al.* 1985) and the lower north shore of the St. Lawrence River (Quebec, Canada) 10,000 years ago (DENTON and TERENCE 1980), so the minimum

time span between colonization of both areas was 3000 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 developed in western Labrador only ~3770 years ago (DE VERNAL and HILLAIRES-MARCEL 1987). The south-north gradient thus also corresponds to a time gradient, whereby northern charr populations, putatively younger, were founded at least 3000 years later than southern populations and possibly as much as 9230 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, distances covered over a season by brook charr in the coastal zone are typically short (WHITE 1942; J. VAN DE SANDE, A. CURRY and F. G. WHORISKEY, unpublished results). Because tolerable temperature and salinity conditions for brook charr are found only in the coastal fringe, distances swum in marine open waters are probably even more limited (WHITE 1942; BESNER and PELLETIER 1991).

Taken together, one can predict from the one-dimensional nature of coastal areas and the restricted movements of anadromous brook charr that IBD 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 and genetic distances. Second, if equilibrium was reached all along the 4992 km of coastline, 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 variation 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 differences in levels of genetic diversity and divergence relative to more southern populations. We thus also tested the null hypothesis of no spatial variation of intrapopulation genetic diversity and the extent of genetic divergence.

MATERIALS AND METHODS

Sampling design: A total of 2087 anadromous brook charr were collected from 52 rivers along the Canadian Atlantic coast and from 7 rivers from Anticosti Island, Quebec, Canada (mean $N = 35.4$, Table 1, Figure 1). This sampling covers nearly 75% of all important rivers inhabited by anadromous brook charr in the region. The brook charr occurs in coastal habitats as far south as North Carolina (McCRIMMON and

CAMPBELL 1969), but no anadromous movements are currently known to occur south of the Gulf of Maine (Figure 1; BIGELOW and SCHROEDER 1953). Therefore, samples were collected from one of the southernmost rivers where anadromous movements currently occur (Hunter's Brook in Acadia National Park, Maine, labeled km 0) and spanned northward over 4992 km of coastline to the lower north shore of the St. Lawrence River (Figure 1). All fish were collected either in river mouths or 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 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.

Microsatellite diversity within and among populations: Total DNA was isolated using a standard phenol-chloroform protocol (SAMBROOK *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 was standardized to the smallest sample size ($N = 13$, *i.e.*, 26 alleles sampled), using a rarefaction method that estimates the expected number of alleles in a sample of a given size (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 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 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 ($\alpha = 0.05$, $k = 59$; 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, p. 593).

Heterogeneity of allele frequencies among samples was tested with Genetix's permutation procedure using 2000 permutations in the global test and 30,000 permutations in the pairwise test to maintain the tablewide significance level at $\alpha = 0.05$ after sequential Bonferroni correction ($k = 1711$ pairwise comparisons). Global population differentiation was estimated in Genetix by WEIR and COCKERHAM's (1984) F_{ST} estimator θ . A neighbor-joining phenogram based on CAVALLI-SFORZA and EDWARDS's (1967) chord distance was constructed using Phylip 3.57c (FELSENSTEIN 1993) to depict the pattern of genetic relationships among populations. Support for the topology was estimated using 1000 bootstrap replicates.

Isolation by distance: Patterns of IBD were analyzed using 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: $F_{ST}/(1 - F_{ST}) \approx A_1/(4N\sigma) + j/(4N\sigma^2\epsilon)$, where

TABLE 1
Anadromous brook charr samples collected

Label	Sample location	Geographic region	Coastal distance from km 0	Latitude N	Longitude W	<i>N</i>
1	Hunter's brook (Acadia National Park)	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, Nova Scotia	Bay of Fundy	1086	43° 46' 00"	65° 14' 00"	29
7	Petite Rivière	Atlantic Coast, Nova Scotia	1166	44° 14' 00"	64° 26' 00"	29
8	West River, St. Mary	Atlantic Coast, Nova Scotia	1406	45° 15' 00"	62° 04' 00"	24
9	Baddeck River	Atlantic Coast, Nova Scotia	1806	46° 05' 00"	60° 52' 00"	39
10	Clyburn Brook	Atlantic Coast, Nova Scotia	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'Anse à Beaufile	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'Anse à Valteau	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 (Saguenay)	North shore St. Lawrence	3958	48° 15' 49"	69° 56' 47"	50
39	Rivière des Escoumins	North shore St. Lawrence	3990	48° 20' 50"	69° 27' 00"	50
40	Rivière Laval	North shore St. Lawrence	4030	48° 46' 00"	69° 03' 00"	68
41	Rivière Godbout	North shore St. Lawrence	4158	49° 19' 00"	67° 35' 00"	22
42	Rivière Trinité	North shore St. Lawrence	4188	49° 25' 05"	67° 18' 16"	50
43	Rivière du Calumet	North shore St. Lawrence	4214	49° 37' 00"	67° 13' 00"	48
44	Rivière Ile de Mai	North shore St. Lawrence	4264	49° 55' 38"	66° 57' 50"	50
45	Rivière Moisie	North shore St. Lawrence	4344	50° 16' 00"	65° 56' 00"	49
46	Rivière St. Jean	North shore St. Lawrence	4472	50° 17' 00"	64° 20' 00"	50

(continued)

N is the 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 method 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

IBD 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. For example, the slope at 100 km was obtained by including pairs of populations separated by 100 km or less, whereas all pairs at 200 km or less were included for the 200-km slope.

TABLE 1
(Continued)

Label	Sample location	Geographic region	Coastal distance from km 0	Latitude N	Longitude W	N
47	Baie-Johann-Beetz	Lower north shore St. Lawrence	4592	50° 17' 00"	62° 48' 00"	13
48	Rivière Washicoutai	Lower north shore St. Lawrence	4736	50° 13' 00"	60° 52' 00"	48
49	Rivière Watasheistic	Lower north shore St. Lawrence	4846	50° 24' 00"	59° 50' 00"	31
50	La Tabatière	Lower north shore St. Lawrence	4896	50° 50' 00"	58° 59' 00"	48
51	Rivière St. Augustin	Lower north shore St. Lawrence	4944	51° 12' 00"	58° 35' 00"	46
52	Rivière St. Paul	Lower north shore St. Lawrence	4992	51° 27' 00"	57° 42' 00"	41
A1	Rivière 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

Geographic regions based on coastal morphology.

Isolation by distance on the way toward equilibrium: The evolution of IBD patterns along the colonization gradient was further investigated using a sliding-window analysis based on ROUSSET's (1997) inference framework described above and programmed in the mathematics computer language Maple 6 (WATERLOO 1999). Because northward colonization most likely followed the coastline, coastal distance from the southernmost population 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 kilometer 4992). Since they are geographically isolated from all others by marine open waters, 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. 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-squares regression line of all possible four-population subsamples were computed within each 600-km window, and their mean over all possible combinations was plotted against the location of the southern end of the window (in kilometers). The window was then shifted by a 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 toward 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 variation in the intercept can reveal variations in σ or variations in the shape of dispersal distances. The variation pattern of the slope and intercept along the coast was investigated using a cubic spline analysis in GLMS 4.0 (SCHLUTER 1988), thus making no prior

assumption about the form of the relationship. Values for parameter λ were chosen to provide smooth curves ($\lambda = 10$), and 10,000 bootstrap replicates were used to depict the sampling variability of the fitted function. As the geographic variation in slope and intercept depicted by the cubic spline analysis closely matched a quadratic model (see RESULTS), the significance of this model was further tested using a permutation method that took into account the nonindependence of data points generated by the sliding-window analysis due to the inclusion of some of the same populations within successive windows. To that end, population locations along the coastline were randomly shuffled 1000 times in a manner that preserved the spatial structure of the sampling design. As above, the variation of IBD slope and intercept for each of these random configurations was described using the sliding-window analysis, except that all populations were considered within each window, such that the variation pattern in random replicates had the same dependence structure as the original pattern. A best-fit second-order regression line was fitted on each replicate, and the quadratic term compared to the observed one to generate the probability that the observed pattern of quadratic variation in either slope or intercept of the IBD relationship did not differ from random expectation.

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 IBD patterns, they may also have left their footprint on allelic richness and on the extent of genetic divergence (F_{ST}). A cubic spline analysis was first used to investigate the variation pattern of the number of alleles and F_{ST} along the coast ($\lambda = 12$ and $\lambda = 10$, respectively), and the significance of the quadratic term was tested for F_{ST} by permuting populations along the coast, as described above. Allelic richness is computed for each population independently, such that successive data points are statistically independent from each other (in contrast with data from the sliding-window analysis). Consequently, the significance of the quadratic term of the best-fit second-order regression line for allelic richness was tested using a backward stepwise model simplification procedure (in Statview) to determine whether a quadratic correlation explained significantly more variance than a linear correlation. Because geographic variations in genetic diversity may compromise the use of the fixation index F_{ST} as an indica-

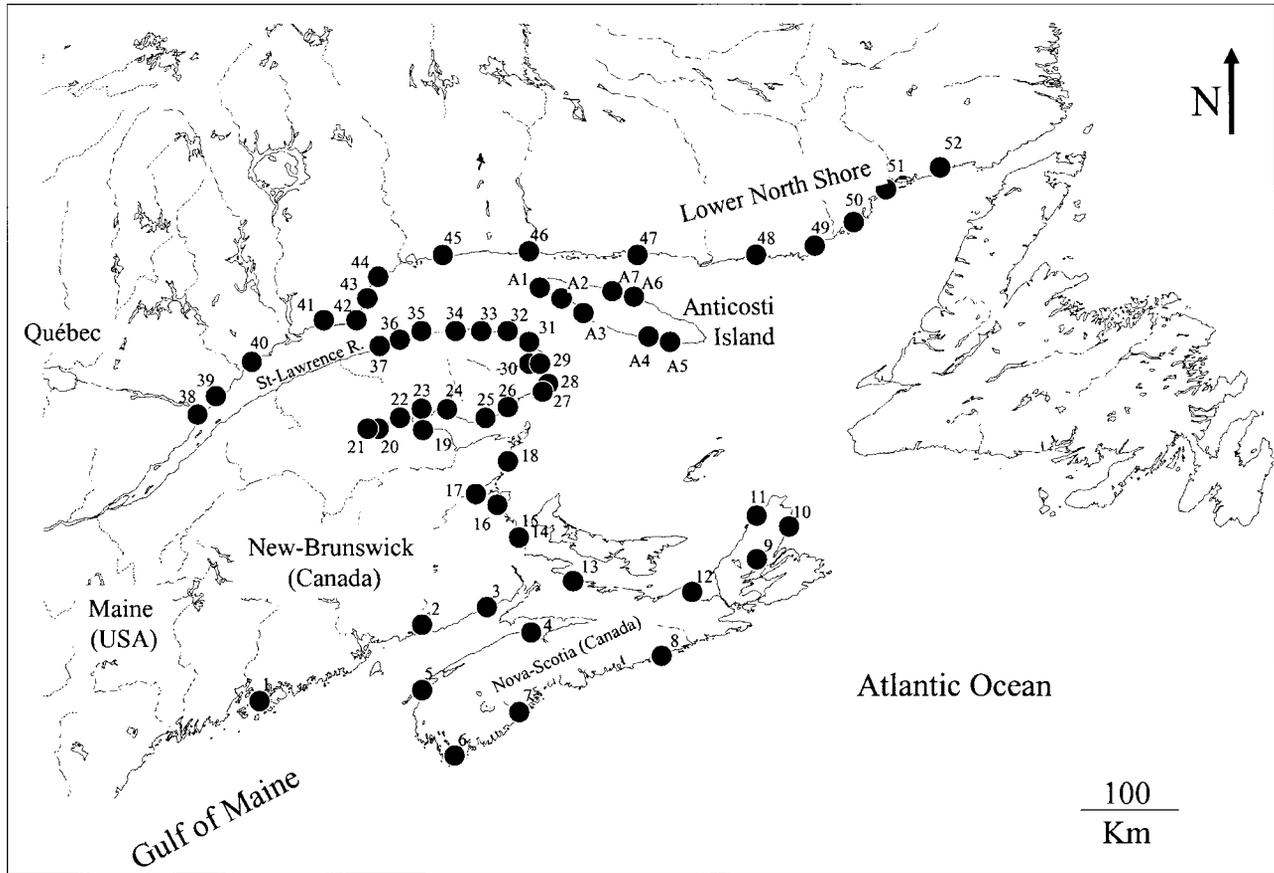


FIGURE 1.—Location of brook charr samples. Numbers refer to locations in Table 1. The southernmost population is labeled kilometer 0 and is close to the southern limit of the anadromous brook charr distribution. Distances were linearly measured along the coast in a northward direction to kilometer 4992.

tor of population differentiation (PETIT *et al.* 1995; HEDRICK 1999; WHITLOCK and MCCAULEY 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: $1 - H_E$.

RESULTS

Microsatellite diversity within and among populations: High levels of allelic richness and genetic diversity were found at all loci (see supplemental appendix at <http://www.genetics.org/supplemental/>; Figure 2A). 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 revealed that several loci were consistently more affected than others ($P = 0.0057$), thus suggesting that technical artifacts such as nonamplifying 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, supplemental appendix at <http://www.genetics.org/supplemental/>), suggesting that nonartifactual explanations also have to be taken into account (CASTRIC *et al.* 2002). Namely, heterozygote deficits could partly result from a Wahlund 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 (Figure 2B). Significant differences in allele frequencies were observed in 1695/1711 pairwise comparisons (99.1%) after sequential Bonferroni correction (final $\alpha = 0.00323$). As indicated by the neighbor-joining phenogram (Figure 3), geographically proximate populations generally 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

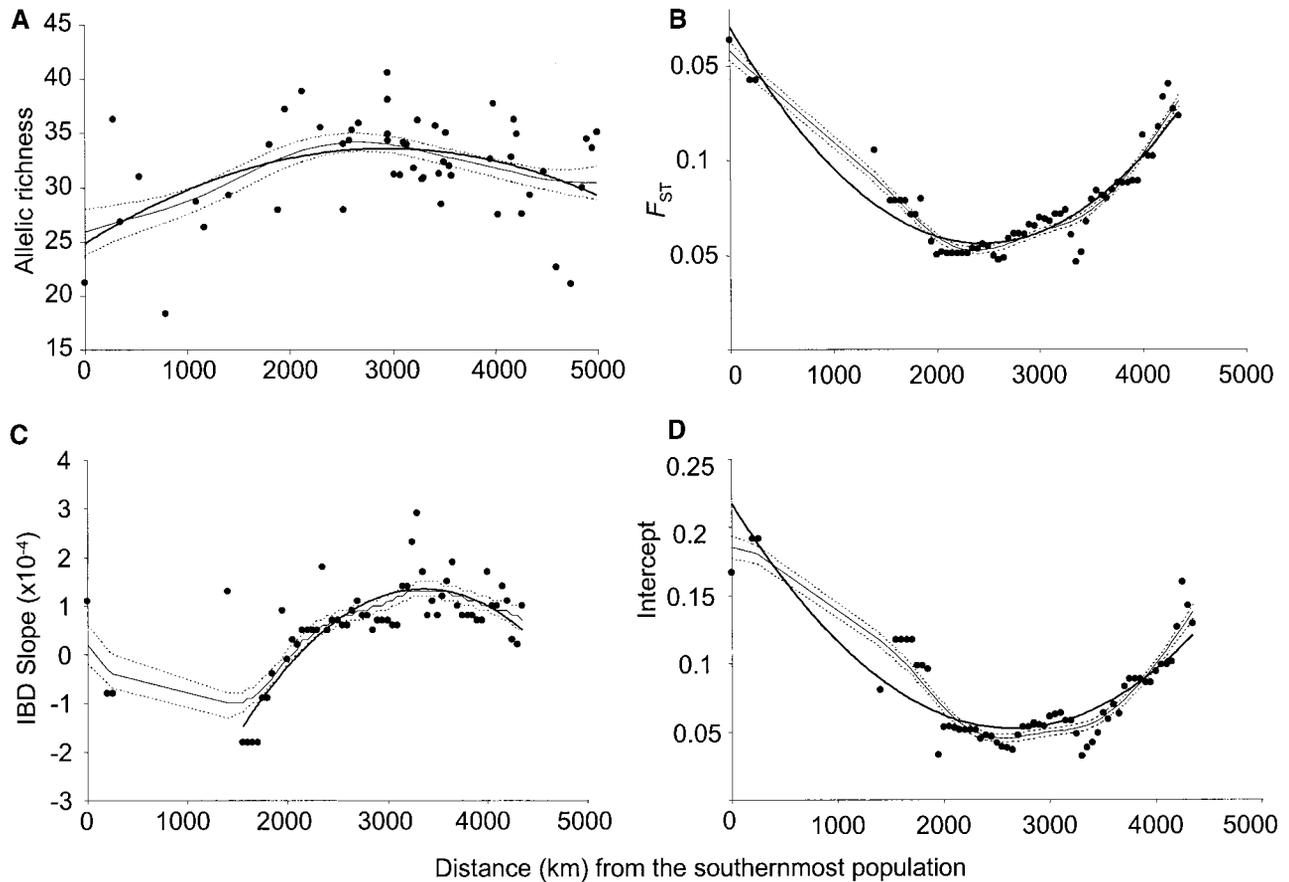


FIGURE 2.—Variation in geographic patterns of genetic diversity along the south-north colonization gradient following the coastline. (A) Number of alleles over the six microsatellite loci. The number of alleles was standardized to a constant sample size ($N = 26$ alleles) using a rarefaction method (PETIT *et al.* 1998). (B) Geographic variation in F_{ST} , depicted using a sliding-window analysis. A 600-km-wide window was shifted along the coast in 10-km increments. Each data point refers to the mean F_{ST} over all possible combinations of four populations within each window. Windows including fewer than four populations were discarded. (C) Geographic variation in the slope of the isolation-by-distance relationship revealed by the sliding-window analysis. (D) Geographic variation in the intercept of the isolation-by-distance relationship revealed by the sliding-window analysis. Thin solid lines are the estimated regression functions from a cubic spline analysis with 1 standard deviation above and 1 standard deviation below represented as dotted lines. Thick solid lines are the best-fit quadratic relationships against which variation patterns were tested.

clustered together with strong statistical support (bootstrap = 86%), thus providing direct support for the hypothesis that open marine 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 (*i.e.*, excluding Anticosti).

Analysis of isolation by distance patterns: The genetic similarity of geographically proximate populations was further confirmed by the strong and highly significant correlation observed over the whole data set between distance and genetic divergence (Figure 4, Mantel's test, $P < 0.0005$). The best-fit regression model had a slope of $3.37 \times 10^{-5} \text{ km}^{-1}$ and an intercept of 0.07743. The slope, however, varied as a function of the spatial scale at which the relationship was examined (Figure 5). When considering only pairs of populations separated by < 50 km, considerable variation in the value of the slope was found (range = -0.00111 – 0.00247). This was followed

by a log-linear decrease of the slope with increasing spatial scale (Figure 5).

Isolation by distance evolving toward equilibrium:

There was considerable geographic variation in the regression slope of the IBD pattern, especially at distances < 1500 km from the southernmost sample, where negative as well as positive values were observed (Figure 2C). However, the median value of slopes was near zero, suggesting the absence of any significant trend in IBD pattern at distances < 1500 km. When excluding southern populations < 1500 km from the analysis, the cubic spline analysis revealed a maximum value of the slope near population 30 at kilometer 3366 with a decline both in more northern and in more southern regions. The permutation test provided further indication that geographic variation in the IBD slope was quadratic. Thus, the probability that the quadratic term of the second-order regression was similar to random expecta-

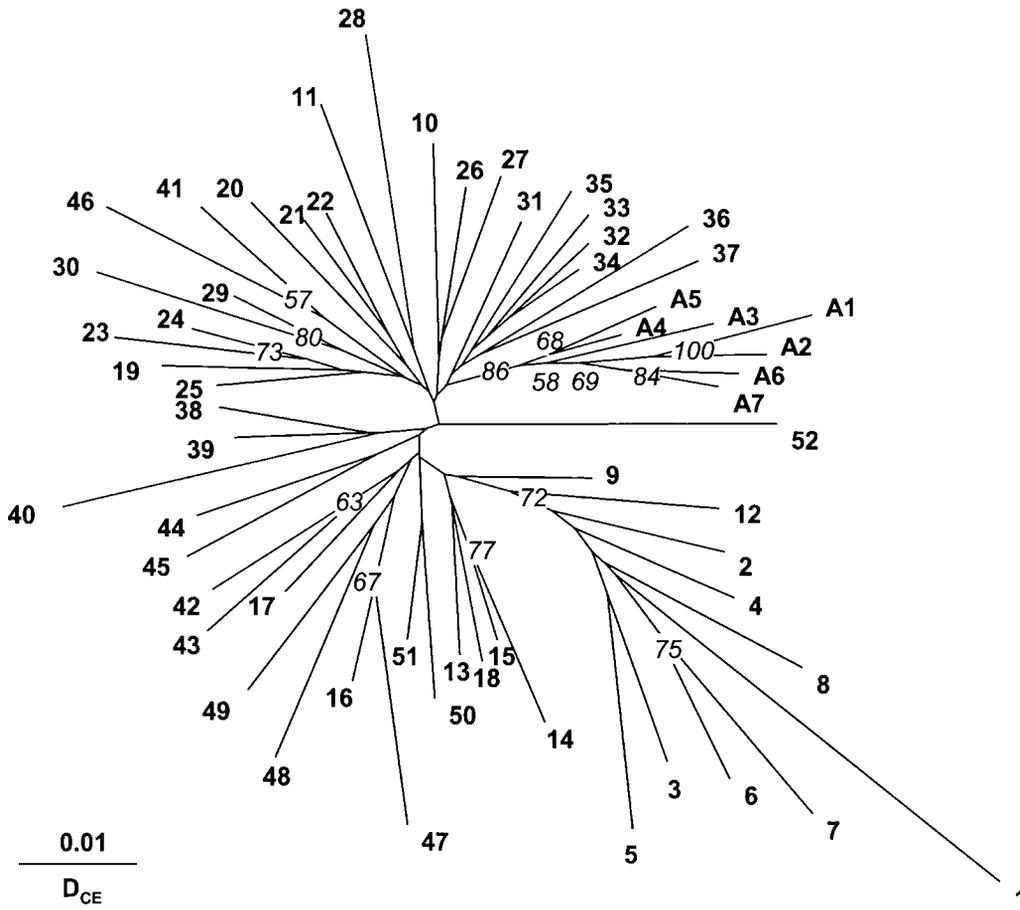


FIGURE 3.—Neighbor-joining phenogram based on D_{CE} distances depicting genetic similarities among populations. Population numbers refer to Table 1. Confidence values for nodes are percentages over 1000 bootstrap replicates. Note the tight clustering with a high bootstrap value of 86% for the Anticosti Island populations. Only bootstrap values $>50\%$ are shown.

tion was only $P = 0.0606$. Similarly, geographic variation in the IBD intercept was more likely to fit a quadratic than a linear model ($P = 0.0196$). Thus, the lowest value for parameter $A_1/(N\sigma)$ was observed at kilometer 2646

between populations 17 and 18 (Figure 2D). Statistics of commercial landings for the species do not indicate any trend of reduction in population size N toward the north (MALOUIN 1996). Consequently, according to

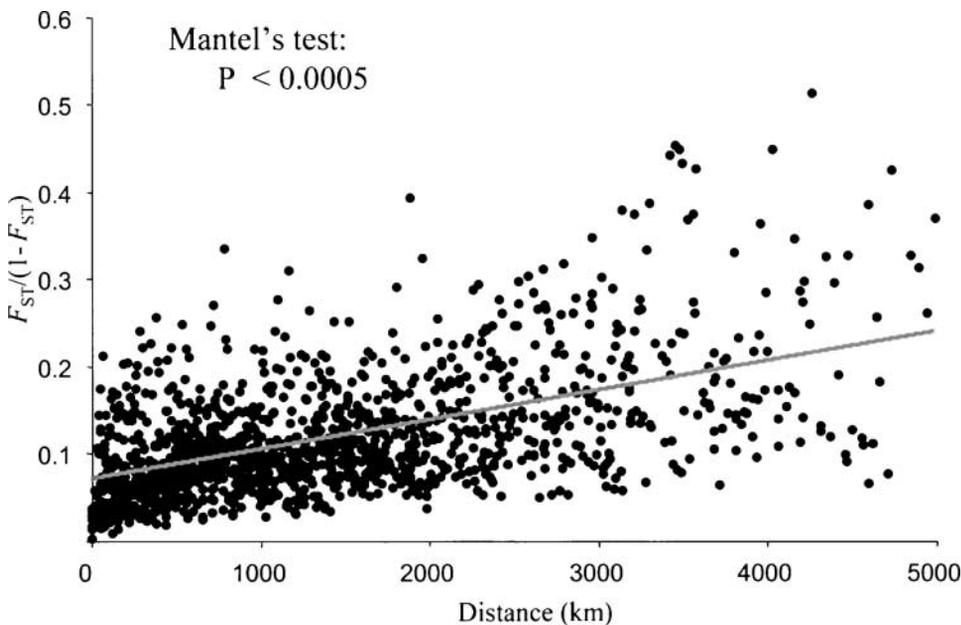


FIGURE 4.—Isolation-by-distance relationship between all population pairs, where $F_{ST}/(1 - F_{ST})$ was regressed over coastal distances.

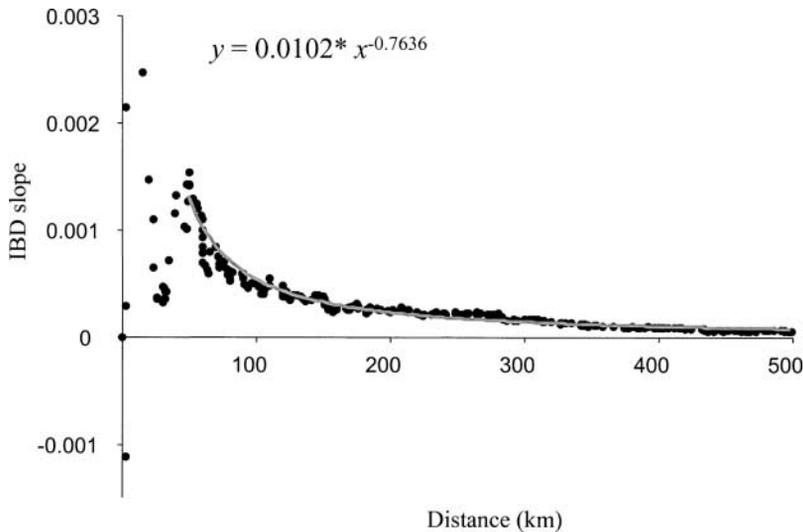


FIGURE 5.—Variation of the slope of the isolation-by-distance regression as a function of the spatial scale of observation. Slopes were computed by progressively including population pairs at increasing geographic distances. To better show initial fluctuations, only the first 500 km are shown.

ROUSSET (1997), the northward increase in intercept values suggests either higher A_1 (e.g., due to a more leptokurtic dispersal pattern) or lower σ (e.g., due to reduced migration rate).

Joint evolution of IBD, F_{ST} , and allelic richness: As observed for IBD slope and intercept, allelic richness varied geographically, with a quadratic model capturing significantly more variance than a linear model (Figure 2A, $P = 0.002$). The highest number of alleles was found at intermediate distance (kilometer 2945 in Chaleur's Bay near population 19; Figures 1 and 2A) with a lower allelic richness observed either northward or southward. The sliding-window analysis revealed that F_{ST} reached a minimum value at intermediate distances (kilometer 2444 between populations 13 and 14) compared to either farther north or farther south, with a significant pattern of quadratic variation (Figure 2B, $P < 0.001$). Correcting for variation in intrapopulation diversity also provided a significant quadratic pattern of latitudinal variation ($P < 0.001$, 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.

DISCUSSION

This study provided evidence for important variation in geographic patterns of genetic diversity and structuring among anadromous brook charr populations. As predicted from its life history, IBD 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 varied with the putative time since population founding. This suggests that the timescale 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. However, contrary to the expected variation if the system had been progressively approaching a single equilibrium state, spatial patterns did not remain constant at the southern end of the range, where populations have most likely 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 the interaction between 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.

Biology of seawater migrations: This study also provided insights into the patterns of coastal movement in the brook charr. Higher levels of intrapopulation genetic diversity were found compared to landlocked populations from Maine (CASTRIC *et al.* 2001), indicating that the higher opportunities for migration provided by the coastal habitat translate into a more even distribution of genetic diversity among populations. 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 behavior is precise. This was most obvious among southern populations, where the regression model predicted 24.8 alleles over the six microsatellite loci for the southernmost population (kilometer 0). This value was similar to levels found in lacustrine populations from Maine (CASTRIC *et al.* 2001), suggesting that reduction in expression and, perhaps, loss of anadromy toward the south 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 move-

ments of brook charr in high-salinity waters (WHITE 1942) and precluded the possibility of cross-inlet migration, thus providing additional support for the one-dimensional migration model. Such limited movements may be due to the species' limited tolerance for high salinity water, although other mechanisms may also be involved. The observation of repeated incursions of fish into nonnatal rivers before entering their "home" river (SMITH and SAUNDERS 1958) suggests that the potential for straying is higher than the actual level of genetic exchanges among rivers and consequently that the homing behavior is active and strong in brook charr. Direct observations and experimental data, however, remain elusive (but see KEEFE and WINN 1991). Field observations of fish repeatedly returning to spawn on the same spawning grounds within a river (S. LENORMAND and J. J. DODSON, unpublished data) and evidence for genetic distinctiveness of fish spawning on different spawning grounds within the same river system (BOULA *et al.* 2002) provide further support for the hypothesis that homing can be very precise.

Initial formation of spatial patterns: "The rise . . .": Given the current knowledge on the species' biology and assuming equilibrium conditions, no pronounced variation in the spatial patterns of allelic richness, population divergence, or IBD would be expected. Yet, each of these patterns decreased with increased distance northward. Because northern latitudes are also the most recently colonized regions along the temporal gradient, our data support the hypothesis that colonization processes are still prevailing in shaping spatial patterns of genetic diversity among northern charr populations. Such a gradient of genetic diversity has also been reported in phylogeographic studies and has been interpreted as the result of sampling processes during colonization from southern glacial refugia (HEWITT 1996; AVISE 2000). These studies also suggested that mutation rate 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 (SLATKIN 1993; BERNATCHEZ and WILSON 1998). In contrast, with a 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 suggest 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 dynamic of migration of new areas would differ from that observed among populations that were established earlier in time. Contrasts between early colonization and subsequent migration dynamics have been proposed in other studies, especially for plants where colonization occurs through seeds while subsequent gene flow primarily occurs through pollen (COMPS *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.* 2001). Competition may thus quickly intensify following population founding, resulting in reduction of fitness of subsequent migrants compared to colonists (NICHOLS and HEWITT 1994; DAVIS and SHAW 2001).

" . . . and fall": disruption of spatial patterns and the evolution of dispersal: Assuming that nonequilibrium 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 observed patterns were more likely to be quadratic than linear. Thus, allelic richness and IBD slope decreased, while the extent of population differentiation F_{ST} increased among southern populations compared to those at intermediate distances from the south. That is, a trend toward increased fixation and spatial patterns of population structuring that varied randomly was evidenced among the most southern populations. Similar trends of increased population fixation 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 *et al.* 1999), and have been interpreted as reflecting a lack of adaptation of the species to the marginal habitat. Why then have southern populations of anadromous brook charr evolved toward increased fragmentation? Increased population fixation could be due to a decrease in either population size or the species' dispersal capability. Although no anadromous individuals occur farther south than the Gulf of Maine, coastal populations of freshwater resident brook charr still exist and show no dramatic decline in census size. For example, CURRY *et al.* (2002) counted >1500 adult fish in the Kennebecasis river (sample 2) in a single season. Thus, lower population size seems unlikely to explain the changes observed in spatial patterns of genetic diversity among the most southern populations. In contrast, CURRY *et al.* (2002) reported that fish from the Kennebecasis river remained in salinity <5‰ (compared to 35‰ for typical seawater), thus precluding any possibil-

ity for movement among rivers. We therefore propose two nonexclusive hypotheses for reduction of anadromy and increased fragmentation among southern brook charr populations. Because body growth is enhanced in the marine environment due to higher food availability, the benefits for switching between habitats may outweigh the costs of physiological acclimations to a hyper- and a hypoosmotic environment (BOULA *et al.* 2002). As such, anadromy may be viewed as a form of seasonal migration driven by the productivity gradient between fresh- and saltwater. Because this gradient declines in intensity from north to south, selective pressures for anadromous behavior are predicted to become weaker and eventually disappear (GROSS *et al.* 1988). On the other hand, since 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). Habitat instability ranks among the most powerful forces selecting for dispersal (GANDON and MICHALAKIS 2001), while a costly dispersal form should decline in frequency in a stable environment (VAN VALEN 1971; OLIVIERI *et al.* 1995, Figure 3; CODY and OVERTON 1996). Assuming that the habitat occupied by the brook charr in postglacial times can be considered as stable, theory therefore predicts that anadromy should have decreased more among southern 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 explanations for the loss of anadromy our results clearly indicate that southern brook charr populations are highly fragmented relative to more northern ones. As genetic exchanges decrease between them, populations drift independently from each other, thus disrupting the pattern of IBD observed among more northern populations.

Scale dependence of IBD patterns: As pointed out by ROUSSET (1997, 2001) but rarely considered in empirical studies (but see HELLBERG 1995; RUCKELSHAUS 1998; EHRLICH and STENSETH 2001), the estimation of demographic parameters from the slope of the IBD relationship is strongly affected by the spatial scale of observation. Our results showed that the IBD slope varied greatly until scales of 50 km were considered and then decreased with increasing geographic scale. Similar fading of IBD at larger geographic scales has been observed in several species (HELLBERG 1995; JOHNSON and BLACK 1998; EHRLICH and STENSETH 2001) and has received various explanations. First, as genetic differences increased with geographic distances, F_{ST} may plateau if it reaches its upper bound at large geographic distances. The mean expected heterozygosity was 0.72, such that the maximum theoretical F_{ST} value should be ~ 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 of IBD could reflect a nonequilibrium situation. The spatial scale over which an IBD signal should be apparent during the transitory period toward equilibrium in a one-dimensional array of populations depends upon the parameter $\sqrt{2 Nm\tau}$ (SLATKIN 1993). Thus, for recent systems (small τ values), IBD may be weak over large geographic scales and may consequently remain undetected. Third, and nonexclusively, mutation may not remain negligible relative to migration over large geographic scales. Because mutations arise randomly in space, theory predicts that their effect should be similar to island migration (CROW and KIMURA 1970), therefore weakening the relationship between genetic and geographic distances. Regardless of the exact explanation for this scale dependence, it is problematic since the slope of IBD is commonly 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 addition to scale dependence, important latitudinal variation in IBD slope was observed even when controlling for the scale of analysis and sampling density. As detailed above, those variations probably arise from the spatio-temporal variation in migration rate and patterns of dispersal, which compromises the use of inference methods assuming spatial homogeneity and temporal stability. New analytical methods, such as maximum-likelihood frameworks (BEERLI and FELSENSTEIN 1999; BAHLO and GRIFFITH 2000), represent promising avenues that may allow inclusion of parameters for an explicit colonization scenario and the rate of decrease of the migrating phenotype. The joint estimation of migration rates, rate of colonization, and cost of dispersal that would maximize the likelihood of observing the data may thus become possible in the near future.

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 consideration for their evolution through time. The assumption of temporal stability may prove especially unlikely in evolutionarily young systems, because it may fail to capture the dynamic essence of spatial patterns of genetic diversity, as was exemplified in this study. Furthermore, because a species' form of dispersal can evolve, the assumption of spatial homogeneity and temporal stability of demographic parameters may also be questioned. Most attempts to characterize the genetic impacts of

habitat fluctuations have been focused on relatively small geographic scales in the framework of an extinction-recolonization dynamic of 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 the cycling nature of climatic changes (PIELOU 1991). This study thus reinforces the view that a biogeographic perspective is essential to fully understand the evolution of geographic patterns of genetic variation.

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