Consequences of unequal population size, asymmetric gene flow and sex-biased dispersal on population structure in brook charr (*Salvelinus fontinalis*)

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Abstract

Unravelling relationships between dispersal and population structure requires considering the impacts of assumption violations of indirect gene flow models in a given system. We combined temporal, individual and coalescent-based analyses of microsatellite DNA variation to explore the general hypothesis that unequal effective population size (N_e), asymmetric gene flow (m) and nonrandom (sex-biased) individual dispersal had an important effect on spatiotemporal population structuring in lake-dwelling brook charr (*Salvelinus fontinalis*). This integrative examination shed light on the dichotomous structuring observed between an outlet and three tributary-spawning populations and their potential for adaptive divergence. It revealed further that finer tributary population structuring incongruent with drainage structure has been shaped by asymmetric m from one population with a large N_e towards two populations of smaller N_e. Gene flow among the tributaries was also mediated mainly by male-biased dispersal. However, longer distance dispersal from tributaries to the outflow was female-biased. Spatially dependent sex-biased dispersal may have contributed therefore to gene flow at different levels of population structuring. Our results demonstrate how dispersal and population structure may interrelate to produce spatial variation in intraspecific diversity, and are therefore relevant for conservation programmes seeking to define conservation units or predict recolonization rates of extirpated populations.

Keywords: assignment test, dispersal, local adaptation, metapopulation, philopatry, recolonization, social behaviour

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Introduction

Population geneticists and ecologists are often interested in understanding how dispersal and population structure interrelate. Dispersal may affect genetic variation within and among populations through gene flow (Wright 1931; Slatkin 1985), thereby influencing population persistence and spatial organization at both local population and metapopulation levels (Hanski & Gilpin 1997). In addition, dispersal and population structure are often linked with social behaviour (Ross & Keller 1995; Sugg *et al*. 1996). Further resolution of these relationships is in turn critical for conservation strategies aiming to protect evolutionarily

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distinct populations (Fraser & Bernatchez 2001) or rehabilitate extirpated populations (Blundell *et al*. 2002).

It is recognized increasingly that commonly used indirect estimators of gene flow for inferring dispersal, such as $N_e m = (1/F_{ST} - 1)/4$ (Wright 1931), are overly simplified in assuming uniform effective population sizes (N_e), symmetric effective migration rates (m) between populations and random individual dispersal (e.g. between sexes) (Bohonak 1999; Whitlock & McCauley 1999). Overcoming such limitations requires testing the very assumptions of these estimators to consider what impacts their rejection (e.g. unequal N_e and m) will have on how dispersal and population structure interrelate in a given system. For instance, because N_e is often a function of the census population size N (Frankham 1995), population differences in N_e may reflect the use of habitats of varying quality which in

turn can affect animal movements (e.g. McCauley 1991). Asymmetric *m* may shape population structure and connectivity because *m* illuminates the potential for gene flow to influence adaptive divergence among populations (e.g. Hendry *et al.* 2001). Non-random individual dispersal, such as sex-biased dispersal, can also impinge on gene flow patterns among populations by affecting rates of dispersal from source populations (Aars & Ims 2000; Blundell *et al.* 2002).

A useful species for addressing these issues is the brook charr (*Salvelinus fontinalis*), an endemic salmonid fish of eastern North America. Like many salmonids, brook charr demonstrate a natal philopatry life history (O'Connor & Power 1973) that, combined with their use of discrete spawning and rearing habitats within rivers (Boula *et al.* 2002), limits dispersal between genetically distinct populations (Castric & Bernatchez 2003). Populations of this species also show high variability in *N* (Power 1980), and the periodic dispersing of individuals ('strays') as observed in similar species may have an important effect on population connectivity and the colonization of new habitats (Quinn 1984; Rieman & Dunham 2000; Hendry *et al.* 2004). Furthermore, brook charr have a polygynous breeding system where male fitness is limited by female availability (Blanchfield & Ridgway 1997) and female fitness is limited predominantly by the number of eggs they produce (Hutchings & Gerber 2002). These characteristics could lead to nonrandom dispersal of males from increased breeding competition (Dobson 1982), given that male-biased dispersal is common and predicted theoretically in such mating systems (Greenwood 1980; Perrin & Mazalov 2000; Hutchings & Gerber 2000).

In large postglacial lakes, brook charr often exhibit a freshwater migratory life history whereby foraging migrations of maturing adults link the tributary river juvenile-rearing and spawning stages of the life cycle. Globally, such systems offer distinct advantages over other environments for pulling apart dispersal dynamics and population structure in philopatric animals, because they are essentially closed and made up of small numbers of populations. Literature on the population structure of brook charr and other salmonids is pervasive (e.g. Angers & Bernatchez 1998; Danzmann *et al.* 1998; Altukhov *et al.* 2000; Castric & Bernatchez 2003). However, studies on these systems (see also Taylor *et al.* 1997; Tessier *et al.* 1997) may reveal further insight into the evolutionary ecology of these animals, and are timely given conservation concerns in some systems (e.g. Newman *et al.* 2003).

This study employs temporal, individual and coalescent-based analyses of microsatellite DNA variation to characterize the relationships between dispersal and genetic population structure in brook charr inhabiting Mistassini Lake, a large (2150 km²) postglacial lake in central Québec, Canada (Fig. 1). We consider dispersal (straying) as 'the interpopulation movement between the natal area and the area where breeding first takes place' (modified from
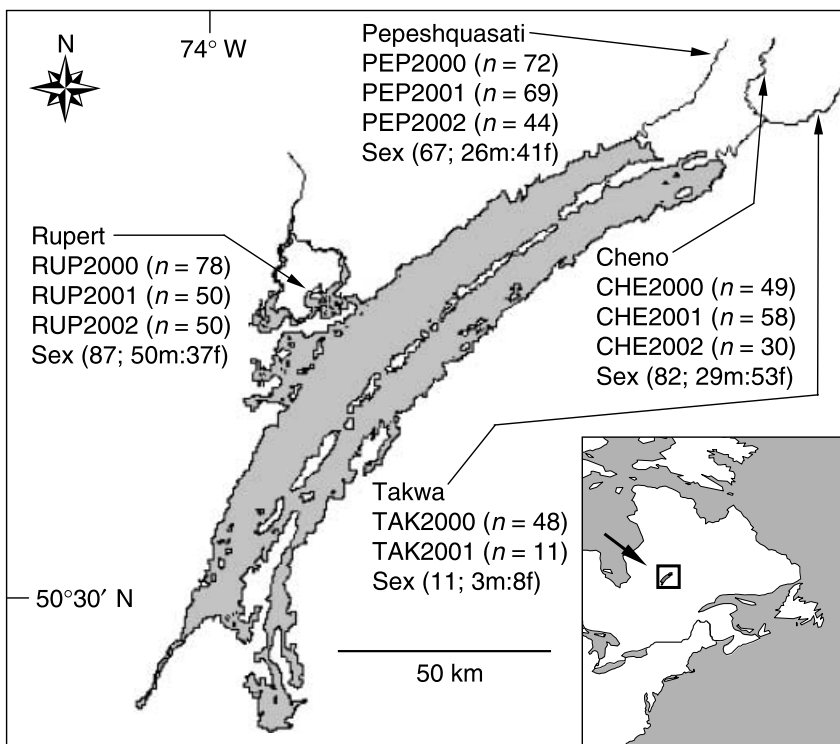

Fig. 1 Map showing sampling localities for brook charr in Mistassini Lake, Québec, as well as sample sizes for each sampling year and numbers of individuals sexed for sex bias dispersal tests (m = male, f = female).

Clobert *et al.* 2001), and gene flow as 'the outcome of successful reproduction after dispersal', because these terms are often used interchangeably but are not necessarily synonymous (see Verhulst & van Eck 1996). We first quantify the genetic population structure of charr spawning in the outflow and three tributary rivers to (i) test the hypothesis that each river forms a genetically distinct and temporally stable population and to (ii) evaluate the potential role of habitat divergence in maintaining population differentiation since postglacial dispersal (Mistassini: 8000 years ago; Bouchard 1980). We then explore the general hypothesis that unequal N_e, asymmetric m and sex-biased dispersal (or a combination thereof) have an important bearing on the interplay between dispersal and population structure in the system, and predict a male bias in dispersal given the preponderance for polygynous mating.

Materials and methods

Sampling design

Mistassini Lake's outflow, the Rupert (RUP), and its three northeast tributaries, the Cheno (CHE), Pepeshquasati (PEP) and Takwa (TAK), are known historically by Cree First Nation peoples as spawning grounds for adult brook charr and as nurseries for juveniles (Fig. 1). Juveniles remain in rivers for 1–2 years before migrating to foraging grounds in the lake and return to rivers in the fall as spawning adults 1–4 years later (D. Fraser, unpubl. data). There has never been any stocking of the species in the lake. A total of 559 prespawning adult brook charr were sampled by angling on spawning grounds in the four rivers over three autumns (three replicates for each river except two for TAK) and subsequently released. Adipose fin tissue was collected from each individual and stored in 95% ethanol until DNA was extracted following Olsen *et al.* (1996). The sex, total length (mm) and age of a subset of individuals from each river was determined for sex-biased dispersal tests and N_e estimation. Dimorphic secondary morphological characters were used to distinguish males and females. Age was assessed from standard scale analysis and defined as the number of completed winter seasons, e.g. 2 +, 3 +, 4 +. Average age of spawning adults (generation time, g) in each river was also used for estimating N_e (see below).

Microsatellite DNA analyses

Microsatellite polymorphism was analysed at 10 loci using fluorescently labelled primers (*SfoB52*, *SfoC86*, *SfoC129*, *SfoD75*, *SfoD91*, *SfoD100*, T. L. King, US Geological Survey, unpublished; *Sfo12*, *Sfo18*, *Sfo23*, Angers *et al.* 1995; *Mst85*, Presa & Guyomard 1996). Two polymerase chain reaction (PCR) profiles carried out on a Perkin-Elmer 9600 thermo-

cycler (version 2.01) were used: (1) two duplexes [*SfoB52*, *SfoC86* (A); *SfoD75*, *SfoC129* (B)], and *SfoD91* and *SfoD100* alone involved a denaturing step of 2 min at 94 °C, followed by 35 cycles of 45 s at 94 °C, 45 s at 56 °C and 1 min 30 s at 72 °C, with 10 μL reaction volumes containing 1.0 μL 10X reaction buffer (10 mM Tris-HCL [ph 9.0], 1.5 mM MgCl$_2$, 0.1% TritonX-100, 50 mM KCl), 1.0 μL dNTPs (10 mM each dNTP), 1.0 U *Taq* polymerase and 40 ng of DNA template and (2) two duplexes [*Sfo18*, *Sfo23* (C); *Mst85*, *Sfo12* (D)] involved a denaturing step of 4 min followed by 34 cycles of 1 min at 95 °C, 45 s at 58 °C and 45 s at 72 °C with a final elongation step of 10 min at 72 °C and with 10 μL volumes as above. All PCR products were separated electrophoretically using an ABI™ 377 automated sequencer (Perkin Elmer) (gel 1: duplexes A, C, D; gel 2 duplex B, *SfoD91*, *SfoD100*). Allelic sizes were scored against the size standard GS350 Tamra (Perkin Elmer) using GENESCAN™ analysis 2.1 and GENOTYPER™ 2.1 software.

Intrasample genetic diversity

Genetic variability for each temporal sample was quantified with standard descriptive statistics (alleles per locus (A), observed (H_O) and expected (H_E) heteroygosities) and analysed by verifying Hardy–Weinberg equilibrium (HWE) expectations of genotypic frequencies (across all loci in each temporal sample and at each locus), using GENEPOP 3.3 (Raymond & Rousset 1995). Tests for genotypic disequilibrium between all loci pairs were also performed with GENEPOP 3.3. Allelic richness ($\hat{A}$) in temporal samples at each locus was corrected (using the rarefaction method of FSTAT 2.9.3; Goudet 2001) to the smallest sample after TAK2001 (CHE2002, $n = 30$) to increase the power of detecting differences in $\hat{A}$ (Leberg 2002).

Spatiotemporal population genetic structure analyses

The hypothesis of genic (allelic frequency) differentiation at individual loci between all pairs of temporal samples was tested following Guo & Thompson (1992) (in GENEPOP 3.3), with significance values obtained over all loci using Fisher's method (Ryman & Jorde 2001). We then compared variance in allelic identity (*F*-statistics, e.g. θ_{ST}; Weir & Cockerham 1984) and allelic size (*R*-statistics, e.g. R_{ST}; Michalakis & Excoffier 1996) measures of differentiation to determine the relative importance of drift (θ_{ST}) vs. mutation (R_{ST}) for population differentiation (following Hardy *et al.* 2003 in SPAGeDi 1.1; Hardy & Vekemans 2002). Global and pair-wise population θ_{ST} and R_{ST} estimates (1000 permutations of allele sizes) were computed to provide a simulated distribution of R_{ST} values (ρR_{ST}) for testing between the null hypothesis ($R_{ST} = \theta_{ST}$; θ_{ST} is more appropriate as differentiation is caused mainly by drift) and the alternative hypothesis ($R_{ST} > \theta_{ST}$; R_{ST} is more

suitable because stepwise mutation model (SSM)-like mutations have contributed to differentiation) (Hardy *et al.* 2003). Nonrejection of the null hypothesis ($P > 0.05$) led to the calculation of genetic differentiation between rivers or temporal samples within rivers using θ_{ST}. Corresponding 95% confidence intervals were determined by bootstrapping 1000 times over loci (FSTAT 2.9.3). When applicable, the sequential Bonferroni procedure was used to maintain Type I probability error at $\alpha = 0.05$ ($p_{adj} = \alpha/k_i$; Rice 1989). All other statistical tests were at the 0.05 level unless stated otherwise.

To test if substructure was present within each river, the Bayesian clustering model used to infer *k* subpopulations was implemented in STRUCTURE (Pritchard *et al.* 2000). Briefly, STRUCTURE reduces linkage disequilibrium and maximizes HWE to cluster individuals into groups, irrespective of a priori knowledge of origin. Following Pritchard *et al.* (2000), simulations were conducted to determine how long to run the burn-in period and MCMC simulations on pooled temporal samples in each river for $k = 1$–4 (burn-in 100 000 replications, 700 000 MCMC replicates) under a model assuming admixture and correlated allele frequencies between populations.

An analysis of molecular variance (AMOVA) was performed (using ARLEQUIN 2.0; Schneider *et al.* 2000) in order to assess components of genetic diversity attributable to (i) variance among rivers (spatial component); (ii) variance among temporal samples within rivers (temporal component); and (iii) variance among individuals within temporal samples. AMOVAS were also performed separately on individual rivers [variance components (ii) and (iii)] to ascertain whether certain rivers contributed more to the overall temporal component of variance. Distance-based relationships among river samples were estimated from an unrooted neighbour-joining (NJ) clustering analysis of Cavalli-Sforza & Edwards's (1967) chord distance (D_{CE}) using POPULATIONS 1.2.14 (Langella 2001). Consistency of D_{CE} tree topology was assessed by bootstrapping over loci, with phylogenetic trees visualized in TREEVIEW (Page 1996).

Effective number of breeders (N_b) and effective population size (N_e)

Estimates of N_e based on temporal allele frequency data (e.g. Waples 1989) over short time intervals (< one generation) are prone to biases because sampling noise may be stronger than the signal of genetic drift (Waples 1990). According to Waples (1990), such bias may be reduced in salmonid fishes by estimating the effective number of breeders N_b, another measurable parameter that has a signal determined by N_e. That is, the nondiscrete generation life history of salmonids has the relationship $N_e = gN_b$, where *g* is the mean generation length (Waples

1990). The N_b model was developed specifically for the semelparous yet overlapping year class life history of Pacific salmon (*Oncorhynchus* spp.), but Waples (1990) found it to be applicable to other salmonid populations where iteroparity (repeat spawning) was low. In Mistassini brook charr, low iteroparity is likely as only two age classes dominated spawning individuals in any one river (D. Fraser, unpubl. data), and iteroparity in other salmonids with analogous life histories is low (e.g. Ardren & Kapuscinski 2003).

In each river, N_b was estimated following Waples (1990) for the time intervals 2000–01 and 2001–02. Standardized variance of allele frequency change at each locus ($\hat{F}_j$) was first estimated using Pollak's (1983) formula:

$$\hat{F}_j = \sum_{i=1}^{L} \left[\frac{(X_{i1} - X_{i2})^2}{(X_{i1} + X_{i2})/2} \right] \bigg/ (L_j - 1)$$

where X_{i1} and X_{i2} are sampled allele frequencies of the *i*th allele at the first and second sampling intervals, respectively, and *L* is the number of alleles sampled at the *j*th locus. Low frequency alleles (< 0.02 over both sampling years) were pooled into a single allele class (Waples 1989, 1990). Mean standardized variance ($\hat{F}$) over all 10 loci was calculated as: $\hat{F} = \Sigma[(L_j - 1)\hat{F}_j] \Sigma(L_j - 1)$. Estimates of N_b were then calculated from the equation:

$N_b = \dfrac{b}{2(\hat{F} - 1/S + 1/N)}$ where *b* is an analogue of the number of generations elapsed between two samples in the discrete generation model, *S* is the harmonic mean of the sample sizes in the two sampling intervals (two intervals × 10 loci = 20 sample sizes) and *N* is the number of spawning individuals exposed to the sampling process before reproduction (Waples 1989). The value *b* was taken as a 1-year interval (for a value of $b = 2.31$; see Waples 1990) based on average generation lengths of approximately 4 years in Mistassini populations (see Results) and similar age-class distributions observed to those simulated in Waples (1990). The value *N* was taken as ∞ as Mistassini populations are probably made up of several thousand individuals, and bias is relatively small as long as $N/N_e > 2$ (Waples 1989). The 95% confidence intervals associated with N_b were calculated according to Waples (1989).

N_e was then estimated as a function of both the harmonic (N_{eh}) and arithmetic mean (N_{ea}) of the N_b estimates for each sampling period ($n = 2$) from the general equation $N_e = gN_b$ (Waples 1990). This was performed for comparative reasons because each model makes differing assumptions about the demographic behaviour of salmonid populations. Namely, N_{eh} assumes that the spawning population in a given year contributes equally to the next generation regardless of the number of spawners whereas N_{ea} assumes that each year's spawning individuals contribute to the next generation in proportion to the number of

spawning individuals (Waples 2002). A χ^2 test was then used to test the null hypothesis of equal expectation of N_e among populations using SAS 8.0 (SAS Institute Inc. 1999; unless otherwise stated, all further statistical tests were conducted using SAS).

Levels and patterns of gene flow among populations

To account for yearly variation in gene flow, $N_e m$ among rivers was first estimated in each sampling year using Wright's ($N_e m_{WRIGHT}$) infinite island model ($N_e m_{WRIGHT} = [(1/\theta_{ST}) - 1]/4$) for comparative reasons with other studies. Yearly $N_e m$ was also estimated in a four-population matrix using the maximum-likelihood framework based on coalescent theory of MIGRATE 1.6.9 (Beerli & Felsenstein 2001) ($N_e m_{BEERLI}$). Like $N_e m_{WRIGHT}$, $N_e m_{BEERLI}$ estimates are based on long-term estimates of gene flow, but $N_e m_{BEERLI}$ makes fewer unrealistic assumptions, such as accounting for asymmetric gene flow between population pairs (discussed in Beerli & Felsenstein 1999, 2001).

To test the null hypothesis of symmetric gene flow between populations, m was first estimated yearly for each direction between population pairs (e.g. CHE to PEP, PEP to CHE) using $N_e m_{BEERLI}$ estimates and by substituting in estimates of N_{eh}. These short-term N_e values derived from the temporal method of estimating N_b were applied because the model used to calculate them is specifically tailored to the complex life history of salmonid fishes. Therefore, our estimations of m assume that N_e estimates from N_b have been temporally stable over the long term. A one-way analysis of variance (ANOVA; Type II sum of squares using the GLM procedure of SAS) involving each population pair direction (e.g. CHE to PEP) was then used to test the null hypothesis of equal m between population pairs. We considered temporal estimates of m in each sampling year as sampling replicates for each direction in pairwise comparisons of population pairs, as they provided an indication of whether asymmetries in m were constant through time. However, our data set did not allow us to determine whether m significantly differed in magnitude in one direction or the other among sampling years. The LSMEANS statement was used to calculate adjusted means for m. Total m into each population i for each sampling year was calculated as: $m_i = \sum_{j \neq i} m_{ji}$ where m_{ji} is the migration rate from population j into i.

Testing male-biased dispersal

An assignment test was conducted first to estimate how well individuals were classified back to their river of capture using the Bayesian method implemented in GENECLASS (Cornuet *et al.* 1999). Temporal samples within rivers were pooled because of the within-river temporal stability (see Results) and to increase assignment resolution because larger sample sizes increase accuracy of allele frequency distributions (Cornuet *et al.* 1999). Assignment values for each individual were then transformed to raw likelihood values or 'assignment indices' (*AI*) (Favre *et al.* 1997). Corrected assignment indices (*AIc*) of each individual were computed following Goudet *et al.* (2002: eqn 1). *AIc* values average zero within a population and individuals with a negative value are more likely to be dispersers than individuals with positive *AIc* values (Favre *et al.* 1997). While sex was only available for some of the individuals sampled (Fig. 1), we included all 559 individuals in the calculation of *AIc* values to increase precision in estimating individual *AIc* values within each population. A test of sex-biased dispersal was then initiated by comparing mean *AIc* values between females and males in each river using a Mann–Whitney *U*-test. Variance of *AIc* values between the sexes was also compared using an *F*-ratio test under the hypothesis that it should be larger for the sex dispersing the most (Favre *et al.* 1997).

Results

Length and age at maturity

Differing mean total length (ANOVA: $F_{3,149} = 9.40$, $P < 0.001$) and age (ANOVA: $F_{3,149} = 5.28$, $P = 0.002$) of prespawning adults among rivers provided a first indication of life-history trait variation in Mistassini populations. *Post-hoc* Tukey tests revealed that length and age at maturity (± SE) were significantly lower in RUP (463.8 ± 7.23 mm, 3.56 ± 0.13 years; all $P < 0.05$) than in the three northeast rivers (CHE, PEP, TAK), but not significantly different among northeast rivers (CHE: 512.8 ± 6.70 mm, 4.22 ± 0.12 years; PEP: 504.6 ± 6.77 mm, 4.14 ± 0.12 years; TAK: 503.6 ± 14.31 mm, 4.09 ± 0.26 years; all $P > 0.39$).

Intrasample genetic diversity

Exact tests of genotypic linkage equilibrium revealed a lower proportion of significant adjusted *P*-values than expected by chance (one of 45 comparisons), suggesting independence of the 10 loci utilized. The exact test of global HWE was not significant ($\alpha = 0.00045$, $k = 110$), and no loci departed from theoretical expectations after Bonferroni correction ($\alpha = 0.005$, $k = 10$). Only one temporal sample (RUP2001) and one locus in a temporal sample (*SfoB52*, PEP2002) displayed significant departures from HWE with a heterozygote deficiency (both $\alpha = 0.0045$, $k = 11$). All 10 loci were moderately to highly polymorphic, with four to 15 alleles observed per locus and H_E ranging from 0.38 (*Sfo18*) to 0.80 (*Sfo23*) (Table 1). Mean corrected allelic richness across loci was not significantly different among temporal samples (ANOVA: $F_{9,81} = 0.88$, $P = 0.55$) (Table 1).

Table 1 Summary of genetic diversity at 10 microsatellite loci among Mistassini population temporal samples (Cheno = CHE, Pepeshquasati = PEP, Takwa = TAK and Rupert = RUP): total and corrected number of alleles* ($A/\hat{A}$) at each locus, and expected and observed (H_E/H_O) heterozygosities for each temporal sample; mean number of alleles ($\hat{A}$) per locus and mean allelic richness per locus (mean $\hat{A}$) in each temporal sample, as well as mean expected and observed heterozygosities H_E/H_O and N for pooled temporal samples within each population. The total allele number per locus (A_T) and overall allelic size range at each locus (S) in base pairs are displayed in the two last rows of the table. *Allelic richness ($\hat{A}$) corrected to $n = 30$ (CHE2002) using the rarefaction method of FSTAT 2.9.3 (Goudet 2001)

Sample	Sfo12	Sfo18	Sfo23	SfoB52	SfoC86	SfoC129	SfoD75	SfoD91	SfoD100	Mst85	$\hat{A}$	Mean $\hat{A}$	H_E/H_O	N
CHE2000	4/3.6	4/3.2	11/10.2	4/4	3/2.9	3/3	10/9.1	7/5.8	8/7.6	6/5.9	6.0	5.5		
	0.54/0.55	0.19/0.16	0.72/0.76	0.63/0.57	0.49/0.47	0.55/0.47	0.82/0.81	0.60/0.55	0.81/0.69	0.73/0.78				
CHE2001	3/3	4/3.7	10/9.6	5/4.5	3/3	4/3.8	8/7.4	5/4.9	7/7	7/6.6	5.6	5.4	0.63/0.61	137
	0.56/0.56	0.32/0.29	0.79/0.72	0.70/0.76	0.50/0.59	0.61/0.57	0.81/0.83	0.63/0.52	0.77/0.86	0.69/0.69				
CHE2002	4/4	2/2	10/10	4/4	3/3	4/4	8/8	7/7	8/8	5/5	5.6	5.6		
	0.52/0.33	0.23/0.20	0.82/1.00	0.69/0.70	0.44/0.47	0.55/0.57	0.80/0.90	0.65/0.60	0.73/0.63	0.63/0.65				
PEP2000	5/4.4	4/3.4	12/10.6	6/4.8	3/3	4/3.4	11/9.7	7/5.3	8/7.8	8/7.8	6.8	6.0		
	0.56/0.57	0.28/0.26	0.81/0.79	0.75/0.79	0.46/0.47	0.59/0.58	0.83/0.83	0.64/0.60	0.78/0.78	0.73/0.67				
PEP2001	3/2.9	4/3.4	13/11.4	5/4.8	4/3.4	3/3	10/8.8	9/7.7	8/7.8	9/8.2	6.8	6.1	0.64/0.64	185
	0.54/0.59	0.32/0.35	0.78/0.82	0.70/0.65	0.42/0.33	0.61/0.64	0.82/0.86	0.71/0.62	0.81/0.91	0.71/0.75				
PEP2002	4/3.9	3/3	10/9.7	5/4.7	3/3	3/3	10/9.3	7/6.6	8/7.3	5/4.7	5.9	5.5		
	0.55/0.50	0.28/0.32	0.74/0.86	0.74/0.52	0.47/0.55	0.60/0.59	0.84/0.93	0.64/0.61	0.67/0.73	0.63/0.61				
TAK2000	4/4	4/3.6	12/10.4	5/4.6	3/3	3/3	8/8.0	9/7.8	7/7	8/8	6.3	5.9	0.68/0.69	59
	0.56/0.60	0.46/0.46	0.77/0.77	0.74/0.83	0.58/0.62	0.61/0.43	0.84/0.83	0.72/0.77	0.77/0.78	0.75/0.69				
TAK2001	4	4	7	5	3	3	6	6	8	7	5.4	—		
RUP2000	6/4.4	3/2.8	13/10.5	6/4.8	4/3.6	6/3.6	8/7.2	11/10.1	7/5.6	8/6.9	7.2	5.9		
	0.61/0.64	0.48/0.55	0.80/0.82	0.72/0.46	0.58/0.82	0.50/0.55	0.79/0.91	0.71/0.73	0.70/0.73	0.70/0.64				
RUP2001	3/3	4/3.4	11/10.8	6/5.7	4/3.6	5/3.6	8/7.2	12/10.3	7/6.5	7/7	6.7	6.2	0.65/0.63	178
	0.67/0.69	0.50/0.53	0.86/0.83	0.49/0.49	0.59/0.51	0.38/0.42	0.61/0.64	0.86/0.76	0.72/0.62	0.69/0.72				
RUP2002	3/3	6/4.7	11/10.4	6/5.2	4/3.6	5/3.6	7/6.4	10/9.3	6/5.4	5/5	6.4	5.7		
	0.65/0.67	0.55/0.50	0.85/0.85	0.56/0.64	0.63/0.63	0.49/0.55	0.58/0.52	0.82/0.72	0.67/0.65	0.65/0.57				
A_T	6	10	15	9	5	7	12	15	8	9				
S	197–273	161–187	145–183	199–225	101–122	218–242	172–216	204–268	210–238	138–184				

Spatiotemporal dynamics of intralacustrine population genetic structure

Multilocus R_{ST} values were not significantly higher than the simulated distribution of R_{ST} values (ρR_{ST}) ($P = 0.061$) (Table 2), suggesting that, overall, θ_{ST} was a more appropriate statistic for assessing Mistassini population differentiation (Hardy *et al.* 2003) (Table 2). This test, coupled with significant global tests of genic differentiation over all loci ($P < 0.001$), indicated population structure in the system [θ_{ST} (95% CI): 2000, 0.076 (0.050−0.102); 2001, 0.067 (0.046−0.086); 2002, 0.075 (0.052−0.099)] (Tables 2 and 3).

Differentiation was more pronounced between RUP and the three northeast rivers (CHE, PEP, TAK) than among northeast rivers, as evidenced by (i) mean pairwise numbers of loci with significant genic differentiation [mean (range): 9.1 (5−10) vs. 4.9 (2−8)]; (ii) mean pairwise θ_{ST} values [mean (range): 0.101 (0.078−0.129) vs. 0.019 (0.003−0.033)]; and (iii) patterns of allele frequency distributions at individual loci (Table 3; Fig. 2). Albeit weaker, some population structuring was evident among northeast rivers, particularly between PEP and CHE in all three sampling years [mean (range): loci, 6.3 (4−8); θ_{ST}, 0.022 (0.019−0.026)] (Table 3). Comparisons between these two rivers and TAK were more variable; all tests of genic differentiation were significant, but pairwise θ_{ST} estimates were not significant between TAK & PEP in 2000 and between TAK & CHE in 2001 (Table 3). Pooled TAK temporal samples were genetically closer to PEP than CHE, despite TAK and CHE being sister tributaries in a different drainage from

Table 2 Summary of the allele size permutation test of Hardy *et al.* (2003) for Mistassini population differentiation: θ_{ST} and R_{ST} estimates for each locus employed and the 95% confidence intervals for simulated R_{ST} values (ρR_{ST}) using random permutations of allele sizes. Significance tests ($R_{ST} > \rho R_{ST}$) are denoted with asterisks (*$P = 0.05$, **$P = 0.01$ level)

Locus	θ_{ST}	R_{ST}	ρR_{ST} (95% CI)
Sfo12	0.045	0.004	0.046 (0.000−0.120)
Sfo18	0.106	0.073	0.089 (0.006−0.143)
Sfo23	0.027	0.036	0.026 (0.000−0.117)
SfoB52	0.118	0.087	0.100 (0.001−0.240)
SfoC86	0.037	0.028	0.037 (0.031−0.042)
SfoC129	0.068	0.117*	0.058 (0.002−0.120)
SfoD75	0.093	0.009	0.083 (0.000−0.251)
SfoD91	0.090	0.363**	0.087 (0.003−0.319)
SfoD100	0.012	0.017	0.015 (0.000−0.067)
Mst85	0.114	0.260	0.110 (0.000−0.351)
Multilocus	0.071	0.147	0.079 (0.025−0.176)

Table 3 Summary of spatial genetic population structure by sampling year in Mistassini brook charr populations (Cheno = CHE; Pepeshquasati = PEP; Takwa = TAK; Rupert = RUP): pairwise estimates of θ_{ST} and 95% confidence intervals (CI), with significance values after Bonferroni correction; genic differentiation (G) represented by the number of loci with significantly different allele frequency distributions between each population pair using Fisher's exact tests and significance values based on multilocus *P*-values using Fisher's method; and, effective number of migrants ($N_e m$) following Wright (1931) and Beerli & Felsenstein (1999, 2001). $N_e m_{BEERLI}$ estimates have been averaged for general comparisons with $N_e m_{WRIGHT}$. Unpooled $N_e m_{BEERLI}$ estimates into receiving populations for each pairwise comparison are listed from left to right (e.g. for 2000, CHE vs. PEP, 6.47 into CHE from PEP and 9.05 into PEP from CHE). Significance at the **$P = 0.01$, *** $P = 0.001$ level

| Comparison	θ_{ST}	95% CI	G	$N_e m_{WRIGHT}$	$N_e m_{BEERLI}$	Unpooled $N_e m_{BEERLI}$
2000						
CHE vs. PEP	0.026***	0.012−0.042	8***	9.24	7.76	6.47 vs. 9.05
CHE vs. TAK	0.026***	0.011−0.043	7***	9.49	3.91	3.38 vs. 4.44
PEP vs. TAK	0.006	0.000−0.016	3**	44.00	7.88	7.33 vs. 8.42
CHE vs. RUP	0.129***	0.073−0.192	10***	1.68	2.20	2.11 vs. 2.28
PEP vs. RUP	0.113***	0.073−0.151	10***	2.02	1.96	1.93 vs. 1.99
TAK vs. RUP	0.097***	0.052−0.151	9***	2.32	2.71	2.94 vs. 2.46
2001						
CHE vs. PEP	0.021***	0.010−0.033	7***	11.87	5.90	6.04 vs. 5.76
CHE vs. TAK	0.003	0.000−0.016	2**	90.00	7.53	4.43 vs. 10.62
PEP vs. TAK	0.033***	0.001−0.072	3***	7.36	4.23	2.26 vs. 6.19
CHE vs. RUP	0.104***	0.059−0.149	10***	2.16	1.49	1.35 vs. 1.63
PEP vs. RUP	0.100***	0.067−0.131	10***	2.25	1.39	1.24 vs. 1.53
TAK vs. RUP	0.078***	0.035−0.126	5***	2.86	5.64	7.29 vs. 3.98
2002						
CHE vs. PEP	0.019***	0.008−0.030	4***	13.18	12.56	15.12 vs. 9.99
CHE vs. RUP	0.094***	0.058−0.131	10***	2.40	7.36	7.95 vs. 6.77
PEP vs. RUP	0.091***	0.056−0.123	9***	2.51	3.18	3.11 vs. 3.24
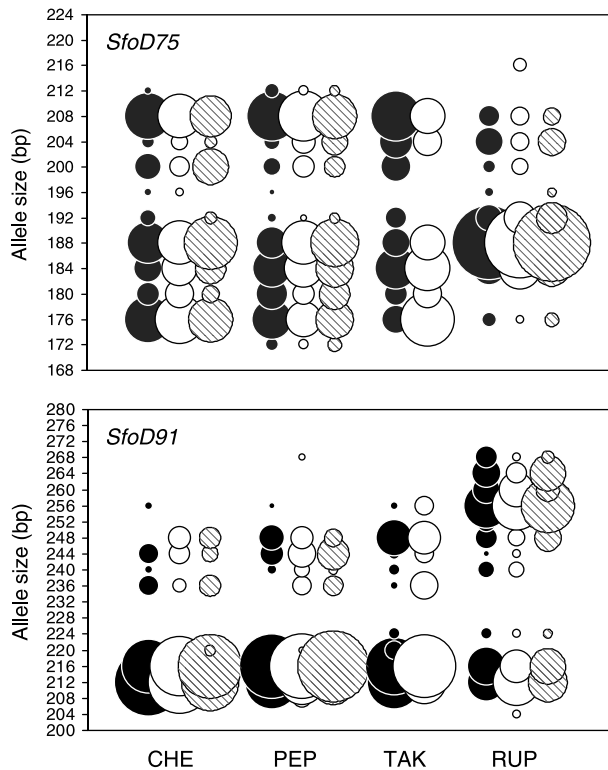
Fig. 2 Temporal allele frequency distributions at two selected microsatellite loci in Mistassini Lake brook charr populations. Columns of black circles represent 2000 samples; white (2001); grey-barred (2002) (Cheno = CHE; Pepeshquasati = PEP; Takwa = TAK; Rupert = RUP). Complete allele frequency distributions for all loci are available upon request from the authors.

PEP (Table 2). No evidence for subpopulation structure within individual rivers was detected, as Bayesian posterior probabilities were much larger for $k = 1$ than for any other model using STRUCTURE (> 0.98). However, $k = 2$ was strongly supported when just considering the three

northeast rivers combined, raising the possibility that TAK did not behave demographically as a genetically distinct unit (see Discussion).

Significant temporal variation of allele frequencies among years within individual rivers from the AMOVA ($P = 0.005$) and tests of genic and genetic differentiation suggested some temporal fluctuation in individual river population structure (Tables 4 and 5). Nevertheless, the temporal component of variance in the AMOVA was 20 times lower than the spatial component (0.0035 vs. 0.0689) and significance in other cases was due mainly to greater temporal variation among sampling years within TAK and RUP (Tables 4 and 5). Temporal samples for three of four rivers (exception TAK) also displayed close clustering in the D_{CE} tree topology with at least 50% bootstrap support (Fig. 3).

Differential N_b and N_e estimates among populations

Population estimates of N_b were stable but consistently higher in one river (PEP) from 2000 to 2002 (Table 6). Consequently, N_e (both N_{eh} and N_{ea}) deviated significantly from equal expectations among rivers (N_{eh}: $\chi^2 = 298$, d.f. = 3, $P < 0.001$) (Table 6). N_{eh} estimates were smaller than N_{ea}; however, differences were not substantial. Upper intervals of N_b were typically infinite, a common problem with calculating N_e from temporal genetic data (Waples 1989) (Table 6).

Heterogeneous m among population pairs

Pairwise estimates of $N_e m$ were not correlated among the methods used (Pearson's $r = 0.42$, $P = 0.12$), but were consistently lower between the RUP and three northeast rivers than among northeast populations (Table 3). Unpooled maximum likelihood $N_e m_{BEERLI}$ estimates were a first indication of asymmetric gene flow between certain rivers and showed some consistent trends, with $N_e m_{BEERLI}$ into TAK

Table 4 Hierarchical partitioning of genetic variance (AMOVA) at microsatellite loci among all Mistassini Lake brook charr populations and individual populations between sampling years (Cheno = CHE; Pepeshquasati = PEP; Takwa = TAK; Rupert = RUP). Significance at the *$P = 0.05$, ***$P = 0.001$ level

	Among all Mistassini Lake populations										
Variance component	d.f.			% total variance				P			
Among populations	3			6.89				***			
Among years within populations	7			0.35				**			
Within populations in each year	1107			92.76				***			
Individual populations	CHE			PEP			TAK			RUP	
Variance component	d.f.	%V	P	d.f.	%V	P	d.f.	%V	P	d.f.	%V	P
Among years	2	0.33	0.16	2	0.20	0.14	1	1.29	*	2	0.41	*
Within sampling years	271	99.67	***	367	99.80	***	116	98.71	***	353	99.59	***

Table 5 Summary of temporal genic and genetic differentiation among sampling years within Mistassini Lake brook populations (Cheno = CHE; Pepeshquasati = PEP; Takwa = TAK; Rupert = RUP): pairwise θ_{ST} estimates between sampling years and 95% confidence intervals, with significant values after Bonferroni correction; genic differentiation (G) represented as the number of loci between sampling years having significant allele frequency differences and significant multilocus values based on Fisher's method. Significance at the *$P = 0.05$, **$P = 0.01$, ***$P = 0.001$ level

Population	θ_{ST}	95% CI	G
CHE2000-01	0.002	0.000–0.006	1*
CHE2000-02	0.014*	0.000–0.028	2
CHE2001-02	0.005	0.000–0.015	2
PEP2000-01	0.002	0.000–0.006	2
PEP2000-02	0.002	0.000–0.006	1
PEP2001-02	0.005	0.000–0.014	1
TAK2000-01	0.012	0.000–0.027	2*
RUP2000-01	0.007*	0.003–0.012	2***
RUP2000-02	0.001	0.000–0.009	1*
RUP2001-02	0.006	0.000–0.011	1**

Table 6 Estimated number of breeders (N_b) and their 95% confidence intervals and effective population size (N_e) based on harmonic and arithmetic mean methods (N_{eh}, N_{ea}, respectively) for Mistassini Lake brook charr populations (Cheno = CHE; Pepeshquasati = PEP; Takwa = TAK; Rupert = RUP)

Population	N_b	95% CI	N_{eh}	N_{ea}
RUP 2000-RUP 2001	88	(39–270)	333	335
RUP 2001-RUP 2002	100	(38–741)		
PEP 2000-PEP 2001	307	(90–∞)	994	1031
PEP 2001-PEP 2002	197	(57–∞)		
CHE 2000-CHE 2001	131	(59–∞)	435	456
CHE 2001-CHE 2002	85	(33–2833)		
TAK 2000-TAK 2001	57	(23–∞)	233	233

Fig. 3 Unrooted neighbour-joining tree of temporal samples in the four Mistassini Lake brook charr populations (Cheno = CHE; Pepeshquasati = PEP; Takwa = TAK; Rupert = RUP) using 10 microsatellite loci and based on Cavalli-Sforza & Edwards's (1967) chord distance (D_{CE}). Phylogenetic trees were bootstrapped over loci with replacement and 5000 replicates, with numbers indicating percentage support of each branch in the topology.
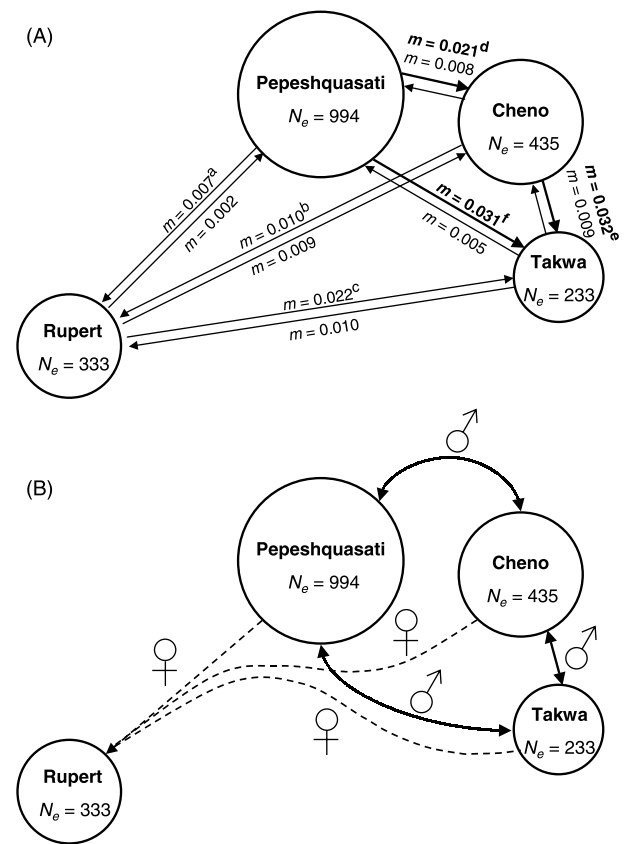

Fig. 4 Schematic summary of gene flow and sex-biased dispersal in Mistassini Lake brook charr populations: (A) dynamics between mean effective population size (N_e based on N_{eh}) and estimates of migration rate (m) between each population pair. Bold lines represent directions between population pairs in which m was significantly asymmetric [P-values indicated by letters a–f ($P = 0.490, 0.770, 0.148, 0.067, 0.010, 0.004$, respectively]; (B) dispersal between the two sexes in northeast rivers: males (solid lines); females (dotted lines). The model assumes both sexes disperse between each population pair but only shows detected asymmetries with one-way arrows. See Discussion for explanation.

being greater than out of this river and PEP generally showing the opposite trend (Table 2). Consequently, the consideration of estimated N_e led to the rejection of the hypothesis of equal m among populations (ANOVA: $F_{5,18} = 3.99$, $P = 0.01$). Significant asymmetric m was found in all pairwise comparisons among the three northeast rivers, where m was consistently higher from both PEP and CHE to TAK than vice-versa and similarly marginally higher from PEP to CHE (Fig. 4A). Total estimates of m into each river

for each sampling year were highest for TAK [mean (range): 0.085 (0.068–0.103)], followed by CHE [0.039 (0.027–0.053)], RUP [0.027 (0.02–0.03)], and PEP [0.015 (0.009–0.018)].

Evidence for differential sex-biased dispersal

The hypothesis that male brook charr disperse more than females was supported in the three northeast rivers, where there was a significant tendency for males to show lower mean AIc values than females (-1.22 ± 0.55 vs. 0.21 ± 0.33; CHE $P = 0.11$; PEP $P = 0.10$; TAK $P = 0.18$; Fisher's method for combining probabilities from tests of significance: $P = 0.05$). Variance in AIc values was also greater among males than among females in northeast rivers ($F = 0.69$, $P = 0.03$) supporting the theoretical prediction that the more-dispersing sex should also have significantly greater variance in assignment indices (Favre *et al.* 1997). The RUP showed, unexpectedly, an opposite trend: females had significantly lower AIc values than males (-1.00 ± 0.75 vs. 0.63 ± 0.53, $P = 0.04$); however, the difference between sexes was less pronounced than in the three northeast rivers and variance in AIc did not differ between the sexes ($F = 0.59$, $P = 0.91$). Overall, proportionally fewer individuals were misclassified to RUP in northeast rivers than vice versa (four of 381 vs. eight of 178; $\chi^2 = 6.97$, d.f. = 1, $P = 0.008$). Misclassified northeast individuals to RUP were male (one) or female (one) where sex was known, whereas misclassified RUP individuals to northeast rivers were all female (seven of eight, deviating from 1:1 expectations, assuming the eighth individual was a male, $\chi^2 = 2.62$, d.f. = 1, $P = 0.02 \pm 0.005$; Roff & Bentzen 1989).

Discussion

A consideration of unequal N_e and m and sex-biased dispersal revealed complex interactions between dispersal and population structure in brook charr. The ensuing discussion treats these relationships first from the standpoint of the role that habitat divergence has played in maintaining population differentiation. It then considers how the observed unequal N_e and m, and differential sex-biased dispersal, may have contributed to population structuring.

Role of habitat divergence in maintaining population differentiation

Genetic analyses revealed a temporally stable dichotomy in population structure between the Rupert and the three northeast rivers in Mistassini Lake. Incomplete ecological and genetic isolating mechanisms probably operate to maintain this divergence. Northeast river charr had similar length and age at maturity compared to the Rupert, as well as earlier spawning times and comparable migration run lengths (D. Fraser, pers. obs.). These characteristics point to different environmental gradients and the possibility of local adaptations to different breeding environments in each population group, as well as similar environmental regimes among the genetically close northeast rivers. This habitat divergence scenario is supported by a combination of: (1) the moderating effects that large lakes have on prolongation of the cooling down of their outflows (e.g. Rupert) each fall relative to the tributaries which enter them (e.g. northeast rivers) and the coinciding importance of water temperature on the spawning time of many salmonids (Carmack *et al.* 1979; Morrison & Smith 1986; Burger *et al.* 1997); (2) the similar geological features shared by northeast rivers that contrast those found in the Rupert (Bouchard 1980); (3) the genetic evidence of a heritable component to salmonid spawning migration run timing (e.g. Quinn *et al.* 2000); and (4) the likelihood that differing length and age at maturity among populations is adaptive in this species (Hutchings 1993).

Several indirect approaches have been used to infer adaptive divergence in empirical genetic studies. Perhaps the most appropriate approach is to employ a quantitative genetic model that considers populations experiencing differing selection regimes and exchanging individuals (e.g. Hendry *et al.* 2001). However, in the absence of detailed quantitative genetic data, local adaptation may be evaluated theoretically using a wide range of N_e and m values and varying selective intensities (s) on traits (Adkison 1995). In this regard, evaluations with similar values of N_e (500–1000) and m (0.005–0.05) to those observed in Mistassini populations [N_e range (233–994) and mean total m (0.015–0.085)] have been considered recently in populations of salmonid fishes (Adkison 1995; Hansen *et al.* 2002). The consensus from these studies was that adaptation is more likely to occur at a regional level of salmonid populations (e.g. geographical scale of several rivers) sharing similar selective regimes than adaptation at the local population level (e.g. individual rivers/populations), unless s was very strong on traits (see Adkison 1995; Hansen *et al.* 2002). Given this and the above discussion, we can expect that the Rupert and the northeast river group are adapted locally. Yet, adaptation may be more likely at the regional level of the three northeast rivers for most traits than in individual northeast rivers, particularly for populations with lower N_e and receiving greater m (e.g. Takwa). A caveat of this approach, is that there is little empirical information regarding actual values of selection coefficients in salmonid populations. Nevertheless, information available suggests that adaptation at the regional rather than the local scale is plausible. For instance, in a recent study that aimed at estimating natural selection acting on stream dwelling Atlantic salmon (*Salmo salar*), Hendry *et al.* (2003) found little evidence that any of the life-history traits they studied were subject to either strong directional or stabilizing selection at the local scale.

Role of varying N_e and asymmetric m in shaping population structure

Unequal N_e and m in Mistassini populations shed additional light on the interplay between dispersal and population structure in the system. Metapopulation theory proposes that asymmetric dispersal between sets of local populations occupying habitats of varying quality influences the demographic connectivity and/or genetics of at least some of the local populations (Hanski & Gilpin 1997; Stacey *et al.* 1997). In the three northeast rivers, such a connectivity scenario may clarify their close genetic relationships, similar heterozygosities and genetic variability. Here, the direction of asymmetric m estimates was always from the population with the highest N_e (Pepeshquasati) to populations of lower N_e (e.g. Takwa and Cheno). Thus, dispersal (in absolute numbers of individuals) from Pepeshquasati may have a greater impact on the genetic structure of the smaller populations in Takwa and Cheno. This is especially probable given that the ratio of N_e to N may become smaller as N_e increases, at least in salmonids (Ardren & Kapuscinski 2003), so N may actually be proportionally greater in Pepeshquasati relative to Takwa and Cheno than N_e estimates suggest. Overall, asymmetric m would explain the unusual closer genetic relationship of Takwa to Pepeshquasati than to its geographically proximate sister river Cheno, which contrasts the commonly observed pattern of congruent population structure with drainage structure in most salmonid fishes (Altukhov *et al.* 2000; but see Tessier *et al.* 1997).

Populations with larger N are also likely to be found in environments of more suitable habitat structure (e.g. quality and size; McCauley 1991) and this pattern may be reflected in northeast rivers. For instance, relative to Takwa and Cheno, Pepeshquasati appears to have a larger drainage area available for spawning adults, a greater availability of juvenile rearing habitat and a lower occurrence of other predatorial and competing species (northern pike, *Esox lucius*; walleye, *Stizostedion vitreum*) (D. Fraser, pers. obs.). Such characteristics have been demonstrated to affect production in salmonid populations (Gibson 1993).

The Bayesian individual-based clustering analysis of Pritchard *et al.* (2000) provided further support for this connectivity scenario in northeast rivers. The observation that only two distinct population clusters ($k = 2$) were found for the three rivers was unexpected, given that salmonid fishes show typically a 'population by river' genetic structuring (Altukhov *et al.* 2000). Along with the dynamics between N_e and m, this suggests that either Takwa may act as a sink habitat (e.g. Dias 1996) or that a recent recolonization has occurred in the river. However, distinguishing between these two possibilities is difficult with the data available. Despite the high posterior probability for $k = 2$ (> 0.98) in all northeast rivers combined, clustering of individuals into each inferred k was not very strong (varied between 0.35 and 0.65). This could have been used to assess confidently whether Takwa individuals reflected pure immigrants from Pepeshquasati or Cheno (which would have given $k = 2$ instead of $k = 1$ for Takwa in the individual river test), or admixtures of the two populations. Moreover, substantial m probably prevented us from detecting recent (40–60 generations) genetic bottlenecks (Luikart *et al.* 1998; data not shown) which could have been used as a proxy to: (1) infer zero or negative population growth and consequently persistence of Takwa, or (2) infer a recent recolonization event had one come about. Nevertheless, we are unaware of any major anthropogenic or environmental influences in the region which could have led to a recent recolonization event. Furthermore, while the Takwa N_e estimate may have been underestimated due to a low sample size in 2001 ($n = 11$), a correspondence between N_e estimates and catch-per-unit effort in each river was observed over the three sampling periods. For instance, catch-per-unit effort based on the number of charr captured per fisher per 8-h fishing day was consistently higher in Pepeshquasati (10.4–12.2), followed by Cheno (2.0–3.2) and lowest in Takwa (0.4–1.5). The Rupert was intermediate in values (3.3–4.0).

Sex-biased dispersal is associated with population structure

Differential sex-biased tendencies detected among Mistassini populations have further relevance for understanding how dispersal and population structure interact in this system. Because individuals captured in a population with negative *AIc* values were potential dispersers from other populations (Favre *et al.* 1997), the few northeast individuals misclassified to the Rupert suggests that male-biased dispersal detected among northeast rivers was not a result of male dispersal from the Rupert but was due instead to male dispersal among northeast rivers (Fig. 4B). Following the same logic, the female bias detected in the Rupert was attributable to female dispersal from northeast rivers and was therefore not reflective of a sex bias in the Rupert population. All misclassified Rupert individuals were female and removing these 'dispersers' resulted in nonsignificant *AIc* values between sexes ($P = 0.17$) (Fig. 4B). These interpretations of disperser origin presume that no other major brook charr populations exist in the lake, an assumption that is probably met (D. Fraser and L. Bernatchez, unpubl. data).

Male-biased dispersal is common in species with polygynous mating systems (Greenwood 1980) and is predicted when male mate competition, alone or in combination with inbreeding avoidance, exceeds female resource competition (Dobson 1982). Some authors have also underscored that avoidance of kin competition leads to male-biased

dispersal by increasing inclusive fitness (Perrin & Mazalov 2000). Avoidance of kin competition and inbreeding were recently invoked to explain male-biased dispersal in the salmonid polygynous mating system (Hutchings & Gerber 2002). However, that study was conducted on a small population occupying a closed stream environment where the chance of straying to other populations was apparently negligible. We suggest that the male-biased dispersal detected among northeast rivers in our study is due predominantly to mate competition. The ~0.1–0.2 ratio of N_e/N in salmonids (Hedrick *et al*. 1995) implies that most Mistassini populations are composed of several thousand individuals. Thus, it is unlikely that kin competition and inbreeding avoidance would be important enough mechanisms in these populations to lead to dispersal to other populations (see also Hendry *et al*. 2004). The fact that northeast males disperse only between northeast rivers may reflect, a selective advantage over dispersing to the Rupert, especially given the apparent similarities in environmental regimes and breeding environments in the three northeast rivers. On the other hand, why northeast females may have a greater propensity for longer-distance dispersal to the Rupert than northeast males is unclear. It is notable that female morphology was variable among three rivers (Rupert, Cheno, Pepeshquasati), whereas male morphology differed only between the Rupert and northeast populations (D. Fraser and L. Bernatchez, unpubl. data). However, female morphological differences were less pronounced than males between population groups (Rupert/northeast). Therefore, one possible explanation could be that dispersing between population groups may incur lower selective costs on northeast females than on northeast males, assuming that body morphology is related to adaptations to reproductive environments (e.g. Blair *et al*. 1993). Longer-distance female-biased dispersal is probable for salmonids, particularly for anadromous populations of some species where sex ratios are often female skewed and where males frequently adopt a nonmigratory life history (e.g. Hansen *et al*. 2001). Thus, in salmonid fishes, sex-biased dispersal and the processes leading to it may be a matter of spatial scale and life history (e.g. migratory vs. nonmigratory).

Patterns of sex-biased dispersal in Mistassini brook charr have therefore had spatially dependent consequences on gene flow at different levels of population structuring. Males may have a greater impact on demographic connectivity and gene flow among northeast rivers than females, an implication that is particularly noteworthy given that these rivers appear to exhibit metapopulation dynamics based on the analyses of N_e and m. Northeast male-biased dispersal also implies that gene flow between these rivers is ongoing. On the other hand, gene flow from northeast rivers to the Rupert may be principally dictated by longer distance dispersal of

females. For the Rupert, our inability to detect a sex-biased dispersal is due probably to an inadequate number of dispersers in our northeast samples. Even so, our data support the hypothesis that Rupert charr disperse less than northeast river charr.

Conclusions

Several implications emerge from considering simultaneously how unequal N_e, m and sex-biased dispersal influence population structuring. First, resolution of dispersal and gene flow processes underlying population structure was clarified, as well as the potential for local adaptation. Such information provides a baseline from which managers can make more informed decisions when defining management or conservation units, evaluating population persistence and prioritizing populations in a given system. Second, our results suggest that sex-specific dispersal strategies are linked with the natural patterns of connectivity among groups of populations and their varying selective regimes. Thus, predominant dispersal of one sex may slow the rate of natural recolonization of extirpated populations (e.g. Blundell *et al*. 2002), but recolonization may be complicated further by such dynamics. They may also act as a buffer against reductions of genetic variability in small N_e populations due to genetic drift, an observation that has been made experimentally (Aars & Ims 2000). Third, our data suggest that dispersal potential may vary among populations, even in the same region (lake). Therefore, applying potential dispersal distances of species may be inadequate to predict the likelihood of recolonization. Ultimately, explorations into the implications of unequal N_e, m and nonrandom individual dispersal will be integral for synthesizing ecological and genetic theory on dispersal and population structure.

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