Evolution, 59(3), 2005, pp. 611–624

ADAPTIVE MIGRATORY DIVERGENCE AMONG SYMPATRIC BROOK CHARR POPULATIONS

DYLAN J. FRASER[1,2] AND LOUIS BERNATCHEZ[1,3]
[1]*Québec Océan, Département de Biologie, Université Laval, Sainte-Foy, Québec G1K 7P4, Canada*
[2]*E-mail: dylan.fraser@giroq.ulaval.ca*
[3]*E-mail: louis.bernatchez@bio.ulaval.ca*

Abstract.—Ecological processes clearly contribute to population divergence, yet how they interact over complex life cycles remains poorly understood. Notably, the evolutionary consequences of migration between breeding and nonbreeding areas have received limited attention. We provide evidence for a negative association between interpopulation differences in migration (between breeding and feeding areas, as well as within each) and the amount of gene flow (m) among three brook charr (*Salvelinus fontinalis*) populations inhabiting Mistassini Lake, Quebec, Canada. Individuals ($n = 1166$) captured throughout lake feeding areas over two consecutive sampling years were genotyped (10 microsatellites) and assigned to one of the three populations. Interpopulation differences in migration were compared based on spatial distribution overlap, habitat selection, migration distance within feeding areas, and morphology. We observed a temporally stable, heterogeneous spatial distribution within feeding areas among populations, with the extent of spatial segregation related to differential habitat selection (represented by littoral zone substrate). Spatial segregation was lowest and gene flow highest ($m = 0.015$) between two populations breeding in separate lake inflows. Segregation was highest and gene flow was lowest (mean $m = 0.007$) between inflow populations and a third population breeding in the outflow. Compared to outflow migrants, inflow migrants showed longer migration distances within feeding areas (64–70 km vs. 22 km). After entering natal rivers to breed, inflow migrants also migrated longer distances (35–75 km) and at greater elevations (50–150 m) to breeding areas than outflow migrants (0–15 km; −10–0 m). Accordingly, inflow migrants were more streamlined with longer caudal regions, traits known to improve swimming efficiency. There was no association between the geographic distance separating population pairs and the amount of gene flow they exchanged. Collectively, our results are consistent with the hypothesis that reduced gene flow between these brook charr populations results from divergent natural selection leading to interpopulation differences in migration. They also illustrate how phenotypic and genetic differentiation may arise over complex migratory life cycles.

Key words.—Assignment test, divergent natural selection, gene flow, local adaptation, migratory connectivity, model selection.

Received June 2, 2004. Accepted December 27, 2004.

Central to evolutionary theory is the notion that ecological processes can affect the evolution and maintenance of phenotypic diversity through divergent natural selection (Dobzhansky 1946; Schluter 2000, 2001). This hypothesis now has support from studies of natural populations, particularly from research examining associations between alternative trophic resources and morphological specialization (e.g., Grant and Grant 1990; Lu and Bernatchez 1999; Schluter 2000). Other interactions may also contribute to divergence (Abrams 2000; Vamosi and Schluter 2004), yet these have received comparatively limited attention (Schluter 2000). To fully understand the basis of population divergence, the consequences of such alternative ecological interactions must also be explored.

Migration, the regular seasonal movement of individuals between breeding and nonbreeding areas, plays a central role in the life cycles of many organisms as an adaptive response to temporally favorable or unstable habitats during distinct life-history stages (Salomonsen 1955; Baker 1978; Dingle 1996). Interpopulation differences in migration, broadly defined here as life-history or phenotypic trait differentiation linked to migration (e.g., migration timing, body morphology, habitat use, migration distance, behavior), are predicted to coevolve to balance the costs and benefits of migrating toward maximizing fitness (fish: Gross et al. 1988; Kinnison et al. 2001; birds: Choinière and Gauthier 1995; Sandberg and Moore 1996; invertebrates: Palmer and Dingle 1986). Populations exhibiting longer migrations, for example, are expected to show adjustments in body shape, age and size at maturity, or reproductive allocation that compensate for the increasing energetic demands and potential reductions in reproductive output that such migrations can incur (fish: Schaffer and Elson 1975; Taylor and McPhail 1985a; Kinnison et al. 2001, 2003; birds: Wiedenfeld 1991; Winkler and Leisler 1992; Alerstam et al. 2003; invertebrates: Dingle 1994). Previous work has also shown a genetic basis for interpopulation differences in migration, and thus the potential for migration to evolve under natural selection in diverse taxa (fish: Raleigh 1971; Taylor and Foote 1991; birds: Berthold et al. 1992; mammals: Rasmuson et al. 1977; invertebrates: McAnelly 1985; Dingle 1994). However, although interpopulation differences in migration have important evolutionary implications, their influence on population divergence and adaptive evolution has rarely been tested (Wood and Foote 1996; Bensch et al. 1999; Taylor 1999). This may be attributable to, until recently, the logistical difficulties of tracking and discerning the population origin of migrating individuals (Webster et al. 2002).

In general, population divergence is a function of the degree of genetic isolation: genetic differences will accumulate and become fixed over time in isolated populations, while gene flow may erase any incipient differences arising among populations in the absence of barriers to dispersal. But if divergent natural selection effectively drives interpopulation differences in migration, dispersers are expected to experience lower fitness than individuals from local populations.

As a consequence, lower levels of gene flow can be expected and a negative relationship between the amount of gene flow and the extent of such differentiation may be predicted (Kirkpatrick 2001; Schluter 2001).

Salmonid fishes are exemplar models for testing this prediction. For instance, life-history and phenotypic traits related to the natal philopatry life cycle of migratory salmonids are well described (Quinn and Dittman 1990; Fleming 1998). Populations of most species show variable degrees of genetic differentiation and may differ in migration distance between environments (e.g., marine vs. freshwater, lakes vs. streams, rivers vs. streams: Northcote 1978; Hendry et al. 2004). Body size and shape may be related to the length and difficulty of migration (Schaffer and Elson 1975; Taylor and McPhail 1985a; Kinnison et al. 2003; Crossin et al. 2004). Parallel interpopulation differences in migration have also arisen independently in separate environments within some salmonids since the last Pleistocene glaciations (15,000–8000 years ago; Taylor et al. 1996; Waples et al. 2004). Although the presence of distinct populations in sympatry may involve multiple colonization events (i.e., an allopatric phase), such parallel patterns of differentiation imply an important role of divergent natural selection in salmonid diversification (Taylor 1999).

Three genetically distinct brook charr (*Salvelinus fontinalis*) populations inhabit Mistassini Lake (Fraser et al. 2004), a large (2150-km^2) postglacial lake in Quebec, Canada (Fig. 1). Juveniles spend 1–2 years in natal rivers and then migrate to feeding areas in the lake; once sexually mature (an additional 1–4 years), individuals migrate back to breeding areas in natal rivers to complete their life cycle. Phylogeographic work supports that outflow and two inflow river breeding populations likely originate from two different ancestral groups (Fraser and Bernatchez 2005). Nevertheless, genetic divergence between outflow and inflow populations is relatively weak (mean $F_{ST} \approx 0.10$), and based on comparisons with other studies, it seems unlikely that their degree of genetic divergence has been sufficient to cause genetic incompatibility between them (Wood and Foote 1990; Hatfield and Schluter 1999). Moreover, other populations originating from the same ancestral groups currently occupy different types of habitats (lacustrine, riverine, anadromous; Fraser and Bernatchez 2005), suggesting that their phenotypic diversity has evolved in postglacial environments (e.g., Mistassini Lake) rather than representing historical differences (Bernatchez 2004).

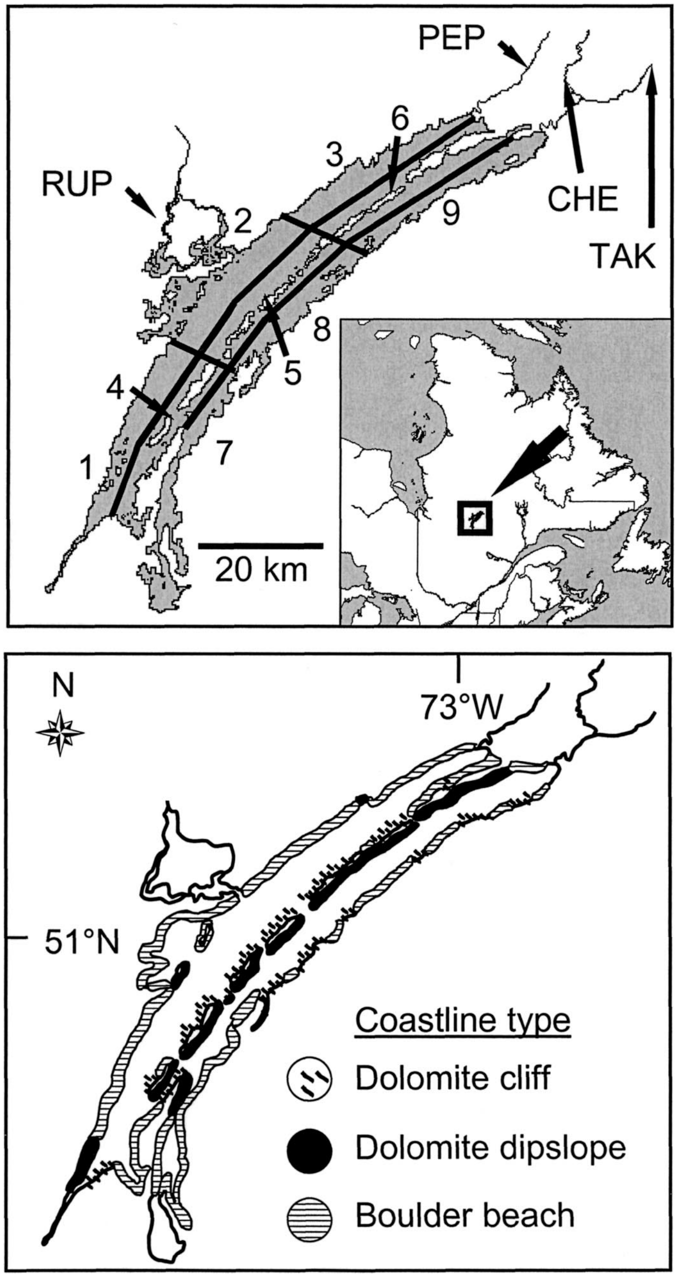

FIG. 1. Geographical locations of Mistassini Lake, Quebec, Canada (inset), the three breeding populations (inflows: Cheno, CHE; Pepeshquasati, PEP; outflow: Rupert, RUP) and the nine lake sectors defined for the spatiotemporal analyses of population migration distributions (north shore, sectors 1–3; island chain, sectors 4–6; south shore, sectors 7–9). Below is a schematic representation of coastline habitat types within the littoral zone of Mistassini Lake used in habitat selection analyses (modified from Laverdière and Guimont 1977). See Materials and Methods for details on a fourth river (Takwa, TAK).

Angler catches indicate that charr are distributed throughout Mistassini Lake in the summer at distances from natal rivers that may exceed 100 km. Thus, charr may potentially migrate hundreds of kilometers both between feeding and breeding areas and within feeding areas, but it is unclear whether populations migrate the same distances and to similar areas within the lake. However, the distance individuals migrate after entering natal rivers to breed, as well as the rate or amount of gene flow (migration rate, *m*; sensu Wright 1931), are known to vary among populations (Fraser et al. 2004). Notably, inflow populations migrate further to breeding areas (35–75 km) and at greater elevations (50–150 m) than the outflow population (0–15 km; −10–0 m). Gene flow is also higher among inflow populations than between inflows and the outflow ($m \approx 0.015$ vs. $m \approx 0.007$, respectively), even though lake shoreline distances are similar between inflows versus the outflow and one inflow (≈90 km, ≈98 km, respectively; Fig. 1).

The above patterns raise the possibility that differences in migration, both between feeding and breeding areas as well as within each, may lead to increased population divergence through adaptive evolution. To test this general hypothesis, 1166 individuals captured throughout the lake over two consecutive sampling years were first genotyped and assigned to one of the three populations. Given that we found evidence for a temporally stable, heterogeneous spatial distribution within feeding areas, we then compared phenotypic trait differentiation related to migration among populations. This was quantified based on spatial overlap, habitat selection, and migration distance in feeding areas, as well as morphology, because these traits likely affect the capacity of individuals to exploit particular resources during migration (Ehrman and Parsons 1981; Taylor and McPhail 1985a; Schluter 2000; Alerstam et al. 2003). A negative association between the extent of interpopulation differences in migration and the amount of gene flow would be consistent with the hypothesis that reduced gene flow between populations is a consequence of divergent natural selection.

MATERIALS AND METHODS

Study Site

Mistassini Lake is located in the boreal forest ecoregion of northern Quebec, Canada (50°25′N, 73°53′W). It is divided into two basins by a distinctive island chain, with basin depths reaching 100–170 m (Fig. 1). The lake is relatively unexploited, there is presently little human development in the region, and much of its shoreline is protected as part of a provincial wildlife reserve. Thus, possible confounding effects from human disturbances on population migrations (e.g., increased dispersal or changes in migration; fish: Labelle 1992; birds: Bechet et al. 2003) are likely minimal.

Migration Sampling and Genetic Analyses

We sampled adipose fin tissue from 1166 individual brook charr captured throughout feeding areas in the lake by recreational fishers and provincial government agencies during the summers (June through early September) of 2000 and 2001 ($n = 471$ and 695, respectively). The date and specific location of capture (e.g., GPS readings or longitudinal-latitudinal coordinates related to landmarks such as nearest islands and bays) were recorded for each individual. Our sampling scheme unavoidably depends on the distribution of brook charr fishing effort in the lake, yet it is reasonable to assume that there is a general correspondence between fish distribution, abundance, and fishers (Hansen and Quinn 1998; Neis et al. 1999). We stored tissue in 95% ethanol until the time of genetic analyses. Details of DNA extractions, polymerase chain reaction conditions, and electrophoresis at 10 microsatellite loci are outlined in Fraser et al. (2004).

Assignment, Exclusion, and Clustering Tests of Individuals

To examine the spatial distribution related to feeding areas among populations, we first needed to quantify the relative proportions of the three populations in lake sectors (see below). With knowledge of population allele frequencies, this can be achieved by either estimating the most likely proportion of each population in an unknown mixed sample according to its allelic composition (mixed-stock analysis; e.g., Wood et al. 1987; Utter and Ryman 1993) or by assigning each individual to its population of origin based on where its multilocus genotype is most likely to occur (e.g., assignment test; Paetkau et al. 1995; Cornuet et al. 1999), and then pooling individuals assigned to the same population to obtain proportion estimates. Potvin and Bernatchez (2001) compared estimates obtained from both methods and found them to be highly correlated ($r^2 = 0.95$, $P < 0.001$), but noted that 95% confidence intervals around estimates were narrower using assignment tests. Consequently, we employed assignment tests for our spatial distribution analyses.

We evaluated precision for assigning lake individuals to populations by using the Bayesian assignment procedure in GENECLASS (Cornuet et al. 1999) on individuals obtained during breeding periods from populations in the outflow (Rupert, RUP: $n = 178$) and two northeast inflows (Cheno, CHE: $n = 137$; Pepeshquasati, PEP: $n = 185$), and by adopting the leave-one-out method, that is, each individual was removed from the dataset, allele frequencies were recalculated, and the individual was then assigned to a population. Such assignment tests only consider the likelihood of originating from a given population. Consequently, individuals originating from more abundant populations may be misclassified to less abundant ones, especially if populations are genetically similar (Wood et al. 1987; Roques et al. 1999). This appeared to be the case between PEP and a third northeast inflow, Takwa (TAK; Fig. 1). Among other factors that suggested strongly that TAK was not a principal population (Fraser et al. 2004), TAK showed no significant genetic differentiation from PEP (despite being geographically closer to CHE), had an eight- to 25-fold lower index of catch-per-unit-effort than PEP over multiple sampling periods, and gene flow was estimated to be six times higher from PEP to TAK than vice versa. Therefore, TAK was not included in assignment tests because doing so blurred assignment success between the two principal inflow populations (CHE, PEP; Table 1A,B).

The assignment tests implemented thus far also assumed that CHE, PEP, and RUP were the only sources of lake individuals. To ensure that we were not missing any unknown sources within the lake, we employed two methods. Both of these supported the assumption that CHE, PEP, and RUP were the only sources of lake individuals (see Results). The first method involved evaluating the accuracy for excluding individuals from populations (collecting during the spawning period) by randomly generating 10,000 genotypes in each population based on their allelic frequencies and adopting a 0.05 exclusion threshold (in GENECLASS). This meant that individuals were rejected from all populations if their multilocus genotypes did not fit within the 95% highest likelihood tail of the assignment distribution in any population. To maximize exclusion precision, we included TAK ($n = 59$) for exclusion tests (Table 1C) because not doing so would risk overexcluding some individuals in the lake that had actually originated from inflow populations. We then conducted similar exclusion tests on lake individuals. A higher frequency of excluded lake individuals than excluded individuals from populations (collected during the spawning period) would be indicative of an unknown source in the lake. Any excluded lake individuals were assumed to have originated from unknown sources and were thus abandoned from further

TABLE 1. (A) Numbers of individuals (proportions in parentheses) from each breeding population correctly classified (bold) and misclassified to other breeding populations using the Bayesian assignment test of GENECLASS (Cornuet et al. 1999). Total sample sizes (*N*) for each breeding population (CHE, Cheno; PEP, Pepeshquasati; RUP, Rupert) were collected from multiple temporal replicates and pooled due to overall temporal stability in population structure to reduce error in estimations of allele frequency distributions. (B) Similar methodology including samples from Takwa River (TAK; see Materials and Methods for details). (C) Numbers of individuals (proportions in parentheses) excluded from each breeding population at the 0.05 threshold. Proportions of the individuals excluded from all breeding population samples are in the far right column.

A Reference population	Assigned to			
	CHE	PEP	RUP	*N*
CHE	**109 (0.796)**	27 (0.197)	1 (0.007)	137
PEP	38 (0.205)	**143 (0.773)**	4 (0.022)	185
RUP	3 (0.017)	2 (0.011)	**173 (0.972)**	178

B Reference population	Assigned to				
	CHE	PEP	RUP	TAK	*N*
CHE	**97 (0.708)**	16 (0.117)	1 (0.007)	23 (0.168)	137
PEP	33 (0.178)	**108 (0.584)**	2 (0.011)	42 (0.227)	185
RUP	3 (0.017)	2 (0.011)	**170 (0.955)**	3 (0.017)	178
TAK	15 (0.254)	17 (0.288)	1 (0.017)	**26 (0.441)**	59

C Reference population	Excluded from				
	CHE	PEP	RUP	TAK	Proportion
CHE	12 (0.088)	9 (0.066)	81 (0.591)	7 (0.051)	4/137 (0.029)
PEP	48 (0.259)	15 (0.081)	115 (0.622)	19 (0.103)	8/185 (0.043)
RUP	155 (0.871)	138 (0.775)	11 (0.062)	120 (0.674)	11/178 (0.062)
TAK	20 (0.339)	5 (0.085)	42 (0.712)	3 (0.051)	2/59 (0.034)

spatiotemporal analyses. Second, we evaluated whether we were missing any unknown sources in the lake by using the Bayesian clustering program STRUCTURE (Pritchard et al. 2000) to infer the number of k population clusters represented in the lake (2000 and 2001 combined). Clustering analyses were performed using three iterations each of $k = 1$ to 7 (burn-in 150,000 replications, 700,000 Markov chain Monte Carlo replicates) and an admixture model with correlated allele frequencies, because gene flow occurs among populations. Strongest likelihood support for the model $k = 3$ would confirm the existence of three populations in the lake, whereas models of $k > 3$ would provide evidence for unknown sources in the lake.

Spatial Distributions and Migration Distance

Because brook charr mainly use coastal habitat in Mistassini Lake, we divided the lake into nine approximately even shoreline distance sectors corresponding to the three major coastline areas in the lake: north shore (sectors 1–3), island chain (sectors 4–6), and south shore (sectors 7–9; Fig. 1; Table 2). With these general sectors, we could test for heterogeneity and temporal stability in spatial distributions related to feeding areas (for details on sample sizes see Table 2). This was assessed by performing a multivariate analysis of variance (MANOVA) to quantify (using Wilk's λ) the relative importance of spatiotemporal variance within the nine sectors under null hypotheses of no overall sector or sampling year effects (using SAS ver. 8.0; SAS Institute 1999; unless stated otherwise, all other statistical analyses were conducted with SAS). Sector proportions of individuals from each population (arcsine transformed) were the multiple dependent variables, with spatial effects (sector) and temporal (sampling year) effects being the independent variables.

TABLE 2. Number of brook charr individuals sampled and genotyped in each year and sector in Mistassini Lake. Sector locations are illustrated in Figure 1.

Region	Sector	Sampling year		Total
		2000	2001	
North shore	1	52	54	106
	2	115	162	277
	3	13	77	90
Island chain	4	25	46	71
	5	51	135	186
	6	103	120	223
South shore	7	49	25	74
	8	53	37	90
	9	10	39	49
Total		471	695	1166

We calculated the degree of spatial overlap between each population pair in 2000 and 2001 with Morisita's (1959) index:

$$C = \frac{2\sum_{i}^{n} p_{ij}p_{ik}}{\sum_{i}^{n} p_{ij}[(n_{ij}-1)/(N_j-1)] - \sum_{i}^{n} p_{ik}[(n_{ik}-1)/(N_k-1)]}, \qquad (1)$$

where p_{ij} is the proportion sector i is of the total sectors used by population j (p_{ik} by population k), n_{ij} and n_{ik} are the number of individuals of populations j and k, N_j and N_k are the total number of individuals of each species in the sample $\Sigma_{i=1}^{n} n_{ij} = N_j$, $\Sigma_{i=1}^{n} n_{ik} = N_k$, and C ranges from zero (no overlap) to one (complete overlap). Simulation studies comparing several spatial (niche) overlap indices have found that Morisita's

(1959) overlap index is the least biased when sample size varies (Ricklefs and Lau 1980; Smith and Zaret 1982). A higher rate of incorrect individual assignment between two populations may bias (i.e., increase) spatial overlap estimates (see Potvin and Bernatchez 2001), so we adjusted C values by correcting the numbers of fish from each population in each sector using:

$$n_{xi\,corr} = (n_{xi} \times assign_{x}) + (n_{yi} \times misassign_{xy}) + (n_{zi} \times misassign_{xz}), \quad (2)$$

where $n_{xi\,corr}$ is the corrected number of fish assigned to population x in sector i, $n_{xi} \times assign_{x}$ is the number of fish assigned to population x in sector i multiplied by the probability of correctly assigning a fish to population x, and $n_{yi} \times misassign_{xy}$ and $n_{zi} \times misassign_{xz}$ are the number of fish assigned to population y and z in sector i multiplied by the probability of incorrectly assigning a fish from population x as a fish from population y and z, respectively.

We used the mean Euclidean distances between latitudinal/longitudinal coordinates of assigned individuals and mouths of their respective river of origin as an index of mean migration distance traveled by each population in feeding areas. We compared this index among populations over sampling years, and within populations over two seasons (early summer: June to mid-July; late summer: mid-July to early September), using an analysis of variance (ANOVA). Although this index likely underestimates actual migration distances covered, as it does not account for physical barriers to intralake movement (e.g., islands), such bias would likely affect all populations equally.

Population Habitat Selection Analyses

We tested for an association between habitat selection and spatial distributions related to feeding areas. To do so, we categorized coastline habitat into three main types based on the major geomorphological characteristics of the littoral zone of Mistassini Lake from Laverdière and Guimont (1977): (1) dolomite cliff, including rocky banks and steep slopes on cuesta (ridge) fronts; (2) dolomite dipslope, including rocky banks on the gently inclined reverse side of cuestas; and (3) boulder beach (Fig. 1). We excluded a fourth habitat type (sandy beach) because it was not used by any charr and only represented 3.5% of the lake's coastline. Prior work has shown that comparable geomorphological features may be related to important composites of habitat in similar species (e.g., alimentation or predator avoidance; Nelson et al. 1992; Lamoureux et al. 2002).

At successive 10-km intervals from each population river mouth, we calculated the number of individuals assigned to that population in each of the three habitats, pooling sampling years because of temporally stable population spatial distributions (see Results), which allowed increased statistical power. We also estimated the proportion of coastline characterized by each habitat using the topographic maps (1: 50,000) of Laverdière and Guimont (1977). To account for unequal habitat availability at each distance interval, we then corrected individual counts for each habitat by dividing them by habitat proportion (following Manly et al. 1993). Corrected individual counts were retained as the dependent variable for log-linear categorical data analyses in PROC CATMOD and arranged according to three independent variables: distance (10-km distance intervals), habitat, and population. These analyses assumed that all individuals had equal capture probabilities and that individuals foraged and/or avoided predators chiefly where they were captured (at least reasonable given that recreational fishing targets foraging fish).

We used model selection based on Akaike information criterion (AIC) to allow comparisons between multiple working hypotheses related to our dependent and independent variables. Following Burnham and Anderson (1998), we calculated AIC_c (AIC corrected for small sample size) for each candidate model (see Table 5). We were especially interested in candidate models involving two-way interactions among variables, as these were often the parameters essential to addressing biologically relevant questions in our system. Namely, inclusion of the population-habitat interaction in the best-fit model would suggest that populations show differential habitat selection. Likewise, retaining of the distance-habitat interaction would suggest that habitat selection differs depending on the distance from river mouths. The value of data overdispersion ($\hat{c}$), the degree to which sampling variance exceeds model based (theoretical) variance, was estimated from the relationship χ^2/df from our most general model (see Table 5). For our data, $\hat{c} = 2.05$ ($\chi^2_{23} = 47.14$, $P = 0.002$). Thus, despite some inherent uncertainty in the choice of candidate models included, this $\hat{c}$ value indicated that our model structure was acceptable for explaining variation in the data (Burnham and Anderson 1998). Quasi-likelihood adjustments were then made using this $\hat{c}$ value to convert AIC_c to QAIC_c values to account for the remaining variance in the data unexplained by the general model. The most parsimonious fit to the data was considered as the model with the smallest QAIC_c value and the largest QAIC_c weight ($\omega\text{QAIC}_\text{c}$, the weight of evidence for each model where the sum of all model weights = 1; Burnham and Anderson 1998).

Morphological Differentiation among Populations

In 2001, we captured prespawning adult brook charr within breeding areas from each population for morphological analyses. To reduce possible effects of temporally dependent development in secondary sex characteristics before breeding (particularly in male salmonids; e.g., Fleming 1998), we sampled charr at comparable times in each river according to their different timing of migration and breeding (i.e., earlier in inflows; Fraser et al. 2004). We also analyzed sexes separately (CHE: males = 23, females = 35; PEP: males = 20, females = 36; RUP: males = 30, females = 20). We anesthetized charr with Euganol (2 mg/l) and positioned each on their right side on a measuring board with the lower jaw closed and caudal fin extended. We took whole body photographs (Nikon FE SLR camera, 50-mm lens, Fuji Sensia 100 ASA slide film) before reviving and releasing each fish. Photographs were digitally scanned before taking measurements using IMAGE J (U.S. National Institute of Health, www.rsbweb.nih.gov/ij/).

Nine traits were measured on each charr based on body depth and length and depth of posterior body sections (Fig. 2). We focused on these nine traits because they have been

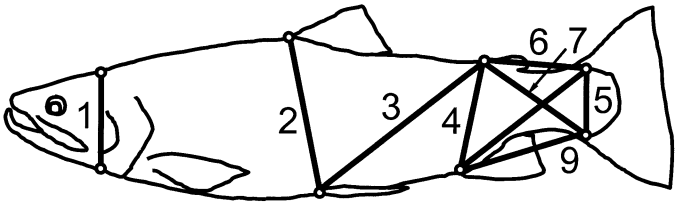

FIG. 2. Lateral view of a brook charr depicting morphological traits measured: (1) head depth (HD); (2) maximum body depth from the dorsal fin to the pelvic fin insertion (MBD); (3) distance from the pelvic fin insertion to the adipose fin insertion (PELVAD); (4) body depth from the adipose fin insertion to the anal fin insertion (BDA); (5) caudal peduncle depth (CPD); (6) distance from the adipose fin insertion to the dorsal (ADDC) and the (7) ventral (ADVC) terminus of the caudal flexure; and distance from the anal fin insertion to the (8) dorsal (ANDC) and the (9) ventral (ANVC) terminus of the caudal flexure.

associated with varying swimming performance related to migration difficulty (e.g., distance, elevation) among populations of other salmonid fishes (Taylor and McPhail 1985a; Taylor and Foote 1991; Kinnison et al. 2003). We used principal component analysis (PCA) as a multivariate approach for describing the similarities and differences among individuals based on covariation among all nine traits.

Potential Effects of Gene Flow

An alternative explanation for potential associations between interpopulation differences in migration and gene flow (m) is that these are the consequence of reduced m rather than the cause (e.g., divergent natural selection). We therefore explored under what conditions m might affect the potential for adaptive divergence in migration within populations. This was based on the quantitative model of Hendry et al. (2001, eq. 7):

$$D^*/D_\theta = (G)/[G(1 - m) + (\omega^2 + P)m], \qquad (3)$$

where D^*/D_θ is the degree of divergence constrained by gene flow for a given trait (assumed for simplicity as morphological differences on PC2 axes; see Results), G is the additive genetic variance (assumed to be $0.3P$ based on h^2 estimates for morphological traits in brook charr; G. Perry, C. Audet, and L. Bernatchez, unpubl. data), P is the phenotypic variance (assumed to be the average between populations on PC2 axes, males and females combined = 0.83), and ω is the strength of stabilizing selection within populations (fitness function width). Estimates of ω are unavailable for brook charr, so we followed Hendry et al. (2001, 2002) and used three values of ω^2 corresponding to strong ($4P$), moderate ($36P$), and weak ($100P$) stabilizing selection in nature (from $\omega^2 = -1/\gamma$, where γ is the quadratic selection gradient: see Arnold at al. 2001; Kingsolver et al. 2001). Single estimates of D^*/D_θ were calculated for RUP-CHE ($m = 0.0097$), RUP-PEP ($m = 0.0044$), and PEP-CHE ($m = 0.0147$). Values of m between populations used in our analyses originate from Fraser et al. (2004). These m values must be considered with some degree of caution because their calculation was intertwined with estimates of effective population size (N_e) in each population, which were themselves derived from a number of assumptions (Fraser et al. 2004; see also Whitlock and McCauley 1999). Nevertheless, our m values represent averages based on samples collected from three consecutive spawning periods in each river (annually between 2000 and 2002), and they overlap with the time period of this study.

RESULTS

Assignment, Exclusion, and Clustering Tests

Overall mean assignment success of individuals to populations was 84.8%, and it reached 98.0% when considering the outflow (RUP) versus the two inflows (CHE, PEP) combined (Table 1A). Most misclassifications were therefore among inflows, consistent with the higher gene flow (m) between these two populations. The proportion of lake individuals excluded from populations did not differ from that excluded in population samples collected in breeding areas ($\chi^2_1 = 2.45$, $P = 0.12$; Table 1C). Clustering analyses with STRUCTURE confirmed the lack of any major unknown population sources within lake individuals, since under the model of $k = 3$, the greatest posterior probability (> 0.90) was obtained, and individual clustering probabilities into any one k were well defined to indicate the presence of real population structuring (data not shown; Pritchard et al. 2000). This was further corroborated by support for $k = 3$ using the same methodology within population samples collected in breeding areas (outflow, RUP: $k = 1$; inflows, including TAK: $k = 2$; Fraser et al. 2004).

Temporal Stability in Population Spatial Distributions and Migration Distance

A heterogeneous spatial distribution related to feeding areas was observed among populations. Outflow (RUP) charr predominated along north shore sectors (1–3: 47.8–93.4%) and to a lesser extent in sector 4 (27.3–41.5%), yet were infrequent in all other island chain and south shore sectors (5–9: 0–16.7%; Table 3, Fig. 3). Conversely, inflow charr (CHE, PEP) were found mainly along island chain and south shore sectors (sectors 4–9: 58.6–100%; Table 3, Fig. 3). These differences in feeding areas were temporally stable, as the MANOVA indicated that variance in the spatial distribution of individual populations in the nine sectors was prominent (Wilk's $\lambda = 0.01$, $F_{24,18} = 2.75$, $P = 0.02$) relative to variance in time (sampling years), which was not significant (Wilk's $\lambda = 0.71$, $F_{3,6} = 0.80$, $P = 0.53$). Reanalysis of the MANOVA with only inflow populations (CHE, PEP) indicated no significant variance in the spatial distribution (Wilk's $\lambda = 0.21$, $F_{16,14} = 1.06$, $P = 0.46$).

In both sampling years, there was a positive association between the degree of population spatial distribution overlap (C) related to feeding areas and gene flow (m). Outflow (RUP) versus the inflow populations (CHE, PEP) had the least amount of spatial overlap and the lowest m (CHE-RUP 2000: $C = 0.173$; 2001: $C = 0.289$; mean $m = 0.0097$; PEP-RUP 2000: $C = 0.225$; 2001: $C = 0.379$; mean $m = 0.0044$). Conversely, despite the fact that shoreline distances from PEP to CHE and PEP to RUP were similar (≈90 km vs. ≈98 km), PEP and CHE had the greatest spatial overlap and highest m (2000: $C = 0.849$; 2001: $C = 0.890$; mean $m = 0.0147$).

Accordingly, there was also higher m between populations

TABLE 3. Estimated proportions (%) and 95% confidence intervals (in parentheses) assigned to Mistassini Lake brook charr populations in the nine lake sectors and two sampling years after excluded individuals were removed from analyses (inflows: CHE, Cheno; PEP, Pepeshquasati; outflow: RUP, Rupert). Sector and overall proportion estimates were taken as the binomial parameter p and bound with 95% confidence intervals (CI) following Brownlee (1965, pp. 148–149).

Sector	CHE		PEP		RUP	
	2000	2001	2000	2001	2000	2001
1	13.6 (5.2–27.2)	10.2 (3.4–22.2)	38.6 (22.6–54.5)	34.7 (21.7–49.0)	47.8 (32.3–63.6)	55.1 (40.1–69.1)
2	1.9 (0.0–6.6)	4.2 (1.6–8.8)	4.7 (1.0–9.3)	15.2 (9.8–22.2)	93.4 (88.2–97.9)	80.6 (73.1–86.6)
3	7.7 (0.0–36.0)	16.0 (8.6–26.3)	7.7 (0.0–36.0)	20.0 (11.6–31.1)	84.6 (54.6–98.1)	64.0 (52.4–75.1)
4	13.6 (2.9–34.7)	19.5 (8.8–38.7)	59.1 (36.3–79.3)	39.0 (23.8–56.0)	27.3 (10.7–49.8)	41.5 (26.5–57.4)
5	30.0 (17.8–44.9)	28.9 (21.5–37.4)	66.0 (51.7–78.6)	59.3 (50.2–68.2)	4.0 (0.0–13.7)	11.8 (6.7–18.8)
6	21.8 (14.2–30.8)	27.4 (19.5–36.9)	68.3 (58.1–77.4)	67.3 (58.0–76.1)	9.9 (4.9–17.5)	5.3 (2.0–11.2)
7	27.1 (15.2–41.9)	50.0 (29.1–70.9)	60.4 (45.5–74.0)	33.3 (15.8–55.4)	12.5 (4.7–25.2)	16.7 (4.7–37.4)
8	22.4 (11.8–36.5)	27.0 (13.9–44.1)	69.4 (54.4–81.8)	67.6 (50.2–82.0)	8.2 (2.3–19.6)	5.4 (0.7–18.2)
9	50.0 (26.3–87.8)	24.3 (11.8–41.4)	50.0 (12.2–73.7)	64.9 (47.2–79.8)	0	10.8 (3.0–25.3)
Overall	17.7 (14.6–21.5)	20.1 (17.5–23.4)	46.0 (42.6–48.7)	43.0 (39.8–45.1)	36.3 (32.5–38.9)	36.9 (34.4–38.0)

with more similar mean Euclidean migration distances in feeding areas: all populations differed in mean migration distance, but this was 3.0–3.5 times longer in inflow populations than in the outflow (Table 4). Neither sampling year nor season (early vs. late summer) had an effect on migration distance (Table 4). While there was significant variation in migration distance between populations among years and seasons, these interactions explained only 1.5% and 1.7% of the total variance compared to 95.8% explained between populations (Table 4).

Population Spatial Segregation and Differential Habitat Selection

Populations differed in lake spatial use and differed concomitantly in their use of coastline habitat in the lake, as the population-habitat interaction was retained in the best-fit model ($\omega QAIC_c > 0.999$; Table 5). Outflow (RUP) charr frequented boulder beach habitat in all but one distance interval, whereas inflow (CHE, PEP) charr were very similar in favoring dolomite cliff coastlines in most distance intervals, including at the same distance intervals as outflow charr (Fig. 4). The inclusion of the population-distance interaction in the best-fit model (Table 5) was also expected given the evidence for different population migration distances (Table 4). The inclusion of the habitat-distance interaction suggested that population habitat selection was variable with distance from river mouths. However, this only occurred at distances greater than 30–40 km than average migration distances of individual populations (see Fig. 4).

Morphological Differentiation

The first three principal components (PC1–PC3) explained 95.6% and 90.4% of the variance in male and female morphology, respectively. All correlations between the nine morphological traits were positive and of similar value along PC1, and PC1 accounted for 85.4% (males) and 72.7% (females) of the total variation (Table 6). Thus, PC1 was considered to represent overall variation in body size and subsequent principal components (PC2, PC3) were interpreted as explaining size-free variation in body shape (Jolliffe 1986).

In both sexes, PC2 contrasted characters related to body depth and caudal peduncle depth (e.g., HD, MBD, BDA, CD) with caudal region length (e.g., ADDC, ADVC, ANDC, ANVC; one-way ANOVAs: males, $F_{2,70} = 37.06$, $P < 0.001$; females $F_{2,88} = 9.04$, $P < 0.001$; Table 6). Outflow (RUP) charr had deeper bodies and caudal peduncles and shorter caudal regions than inflow charr (all Tukey's $P < 0.05$; Fig. 5: plotted as higher negative scores), whereas inflow charr did not differ in mean PC2 scores (all Tukey's $P > 0.30$; Fig. 5). PC3 (explaining 2–3 times less variation than PC2) contrasted head depth and dorsal caudal length regions (e.g., HD, ADDC, ADVC) with ventral caudal length regions (e.g., PELVAD, ANDC, ANVC; Table 6). Mean PC3 scores did not differ among populations in males ($F_{2,70} = 1.04$, $P = 0.36$), but differed in females ($F_{2,88} = 11.04$, $P < 0.001$). Outflow females had longer dorsal relative to ventral caudal regions and deeper heads (plotted as negative scores) than inflow females (all Tukey's $P < 0.05$; Fig. 5).

Potential Constraints of Gene Flow

Variable gene flow (m) among populations (RUP-CHE: $m = 0.0097$; RUP-PEP: $m = 0.0044$; PEP-CHE: $m = 0.0147$; Fraser et al. 2004) suggested that m would be more likely to constrain adaptive divergence among some populations than others. Namely, between the outflow (RUP) and each inflow population (CHE, PEP), m was estimated to constrain adaptive divergence to 87%, 46%, and 24% of its optimum (RUP-CHE) and 94%, 65%, and 40% of its optimum (RUP-PEP) if stabilizing selection was strong, moderate, and weak, respectively. Conversely, although there were overlapping intervals for estimated constraints of m on adaptive divergence between all three interpopulational comparisons, those between inflow populations (CHE, PEP) had the greatest potential impact on adaptive divergence (81% of its optimum if stabilizing selection was strong), particularly if stabilizing selection was moderate or weak (36% and 17%, respectively).

DISCUSSION

Divergent Natural Selection and Interpopulation Differences in Migration

Comparatively limited attention has been paid to ecological interactions other than associations between alternative

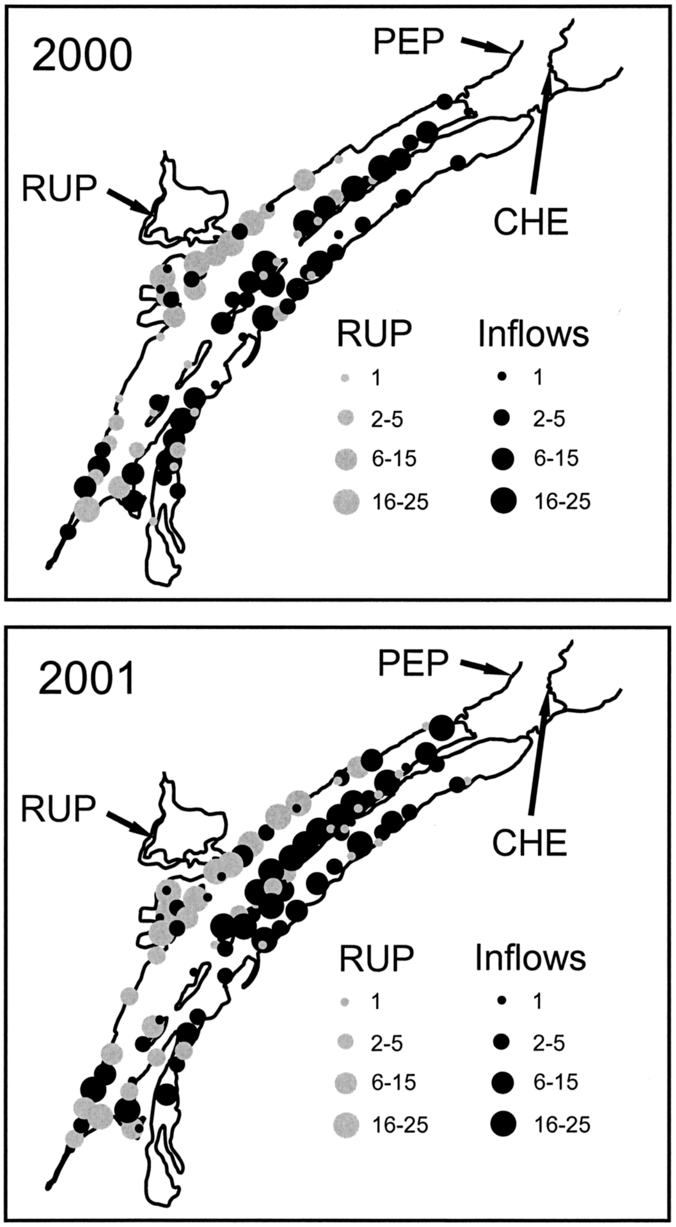

FIG. 3. Spatial representation of the numbers of fish assigned to brook charr populations (inflows: Cheno, CHE; Pepeshquasati, PEP; outflow: Rupert, RUP) among the nine lake sectors in 2000 and 2001, based on assignment tests. Both inflow populations are denoted in black because their spatial distributions did not differ from one another in either year. The size of the circles within legends is proportional to the number of individuals assigned to populations at each sampling location.

trophic resources and morphological specialization in studies of phenotypic diversity and divergent natural selection (Schluter 2000). Our study provided evidence for a temporally stable, heterogeneous spatial distribution in feeding areas during migration among sympatric brook charr populations. We then compared interpopulation differences in migration among populations (spatial overlap, habitat selection, and migration distance within feeding areas, as well as morphology). A match between such differences and the heterogeneous spatial distribution in feeding areas observed would lend support to an adaptive basis for the former (Schluter 2000). In addition, a negative association between the extent interpopulation differences in migration and the amount of gene flow would provide evidence that reduced gene flow between populations is a consequence of divergent natural selection (Schluter 2000, 2001).

The data on interpopulation differences in migration and gene flow among Mistassini Lake brook charr populations were consistent with these expectations. First, the amount of gene flow was lowest between populations having more spatial segregation related to feeding areas during migration, and this was independent of the shoreline distance between rivers where each population breeds. The extent of spatial segregation among populations was also related to a phenotype-environment association for differential habitat selection. Exploitation of different habitats upon expansion into novel resource (e.g., postglacial) environments is considered an adaptive behavioral response for alleviating competitive interactions in the initial stages of population divergence (Ehrman and Parsons 1981; Diamond 1986; Schluter 2000). Habitat selection is also thought to be critical for matching locally adapted phenotypes within heterogeneous landscapes (Davis and Stamps 2004). Furthermore, a genetic basis for habitat selection has previously been demonstrated in various taxa (e.g., mammals: Harris 1952; invertebrates: Doyle 1976; Ehrman and Parsons 1981, references therein), including in other salmonid fishes (Skulason et al. 1993; Rogers et al. 2002). For example, dwarf and normal ecotypes of lake whitefish (*Coregonus clupeaformis*) occupy divergent habitats in the upper (limnetic zone) and lower (benthic zone) water column, respectively, of several North American postglacial lakes (Rogers et al. 2002). Laboratory-bred fish from both ecotypes, having had no previous experience with either natural habitat, showed depth preferences for the type of habitat usually inhabited in nature, and F_1 hybrids were intermediate in depth use (Rogers et al. 2002).

Morphological variation among Mistassini Lake brook charr populations was also consistent with a probable phenotype-environment association. Notably, long-distance feeding migrants of inflow populations were more streamlined with longer caudal regions than short-distance migrants of the outflow. In addition, after entering natal rivers to breed, inflow charr also migrated longer distances (35–75 km) and at greater elevations (50–150 m) to breeding areas than outflow charr (0–15 km; −10–0 m). Overall, a streamlined body form reduces drag during swimming, while a longer caudal region facilitates prolonged swimming (Webb 1984a,b; Taylor and McPhail 1985a; Taylor and Foote 1991). Such phenotypic attributes presumably would increase energetic efficiency for longer and more difficult migrations in inflow charr. This may be critical because migration distance and difficulty have been experimentally shown to affect reproductive success in salmonids. For instance, Kinnison et al. (2001, 2003) inferred differences in migratory costs for Chinook salmon families (*Oncorhynchus tshawychwa*) at distances (17 km vs. 100 km) and elevations (17 m vs. 430 m) within natal rivers comparable to those that divergent Mistassini Lake populations undertake between feeding and breeding areas and within feeding areas. In both males and

TABLE 4. Significance of population of origin and independent variables (sampling year, season: early vs. late summer, i.e., June through mid-July vs. mid-July through early September) on migration distance for Mistassini Lake brook charr based on ANOVA. % MS (mean square) represents the percentage of variance explained by each effect (each effect MS divided by the sum of all effect MS). Means (in kilometers ± 1 SE) for all significant independent variables are shown, with asterisks denoting significant a posteriori comparisons (Tukey test: single variables; contrasts: interaction terms) at the $P = 0.05$ level.

Effect	F	df	P-value	% MS	Effect means
Population	258.37	2	<0.0001	95.82	CHE: 69.6 (±2.1)* PEP: 63.5 (±1.4)* RUP: 21.8 (±1.5)*
Sampling year	1.73	1	0.19	0.64	
Season (early vs. late summer)	0.73	1	0.39	0.27	
Population × sampling year	4.15	2	0.02	1.54	CHE 2000 vs. 2001: 71.5 (±3.9) vs. 68.4 (±2.6) PEP 2000 vs. 2001: 68.2 (±2.2) vs. 60.0 (±1.8)* RUP 2000 vs. 2001: 20.5 (±2.2) vs. 22.7 (±1.5)
Population × season	4.67	2	0.01	1.73	CHE early vs. late: 68.4 (±2.6) vs. 71.2 (±3.5) PEP early vs. late: 62.8 (±2.0) vs. 64.2 (±2.3) RUP early vs. late: 27.3 (±2.1) vs. 18.2 (±1.5)*

females, the longer migration led to reductions in somatic energy reserves for reproduction. The longer migration also led to a reduction in ovarian mass and egg size in females, and reduced dorsal hump size (related to body depth) and upper jaw length in males, all of which are traits related to reproductive output, competitive ability, or mating success in salmonids (Kinnison et al. 2001, 2003).

Similar interpopulation differences in morphology to those observed in Mistassini Lake (e.g., streamlined long caudal region vs. deep-bodied short caudal region) are also genetically based in other migratory salmonids (Taylor and McPhail 1985a; Hawkins and Quinn 1996), including brook charr (G. Perry, unpubl. data). In addition, analogous dichotomies in migration distance between breeding and nonbreeding (e.g., feeding or wintering) areas have been observed within other species. For example, in some bird species that migrate between northern breeding areas and southern wintering areas, the populations breeding at the highest latitudes also winter at the lowest latitudes, thus bypassing more intermediate latitude areas used by other populations (termed ‘‘leap-frog migrations’’: Salomonsen 1955; Pienkowski et al. 1985). Likewise, ocean-type and stream-type Chinook salmon (*Oncorhynchus tshawychwa*) populations generally migrate shorter and longer distances to breeding areas after entering natal rivers, respectively, but ocean-types do not migrate as far from coastal shelf areas within oceanic feeding areas as stream-types (Healey 1983; Waples et al. 2004). Thus, similar interpopulation differences in migration may be selected along parallel ecological axes in a variety of species, in part perhaps because of a compromise in the suites of traits necessary for meeting energetic demands and life-history trade-offs at different migratory life-history stages (Dingle 1996; see below).

Coadapted Life-History Traits and Migration

Seasonal timing of migration and breeding are considered critical life-history traits, as they allow locally adapted individuals to maximize fitness in their environments (fish: Quinn et al. 2000; birds: Hatchwell 1991; insects: Ohgushi 1991). Inflow charr migrate back to natal rivers earlier and tend to breed earlier than outflow charr (Fraser et al. 2004). In other salmonid fishes, variation in migration and breeding timing often has a strong genetic component (Quinn and Adams 1996; Quinn et al. 2000; Bentzen et al. 2001) and is thought to evolve to compensate for environmental conditions such as flow and temperature (Quinn and Adams 1996). In addition to spatially discrete breeding grounds, such temporal breeding differences may further limit gene flow among Mistassini Lake brook charr populations, particularly between inflow and outflow populations.

Life-history theory also predicts that trade-offs between migration, growth, and age at breeding will be optimized to maximize individual fitness in populations (Roff 1992; Dodson 1997). Long-distance inflow migrants were older (4.18 years vs. 3.56 years) and larger (509 mm vs. 464 mm) at maturity than short-distance outflow migrants (Fraser et al. 2004). Yet, variance in breeding age was lower overall in inflows, as was the body size of all fish sampled over three years in breeding areas, and we found no evidence for dif-

TABLE 5. The five best-fit models among the initial candidate model set, and the most general model (in bold) for habitat selection analyses among brook charr populations based on $QAIC_c$, with an overdispersion correction factor of $\hat{c} = 2.05$. Shown for each model are the variables retained, the relative differences (Δ) in model $QAIC_c$ values, parameter number (k), and the model's $QAIC_c$ weight relative to all other models ($\omega QAIC_c$). Pop, population (Cheno, Pepeshquasati, Rupert); hab, habitat (dolomite cliff, dolomite dipslope, boulder beach); dist, successive 10-km distance intervals from river mouths.

Best-fit model	$\Delta QAIC_c$	k	$\omega QAIC_c$
Pop, hab, dist, pop × hab, pop × dist, hab × dist	**0.00**	**74**	**>0.999**
Pop, hab, dist, pop × dist, hab × dist	32.54	70	<0.001
Pop, hab, dist, pop × hab, pop × dist	34.55	48	<0.001
Pop, hab, dist, pop × dist	93.03	44	<0.001
Pop, hab, dist, pop × hab, hab × dist	101.86	48	<0.001

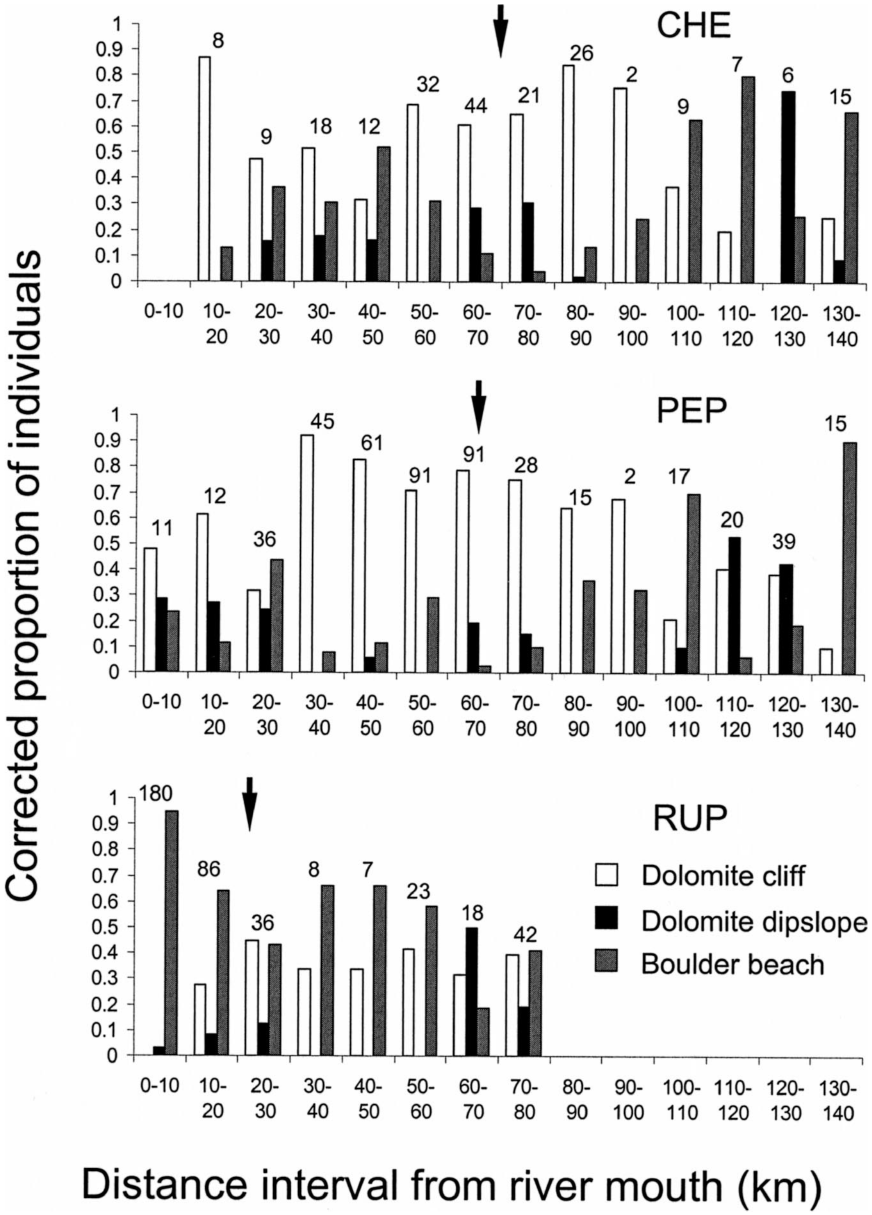

FIG. 4. Summary of population habitat selection at differing distance intervals from river mouths. Sample sizes represented within each distance interval are denoted above each distance interval. Arrows indicate the index of mean migration distance from river mouths in each population (inflows: Cheno, CHE; Pepeshquasati, PEP; outflow: Rupert, RUP).

TABLE 6. Summary of principal component analysis loadings of morphological variation among brook charr populations. Morphological trait definitions are provided in Figure 2.

	Males			Females		
Morphological character	PC1	PC2	PC3	PC1	PC2	PC3
1 (HD)	0.325	−0.198	0.657	0.337	−0.187	0.605
2 (MBD)	0.338	−0.348	−0.034	0.340	−0.127	−0.014
3 (PELVAD)	0.337	−0.245	−0.419	0.351	−0.003	−0.561
4 (BDA)	0.340	−0.344	−0.044	0.319	−0.684	−0.117
5 (CD)	0.336	−0.286	−0.057	0.335	−0.148	0.065
6 (ADDC)	0.312	0.517	0.314	0.340	0.238	0.251
7 (ADVC)	0.341	0.219	0.273	0.365	0.174	0.286
8 (ANDC)	0.329	0.394	−0.344	0.354	0.204	−0.320
9 (ANVC)	0.338	0.331	−0.309	0.374	0.224	−0.231
% Variance accounted for	85.41	7.75	2.41	72.66	11.37	6.34

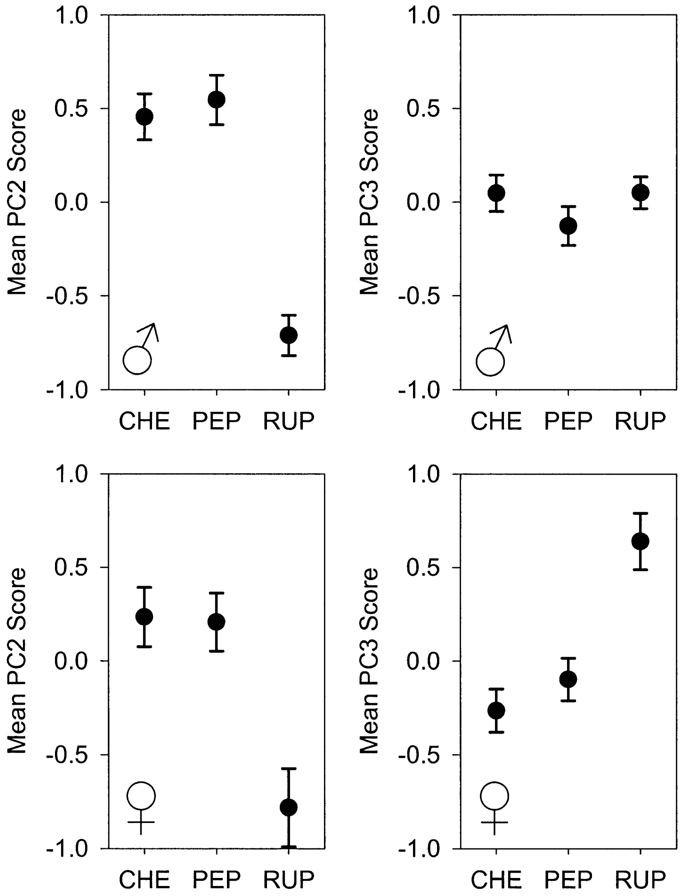

FIG. 5. Mean PC2 and PC3 scores (±1 SE) of morphological variation for male and female brook charr among Mistassini lake populations (inflows: Cheno, CHE; Pepeshquasati, PEP; outflow: Rupert, RUP).

ferent growth rates among populations (D. Fraser, unpubl. data). Although future research should incorporate information on age-specific rates of survival (e.g., Hutchings 1993), these results and observations imply that postbreeding survival, and thus iteroparity (repeat breeding), may be lower in charr from inflows than the outflow. In salmonids, longer migrations can result in lower postbreeding adult survival, and the energy lost in breeding is more difficult to regain for larger fish (Crespi and Teo 2002 and references therein). Thus, delayed reproduction in long-distance inflow migrants could maximize fitness benefits by conferring a larger body size that swims more efficiently (Brett and Glass 1973) for upstream migration and that increases reproductive output (e.g., fecundity; Schaffer and Elson 1975) for their stronger probability of breeding only once.

The Role of Selection versus Gene Flow on Divergence or Other Mechanisms

We have considered that reduced gene flow (m) among sympatric brook charr populations is a consequence of divergent natural selection leading to interpopulation differences in migration. However, this does not rule out the possibility that other mechanisms play a role in population divergence within this system.

Interpopulation differences in migration may also be limited by higher m, such that these may be a consequence of reduced m rather than a cause (Endler 1977; Storfer and Sih 1998; Hendry et al. 2001, 2002; Hendry and Taylor 2004; Nosil and Crespi 2004). Overall, the analysis we used to explore this possibility (albeit with a number of assumptions and imprecise parameter estimates) suggested that adaptive interpopulation differences in migration likely reflected a balance between divergent natural selection and gene flow. However, m may only have had appreciable effects between certain populations in Mistassini Lake. For instance, selection was more likely to be responsible for much of the differentiation between the outflow and two inflows. First, inflows differed little in morphology despite variable m with the outflow (0.0097 vs. 0.0044, respectively). Second, there was no association between shoreline distance among populations and the amount of gene flow. Third, inflow charr are more abundant than outflow charr, based on estimated proportions of charr assigned to each population in this study and estimates of effective population size (N_e) from Fraser et al. (2004). Thus, simply because a larger number of individuals likely emigrate from inflows, we might have expected less differentiation between the outflow and two inflows if m constrains adaptive divergence. In contrast, our data suggested that both smaller differences in selective pressures (or regime) and higher m are likely responsible for migration similarities between the two inflow populations. Gene flow may especially constrain adaptive divergence within Cheno, as Fraser et al. (2004) found evidence for higher m from Pepeshquasati to Cheno than vice versa. Future investigation into the effects of interpopulation differences in migration on ecologically dependent postmating isolation (i.e., reduced hybrid fitness: Rundle and Whitlock 2001; Kirkpatrick 2001) would provide more insight into the role of divergent natural selection in reducing gene flow.

Studies on salmonids have documented a genetic basis for many of the traits related to migration considered here, but these traits also have an important environmental component (their heritabilities are typically 0.1–0.5; Roff 1992). Additional research on this system must confirm the genetic basis of interpopulation differences in migration and consider the role of adaptive phenotypic plasticity, as such plasticity may have been favored within newly formed postglacial lake environments (Robinson and Parsons 2002; Hutchings 2004). Likewise, alternative explanations for the divergent morphology among populations must be ruled out before the nature of relationships between body form and migration can be confirmed. This might involve collecting data on predation regimes of Mistassini populations, since a deeper-bodied form (e.g. outflow charr) in juvenile salmonids can reduce vulnerability to predation via increased burst swimming performance or difficulty in handling (Taylor and McPhail 1985b and references therein). Finally, because inflow and outflow populations likely do not originate from a common ancestor, interactions between the colonization timing and direction of ancestral lineages and aspects of the habitat landscape may have affected and/or may continue to affect the evolutionary mode of interpopulation differences in migration among populations in sympatry (Fraser and Bernatchez 2005).

Evolutionary and Conservation Implications

Breeding and nonbreeding areas within migratory life cycles are necessarily linked (Webster et al. 2002 and references therein). However, the evolutionary implications of these links in the context of population divergence and adaptive evolution remain poorly understood. The results of this study and those of Fraser et al. (2004) expand on previous studies of migration by showing a negative association between the extent of interpopulation differences in migration over the entire life cycle (both between breeding and nonbreeding areas, as well as within each) and the amount of gene flow among brook charr populations. The predictable patterns of intraspecific divergence within this postglacial lake may be relevant for elucidating how interpopulation differences in migration arise in other migratory species where there is pronounced gene flow (birds: Berthold 1988; Scribner et al. 2003; mammals: Baker 1978 and references therein; invertebrates: Dingle et al. 1980; McAnelly 1985). They may also make clear the habitats necessary for preserving or rehabilitating different populations at various life-cycle stages. With respect to migratory salmonids, for example, factors leading to intraspecific divergence within breeding areas have been extensively studied, whereas much less is known of nonbreeding areas (e.g., feeding areas). Main features of our study are the implication of an adaptive component to links between breeding and feeding areas in intraspecific salmonid populations, as well as the evidence that these may shape other aspects of population structuring and evolution (see also Weitcamp et al. 1995; Potvin and Bernatchez 2001; Waples et al. 2004). Whether selection on coadapted traits for migration enhances directly or indirectly the same traits associated with premating isolation (Rice and Hostert 1993; Schluter 2001) will require further study. That these mechanisms may act differently or synergistically at successive life-cycle stages in migratory species reaffirms the value of a comprehensive approach to studying phenotypic diversity and divergence.

ACKNOWLEDGMENTS

We are indebted to A. Calvert, M. Boulet, S. Rogers, D. Veliz, P. Duchesne, S. McCairns, M. M. Hansen, M.-C. Cadieux, N. Lecomte, and G. Perry for discussions throughout manuscript preparation. Comments from G. Orti and two anonymous reviewers thoroughly improved the manuscript. Field sampling funding and help was provided by Cree Nation of Mistissini, Grand Council of the Crees of Québec, Barrette Chapais Ltd., Camp Louis Joliet, Eeyou Namess Corp., Osprey Excursions Reg'd, Réserves Fauniques Assinica et des Lacs-Albanel-Mistassini-et-Waconichi, Ministère des Resources naturelles (Québec), E. Awashish, B. Coon, R. Dion, P. P. Dupont, D. Iserhoff, M. Jimikin, N. Leclerc, J. Loon, R. Loon, M. Prince, and D. Mianscum, L. Mianscum, and S. Mianscum. We also thank C. Lippé for laboratory assistance. Research funding was provided by the Natural Science and Engineering Research Council of Canada (NSERC, Genomic program) to LB, and by NSERC Postgraduate and Northern Research Scholarships and Le Fonds Écologique Anne Vallée to DJF.

LITERATURE CITED

Abrams, P. A. 2000. Character shifts of prey species that share predators. Am. Nat. 156:S4–S16.

Alerstam, T., A. Hedenstrom, and S. Akesson. 2003. Long-distance migration: evolution and determinants. Oikos 103:247–260.

Arnold, S J., M. E. Pfrender, and A. G. Jones. 2001. The adaptive landscape as a conceptual bridge between micro- and macroevolution. Genetica 112–113:9–32.

Baker, R. R. 1978. The evolutionary ecology of animal migration. Hodder and Stoughton, London.

Bechet, A., J. F. Giroux, G. Gauthier, J. D. Nichols, and J. E. Hines. 2003. Spring hunting changes the regional movements of migrating greater snow geese. J. Appl. Ecol. 40:553–564.

Bensch, S., T. Andersson, and S. Akesson. 1999. Morphological and molecular variation across a migratory divide in willow warblers, *Phylloscopus trochilus*. Evolution 53:1925–1935.

Bentzen, P., J. B. Olsen, J. E. McLean, T. R. Seamons, and T. P. Quinn. 2001. Kinship analysis of Pacific salmon, insights into mating, homing, and timing of reproduction. J. Hered. 92: 127–136.

Bernatchez, L. 2004. Ecological theory of adaptive radiation: an empirical assessment from Coregonine fishes (Salmoniformes). Pp. 175–207 *in* A. P. Hendry and S. C. Stearns, eds. Evolution illuminated: salmonids and their relatives. Oxford Univ. Press, New York.

Berthold, P. 1988. Evolutionary aspects of migratory behavior in European warblers. J. Evol. Biol. 1:195–209.

Berthold, P., A. J. Helbig, G. Mohr, and U. Querner. 1992. Rapid microevolution of migratory behaviour in a wild bird species. Nature 360:668–670.

Brett, J. R., and N. R. Glass. 1973. Metabolic rates and critical swimming speeds of sockeye salmon (*Oncorhynchus nerka*) in relation to body size and temperature. J. Fish. Res. Board Can. 30:379–387.

Brownlee, K. A. 1965. Statistical theory and methodology in science and engineering. John Wiley, New York.

Burnham, K. P., and D. R. Anderson. 1998. Model selection and inference: a practical information-theoretic approach. Springer Verlag, New York.

Choinière, L., and G. Gauthier. 1995. Energetics of reproduction in female and male greater snow geese. Oecologia 103:379–389.

Cornuet, J.-M., S. Piry, G. Luikart, A. Estoup, and M. Solignac. 1999. New methods employing multilocus genotypes to select or exclude populations as origins of individuals. Genetics 153: 1989–2000.

Crespi, B. J., and R. Teo. 2002. Comparative phylogenetic analysis of the evolution of semelparity and life history in salmonid fishes. Evolution 56:1008–1020.

Crossin, G. T., S. G. Hinch, A. P. Farrell, D. A. Higgs, A. G. Lotto, J. D. Oakes, and M. C. Healey. 2004. Energetics and morphology of sockeye salmon: effects of upriver migratory distance and elevation. J. Fish Biol. 65:788–810.

Davis, J. M., and J. A. Stamps. 2004. The effect of natal experience on habitat preferences. Trends Ecol. Evol. 19:411–416.

Diamond, J. 1986. Evolution of ecological segregation in the New Guinea montane avifauna. Pp. 98–125 *in* J. Diamond and T. J. Case, eds. Case community ecology. Harper and Rowe, New York.

Dingle, H. 1994. Genetic analyses of animal migration. Pp. 145–164 *in* C. R. B. Boake, ed. Quantitative genetic studies of behavioral evolution. Univ. of Chicago Press, Chicago.

———. 1996. Migration: the biology of life on the move. Oxford Univ. Press, New York.

Dingle, H., N. R. Blakley, and E. R. Miller. 1980. Variation in body size and flight performance in milkweed bugs (*Oncopeltus*). Evolution 34:371–385.

Dobzhansky, T. 1946. Complete reproductive isolation between two morphologically similar species of *Drosophila*. Ecology 27: 205–211.

Dodson, J. J. 1997. Fish migration: an evolutionary perspective. Pp. 10–36 *in* J. D. J. Godin, ed. Behavioural ecology of teleost fishes. Oxford Univ. Press, New York.

Doyle, R. S. 1976. Analysis of habitat loyalty and habitat preference in the settlement behavior of planktonic marine larvae. Am. Nat. 110:719–730.

Ehrman, L., and P. A. Parsons. 1981. Behavior genetics and evolution. McGraw-Hill, New York.

Endler, J. A. 1977. Geographic variation, speciation, and clines. Princeton Univ. Press, Princeton, NJ.

Fleming, I. A. 1998. Pattern and variability in the breeding system of Atlantic salmon (*Salmo salar*) with comparisons to other salmonids. Can. J. Fish. Aquat. Sci. 55(Suppl. 1):59–76.

Fraser, D. J., and L. Bernatchez. 2005. Allopatric origins of sympatric brook charr populations: Colonization history and admixture. Mol. Ecol. *In press*.

Fraser, D. J., C. Lippé, and L. Bernatchez. 2004. Consequences of unequal population size, asymmetric gene flow and sex-biased dispersal on population structure in brook charr (*Salvelinus fontinalis*). Mol. Ecol. 13:67–80.

Grant, B. R., and P. R. Grant. 1990. Natural selection in a population of Darwin's finches. Am. Nat. 133:377–393.

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

Hansen, L. P., and T. P. Quinn. 1998. The marine phase of the Atlantic salmon (*Salmo salar*) life cycle, with comparisons to Pacific salmon. Can. J. Fish. Aquat. Sci. 55(Suppl. 1):104–118.

Harris, V. T. 1952. An experimental study of habitat selection by prairie and forest races of the deermouse *Peromyscus maniculatus*. Contrib. Lab. Vertebr. Biol. Univ. Mich. 56:1–53.

Hatchwell, B. J. 1991. An experimental study of the effects of timing of breeding on the reproductive success of common guillemots (*Uria aalge*). J. Anim. Ecol. 60:721–737.

Hatfield, T., and D. Schluter. 1999. Ecological speciation in sticklebacks: environment-dependent fitness. Evolution 53:866–873.

Hawkins, D. K., and T. P. Quinn. 1996. Critical swimming velocity and associated morphology of juvenile coastal cutthroat trout (*Oncorhynchus clarki clarki*), steelhead trout (*Oncorhynchus mykiss*), and their hybrids. Can. J. Fish. Aquat. Sci. 53:1487–1496.

Healey, M. C. 1983. Coastwide distribution and ocean migration patterns of stream- and ocean-type Chinook salmon, *Oncorhynchus tshawytscha*. Can. Field Nat. 97:427–433.

Hendry, A. P., and E. B. Taylor. 2004. How much of the variation in adaptive divergence can be explained by gene flow? An evaluation using lake-stream stickleback pairs. Evolution 58: 2319–2331.

Hendry, A. P., T. Day, and E. B. Taylor. 2001. Population mixing and the adaptive divergence of quantitative traits in discrete populations: a theoretical framework for empirical tests. Evolution 55:459–466.

Hendry, A. P., E. B. Taylor, and J. D. McPhail. 2002. Adaptive divergence and the balance between selection and gene flow: lake and stream stickleback in the Misty system. Evolution 56: 1199–1216.

Hendry, A. P., T. Bohlin, B. Jonsson, and O. K. Berg. 2004. To sea or not to sea? Anadromy vs. non-anadromy in salmonids. Pp. 92–126 *in* A. P. Hendry and S. C. Stearns, eds. Evolution illuminated: salmonids and their relatives. Oxford Univ. Press, New York.

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

———. 2004. Norms of reaction and phenotypic plasticity in salmonid life-histories. Pp. 154–174 *in* A. P. Hendry and S. C. Stearns, eds. Evolution illuminated: salmonids and their relatives. Oxford Univ. Press, New York.

Jolliffe, I. T. 1986. Principal component analysis. Springer, New York.

Kinnison, M. T., M. J. Unwin, A. P. Hendry, and T. P. Quinn. 2001. Migratory costs and the evolution of egg size and number in introduced and indigenous salmon populations. Evolution 55: 1656–1667.

Kinnison, M. T., M. J. Unwin, and T. P. Quinn. 2003. Migratory costs and contemporary evolution of reproductive allocation in male Chinook salmon. J. Evol. Biol. 16:1257–1269.

Kingsolver, J. G., H. E. Hoekstra, J. M. Hoekstra, D. Berrigan, S. N. Vignieri, C. E. Vignieri, C. E. Hill, A. Hoang, P. Gibert, and P. Beerli. 2001. The strength of phenotypic selection in natural populations. Am. Nat. 157:245–261.

Kirkpatrick, M. 2001. Reinforcement during ecological speciation. Proc. R. Soc. Lond. Biol. Ser. B 268:1259–1263.

Labelle, M. 1992. Straying patterns of coho salmon (*Oncorhynchus kisutch*) from southeast Vancouver Island, British Columbia. Can. J. Fish. Aquat. Sci. 49:1843–1855.

Lamouroux, N., N. LeRoy, and P. L. Angermeier. 2002. Intercontinental convergence of stream fish community traits along geomorphic and hydraulic gradients. Ecology 83:1792–1807.

Laverdière, C., and P. Guimont. 1977. Le littoral des lacs Albanel et Mistassini. Rapport de reconnaissance. Société de Développement de la Baie James, Montreal, Canada.

Lu, G., and L. Bernatchez. 1999. Correlated trophic specialization and genetic divergence in sympatric lake whitefish ecotypes (*Coregonus clupeaformis*): support for the ecological speciation hypothesis. Evolution 53:1491–1505.

Manly, B. F. J., L. L. McDonald, and D. L. Thomas. 1993. Resource selection by animals: statistical design and analysis for field studies. Chapman and Hall, London.

McAnelly, M. L. 1985. The adaptive significance and control of migratory behavior in the grasshopper *Melanoplus sanguinipes*. Pp. 687–703 *in* M. A. Q. Rankin, ed. Migration: mechanisms and adaptive significance. Contributions to Marine Science no. 27 (Suppl.). University of Texas Marine Science Institute, Austin, TX.

Morisita, M. 1959. Measuring interspecific association and similarity between communities. Mem. Fac. Sci. Kyushu Univ. Ser. E Biol. 3:65–80.

Neis, B., D. C. Schneider, L. Felt, R. L. Haedrich, J. Fischer, and J. A. Hutchings. 1999. Fisheries assessment: What can be learned from interviewing resource users? Can. J. Fish. Aquat. Sci. 56: 1949–1963.

Nelson, R. L., W. S. Platts, D. P. Larsen, and S. E. Jensen. 1992. Trout distribution and habitat in relation to geology and geomorphology in the North Fork Humboldt River drainage, northeastern Nevada. Trans. Am. Fish. Soc. 121:405–426.

Northcote, T. G. 1978. Migratory strategies and production of freshwater fishes. Pp. 326–359 *in* S. D. Gerking, ed. Ecology of freshwater fish production. John Wiley and Sons, New York.

Nosil, P., and B. J. Crespi. 2004. Does gene flow constrain adaptive divergence or vice versa? A test using ecomorphology and sexual isolation in *Timema cristinae* walking-sticks. Evolution 58: 102–112.

Ohgushi, T. 1991. Lifetime fitness and evolution of reproductive patterns in the herbivorous lady beetle. Ecology 72:2110–2122.

Paetkau, D., W. Calvert, I. Stirling, and C. Strobeck. 1995. Microsatellite analysis of population structure in Canadian polar bears. Mol. Ecol. 4:347–354.

Palmer, J. O., and H. Dingle. 1986. Direct and correlated responses to selection among life-history traits in milkweed bugs (*Oncopeltus fasciatus*). Evolution 40:767–777.

Pienkowski, M. W., P. R. Evans, and D. J. Townshend. 1985. Leapfrog and other migration patterns of waders: a critique of the Alerstam and Hogstedt hypothesis, and some alternatives. Ornis Scand. 16:61–70.

Potvin, C., and L. Bernatchez. 2001. Lacustrine spatial distribution of landlocked Atlantic salmon populations assessed across generations by multilocus individual assignment and mixed-stock analyses. Mol. Ecol. 10:2375–2388.

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

Quinn, T. P., and D. J. Adams. 1996. Environmental changes affecting the migratory timing of American shad and sockeye salmon. Ecology 77:1151–1162.

Quinn, T. P., and A. H. Dittman. 1990. Pacific salmon migrations and homing: mechanisms and adaptive significance. Trends Ecol. Evol. 5:174–177.

Quinn, T. P., M. J. Unwin, and M. T. Kinnison. 2000. Evolution of temporal isolation in the wild: genetic divergence in timing of migration and breeding by introduced chinook salmon populations. Evolution 54:1372–1385.

Raleigh, R. F. 1971. Innate control of migrations of salmon and trout fry from natal gravels to rearing areas. Ecology 52: 291–297.

Rasmuson, B., M. Rasmuson, and J. Nygren. 1977. Genetically controlled differences in behavior between cycling and noncycling populations of field voles (*Microtus agrestis*). Hereditas 87:33–42.

Rice, W. R., and E. E. Hostert. 1993. Laboratory studies on speciation: What have we learned in 40 years? Evolution 47: 1637–1653.

Ricklefs, R. E., and M. Lau. 1980. Bias and dispersion of overlap indices: results of some Monte Carlo simulations. Ecology 61: 1019–1024.

Robinson, B. W., and K. J. Parsons. 2002. Changing times, spaces, and faces: tests and implications of adaptive morphological plasticity in the fishes of northern postglacial lakes. Can. J. Fish. Aquat. Sci. 59:1819–1833.

Roff, D. A. 1992. The evolution of life histories: theory and analysis. Chapman and Hall, New York.

Rogers, S. M., V. Gagnon, and L. Bernatchez. 2002. Genetically based phenotype association for swimming behavior in lake whitefish ecotypes (*Coregonus clupeaformis* Mitchill). Evolution 56:2322–2329.

Roques, S., P. Duchesne, and L. Bernatchez. 1999. Potential of microsatellites for individual assignment: the North Atlantic redfish (genus *Sebastes*) species complex as a case study. Mol. Ecol. 8:1703–1707.

Rundle, H. D., and M. C. Whitlock. 2001. A genetic interpretation of ecologically dependent isolation. Evolution: 55:198–201.

Salomonsen, F. 1955. The evolutionary significance of bird migration. Dan. Biol. Medd. 22:1–62.

Sandberg, R., and F. R. Moore. 1996. Fat stores and arrival on the breeding grounds: reproductive consequences for passerine migrants. Oikos 77:577–581.

SAS Institute. 1999. SAS version 8.0. SAS Institute, Inc., Cary, NC.

Schaffer, W. M., and P. F. Elson. 1975. The adaptive significance of variations in life history among local populations of Atlantic salmon in North America. Ecology 56:577–590.

Schluter, D. 2000. The ecology of adaptive radiation. Oxford series in Ecology and Evolution. Oxford Univ. Press, New York.

———. 2001. Ecology and the origin of species. Trends Ecol. Evol. 16:372–380.

Scribner, K. T., R. A. Malecki, B. D. J. Batt, R. L. Inman, S. Libants, and H. H. Prince. 2003. Identification of source population for Greenland Canada geese: genetic assessment of a recent colonization. Condor 103:771–782.

Skulason, S., S. S. Snorrason, D. Ota, and D. L. G. Noakes. 1993. Genetically based differences in foraging behaviour among sympatric morphs of arctic charr (Pisces: Salmonidae). Anim. Behav. 45:1179–1192.

Smith, E. P., and T. M. Zaret. 1982. Bias in estimating niche overlap. Ecology 63:1248–1253.

Storfer, A., and A. Sih. 1998. Gene flow and ineffective antipredator behavior in a stream-breeding salamander. Evolution 52: 558–565.

Taylor, E. B. 1999. Species pairs of north temperate freshwater fishes: taxonomy, evolution, and conservation. Rev. Fish Biol. Fish. 9:299–324.

Taylor, E. B., and C. J. Foote. 1991. Critical swimming velocities of juvenile sockeye salmon and kokanee, the anadromous and non-anadromous forms of *Oncorhynchus nerka* (Walbaum). J. Fish Biol. 38:407–419.

Taylor, E. B., and J. D. McPhail. 1985a. Variation in body morphology among British Columbia populations of coho salmon, *Oncorhynchus kisutch*. Can. J. Fish. Aquat. Sci. 42:2020–2029.

———. 1985b. Variation in burst and prolonged swimming performance among British Columbia populations of coho salmon, *Oncorhynchus kisutch*. Can. J. Fish. Aquat. Sci. 42:2029–2033.

Taylor, E. B., C. J. Foote, and C. C. Wood. 1996. Molecular genetic evidence for parallel life-history evolution within a Pacific salmon (sockeye salmon and kokanee, *Oncorhynchus nerka*). Evolution 50:401–416.

Utter, F., and N. Ryman. 1993. Genetic markers and mixed stock fisheries. Fisheries 18:11–21.

Vamosi, S. M., and D. Schluter. 2004. Character shifts in the defensive armor of sympatric sticklebacks. Evolution 58:376–385.

Waples, R. S., D. J. Teel, J. M. Myers, and A. M. Marshall. 2004. Life history variation in Chinook salmon: historic contingency and parallel evolution. Evolution 58:386–403.

Webb, P. W. 1984a. Body form, locomotion and foraging in aquatic vertebrates. Am. Zool. 24:107–120.

———. 1984b. Form and function in fish swimming. Sci. Am. 251: 72–82.

Webster, M. S., P. P. Marra, S. M. Haig, S. Bensch, and R. T. Holmes. 2002. Links between worlds: unraveling migratory connectivity. Trends Ecol. Evol. 17:76–83.

Weitcamp, L. A., T. C. Wainwright, G. J. Bryant, G. B. Milner, D. J. Teel, R. G. Kope, and R. S. Waples. 1995. Status review of coho salmon from Washington, Oregon and California. U.S. Dept. Commerce, NOAA Tech. Memo NMFS-NMFSC-24.

Whitlock, M. C., and D. E. McCauley. 1999. Indirect measures of gene flow and migration: $F_{ST} \neq 1/(4Nm + 1)$. Heredity 82: 117–125.

Wiedenfeld, D. A. 1991. Geographical morphology of male yellow warblers. Condor 93:712–723.

Winkler, H., and B. Leisler. 1992. On the ecomorphology of migrants. Ibis 134(Suppl):21–28.

Wood, C. C., and C. J. Foote. 1990. Genetic differences in the early development and growth of sympatric sockeye and kokanee (*Oncorhynchus nerka*) and their hybrids. Can. J. Fish. Aquat. Sci. 47:2250–2260.

———. 1996. Evidence for sympatric genetic divergence of anadromous and nonanadromous morphs of sockeye salmon (*Oncorhynchus nerka*) Evolution 50:1265–1279.

Wood, C. C., S. McKinnell, T. J. Mulligan, and D. A. Fournier. 1987. Stock identification with the maximum-likelihood mixture model: sensitivity analysis and application to complex problems. Can. J. Fish. Aquat. Sci. 44:866–881.

Wright, S. 1931. Evolution in Mendelian populations. Genetics 16: 97–159.

Corresponding Editor: G. Ortí