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[Article]

Matching Management to Biological Scale: Connectivity among Lacustrine Brook Trout Populations

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Abstract.—Determining appropriate spatial scales for managing fisheries is a key element of sustainable management. For inland fisheries, management or harvest regulations are often implemented as general regional guidelines or on a lake-by-lake basis. Wild lacustrine brook trout *Salvelinus fontinalis* from four waterbodies in the Galipo River watershed of Algonquin Provincial Park, Ontario, were used as a model system to determine the extent of population structure among lakes and to identify appropriate scale(s) for managing inland brook trout fisheries. Individual multilocus genotypes were measured using 10 microsatellite loci and were used to characterize movement and gene flow among lakes. Both population- and individual-based analyses showed very little genetic structure among all pairs of waterbodies, suggesting high levels of movement and gene flow between all pairs of lakes. Varying levels of limited genetic structure between pairs of lakes indicate that gene flow may not be uniform within the study system. These results suggest that contrary to previous studies, local watersheds may be the most appropriate management scale for lacustrine brook trout populations in watersheds where physical characteristics provide the potential for migration and gene flow.

Conservation and sustainable management of exploited species are dependent on a good understanding of population parameters and their dynamic relationship with exploitation (Lester et al. 2003). Typically, inland lacustrine fisheries are managed on a lake-by-lake basis and managers rely on catch limits to maintain harvest at a level that is suitable to population maintenance (Lester et al. 2003). This management strategy relies on the assumption that individuals are sedentary and that populations are defined by the confines of each lake. This may hold true in lakes that have low connectivity to other lakes within the same watershed or for obligate coldwater species, such as lake trout *Salvelinus namaycush*, but may be more problematic for mobile species that support recreational fisheries.

Brook trout *S. fontinalis* inhabit cold, well-oxygenated freshwater riverine and lacustrine habitats across their native range in eastern North America (Scott and Crossman 1973). A significant body of work focusing on genetic structure of lacustrine and riverine brook trout suggests that brook trout populations in general are highly structured within and among watersheds, which implies low rates of gene flow across a range of scales (Angers et al. 1995, 1999; Jones et al. 1996; Hébert et al. 2000; Castric et al. 2001; Adams and Hutchings 2003; but see Rogers and Curry 2004). In contrast, ecological studies utilizing mark–recapture methods suggest that brook trout are highly mobile in both riverine and lacustrine environments (Gowan and Fausch 1996; Josephson and Youngs 1996; Curry et al. 2002; but see Adams and Hutchings 2003). Movement of brook trout is hypothesized to be associated with access to groundwater upwelling areas used for spawning (Josephson and Youngs 1996) and areas that provide optimal feeding opportunities (Gowan and Fausch 1996). In combination, these results suggest that brook trout are highly mobile but have the potential to display strong philopatry to natal sites when spawning, as was suggested by O'Connor and Power (1973).

Assessing levels of migration and gene flow in watersheds with interconnected environments should be an integral component of managing brook trout as these parameters will dictate the most appropriate management strategies. This study investigated contrasting hypotheses pertaining to the population structure of brook trout among interconnected lacustrine environments in a tertiary watershed of Algonquin Provincial Park, Ontario, using microsatellite DNA analysis to assess movement and gene flow among lakes. The results support the hypothesis that brook trout can form panmictic populations across multiple connected habitats within a watershed, suggesting that in some cases, local watersheds rather than individual lakes may be the most appropriate scale for management of exploited mobile species.

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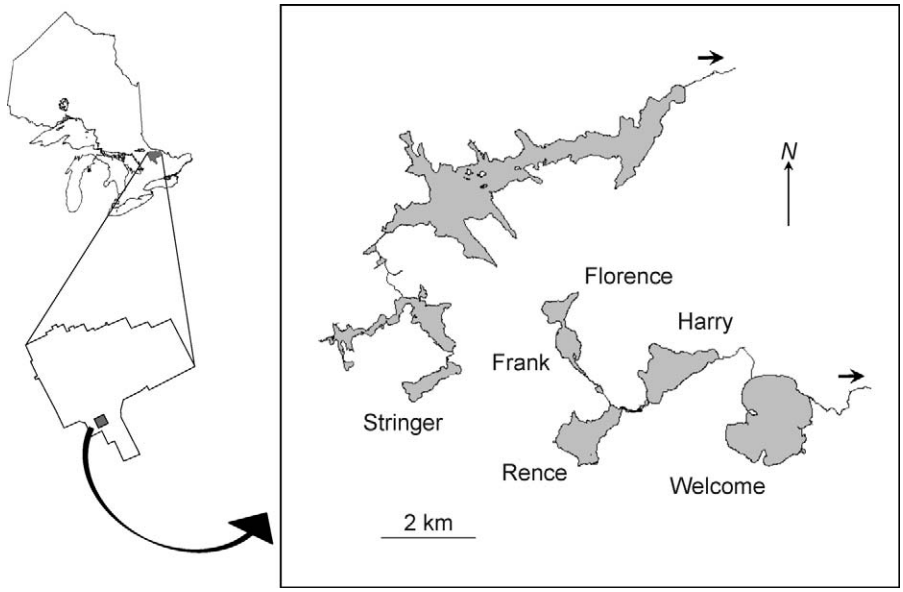

FIGURE 1.—Map of the study area, showing the location of Florence–Frank (considered to be one waterbody for this study), Rence, Harry, and Welcome lakes (Galipo River watershed) and Stringer Lake (outgroup) within Algonquin Provincial Park, Ontario. Arrows show the direction of water flow within the watersheds.

Study Site

This study focused on natural brook trout in four interconnected lacustrine environments in the Galipo River watershed, located in the Algonquin Provincial Park, Ontario, Canada. Waterbodies included Welcome, Harry, Rence, Florence, and Frank lakes; the latter two lakes were considered to be one waterbody for the purposes of this study (Figure 1). Connecting streams range from 700 to 2,000 m in length, 1 to 30 m in width, and 0.1 to 3.0 m in depth. Tagging data from Rence, Harry, and Welcome lakes suggest that individual brook trout often migrate between waterbodies (Norm Quinn, Ontario Ministry of Natural Resources [OMNR], unpublished data), raising the question whether this movement has resulted in a single panmictic population rather than neighboring populations in separate lakes. Natural brook trout from Stringer Lake were used as a genetic outgroup due to this lake's close proximity and similar stocking history but lack of connections to the Galipo River watershed.

Periodically between 1940 and 1978, Frank, Rence, Harry, Welcome, and Stringer lakes received supplementary stocking with a domestic strain of brook trout (OMNR Hills Lake Hatchery strain). No stocking has occurred in the past 29 years or approximately eight generations. Allozyme data suggest that current populations in Harry, Rence, and Welcome lakes have mixed ancestry from introgression between native and hatchery (Hills Lake Hatchery strain) fish (C. C. Wilson et al., unpublished data); no previous genetic data are available for Frank Lake. Hills Lake Hatchery strain brook trout were therefore included in this study to provide insight into the potential impacts of historical stocking on the assessment of population structure.

Methods

Sample collection.—A total of 222 brook trout were sampled, with sample sizes ranging from 33 to 43 fish for individual waterbodies and the hatchery source (Table 1). The Galipo River watershed lakes (Harry, Rence, Welcome, and Florence–Frank; hereafter, "Galipo lakes") were sampled by nonlethal angling and gillnetting between July and August 2002. Stringer Lake was sampled by angling during June 2005. Hills Lake Hatchery strain brook trout were obtained in 2003 from the OMNR Codrington Research Hatchery. A small fin clip from each individual was preserved in 95% ethanol for subsequent extraction of genomic DNA.

Data collection.—The DNA was extracted from ethanol-preserved fin tissue using QIAGEN DNeasy spin columns according to the manufacturer's protocol (QIAGEN, Inc., Valencia, California). Extracted DNA was quantified and diluted to 3 ng/μL. Individuals were genotyped for 11 fluorescently labeled microsatellite loci (*Sfo18* and *Sfo23*: Angers et al. 1995; *SfoC24*,

TABLE 1.—Summary of study lakes in Ontario, showing waterbody names and abbreviations (Abr.), latitude and longitude (Lat/long), surface area (SA), and numbers of individual brook trout that were genotyped (*N*). Values of expected heterozygosity (H_E) and observed heterozygosity (H_O), mean allelic richness (N_A), and the inbreeding coefficient (F_{IS}) are based on mean values for 10 microsatellite loci. Standard deviation (in parentheses) is provided for H_E, H_O, and N_A.

Lake	Abr.	Lat/long	SA (ha)	*N*	H_E	H_O	N_A	F_{IS}
Florence–Frank	FF	45°26′N, 78°28′W	46.1	36	0.72 (0.04)	0.70 (0.02)	7.4 (3.6)	0.034
Rence	RE	45°24′N, 78°28′W	95.6	35	0.75 (0.03)	0.69 (0.02)	8.4 (4.0)	0.099
Harry	HA	45°25′N, 78°26′W	114.1	33	0.72 (0.04)	0.72 (0.02)	7.5 (3.6)	−0.003
Welcome	WE	45°25′N, 78°24′W	260	43	0.74 (0.04)	0.70 (0.02)	8.0 (3.6)	0.050
Stringer (outgroup)	ST	45°25′N, 78°30′W	33.5	40	0.64 (0.06)	0.67 (0.02)	5.4 (1.6)	−0.043
Hills Lake (hatchery)	HI	—		35	0.76 (0.03)	0.72 (0.02)	7.5 (2.9)	0.070

SfoD28, *SfoC38*, *SfoC88*, *SfoC100*, *SfoC113*, *SfoC115*, *SfoC129*, and *SfoB52*: T. King and M. Burnham-Curtis, U.S. Geological Survey, unpublished data) using three 10-μL multiplex reactions. Each multiplex reaction contained approximately 6 ng of DNA, 1.0 μL of 10× polymerase chain reaction (PCR) buffer, 2 μg of BSA, 200 μmol of deoxynucleotide triphosphates, 0.025 units of *Taq* polymerase (QIAGEN), and from 0.075 to 0.25 μM of each primer pair. All amplifications were completed using a PTC-100 thermocycler (MJ Research, Inc., Waltham, Massachusetts) using the following conditions: 94°C for 5 min, 36 cycles of 94°C for 1 min, 58°C or 60°C (multiplex specific) for 1 min, 72°C for 1.5 min, and a final extension at 60°C for 45 min. The PCR products were diluted with 10 μL of double-distilled H_2O. A 1-μL aliquot of the diluted product was added to a 1-μL solution of formamide, fluorescent size standard (GeneScan ROX350), and Applied Biosystems, Inc. (ABI), loading buffer. Electrophoresis and visualization of microsatellite genotypes were carried out on an ABI 377 automated sequencer. Genotypes were scored using ABI GENOTYPER version 2.5 and visual proofreading.

Data analysis.—Estimates of genetic polymorphism for each locus were measured as number of alleles corrected for variation in sample size (N_A) using FSTAT (Goudet 1995); expected heterozygosity and observed heterozygosity (H_O) were also calculated using GENEPOP version 3.4 (Raymond and Rousset 1995). Individual multilocus genotypes were grouped by population, and populations were tested individually and pooled (in the case of the Galipo lakes) for deviations from Hardy–Weinberg equilibrium (HWE) using GENEPOP. Conformity of loci to HWE expectations was calculated using Markov-chain Monte Carlo (MCMC) methods (Guo and Thompson 1992) available in GENEPOP. The H_O values of six loci deviated significantly ($P < 0.05$) from HWE expectations across all lakes; one of these (*SfoC129*) remained significant after correction for multiple comparisons and was removed from subsequent analyses.

Divergence among populations was estimated using variance in allele frequencies (F_{ST}; Weir and Cockerham 1984) and allele sizes (R_{ST}; Michalakis and Excoffier 1996) by use of FSTAT. Genetic distances among populations (D_A) were estimated using the formula of Nei et al. (1983) and were used to construct a neighbor-joining dendrogram with associated bootstrap values based on 1,000 iterations in POPULATIONS version 1.2.28 (Langella 2002). The resulting tree was displayed using TREEVIEW version 1.66 (Page 1996).

To complement the population-level analyses, individual-based genetic structure and the number of populations present were assessed without using a priori sampling information in STRUCTURE version 2.1 (Pritchard et al. 2000). STRUCTURE uses a Bayesian approach to cluster individual genotypes into a putative number of groups (*K* clusters) while minimizing Hardy–Weinberg disequilibrium and gametic phase disequilibrium. This method is analogous to generalized centroid clustering, where the user specifies the number of groups (centroids) and the analysis infers the proportional membership of an individual to each group (Pritchard et al. 2000). Twenty independent runs for *K*-values from 1 to 6 were completed on the entire data set. Run parameters included a burn-in and data collection periods of 50,000 MCMC iterations each. The best estimates of the number of genetic groups (*K*) were determined by comparing the estimated log probability, $\log_e(\Pr[X \mid K])$, of the data under each value of *K* (Pritchard et al. 2000). Waples and Gaggiotti (2006) suggested that this method provides the best metric for estimating the number of genetic groups when using STRUCTURE.

Theoretical expectations of divergence among populations based on neutral DNA markers.—The program EASYPOP version 2.0.1 (Balloux 1999) was used to simulate multilocus genotypes to determine whether reported divergence (F_{ST}) among the four waterbodies was consistent with differentiation expected from four reciprocally isolated populations founded by common ancestors eight generations previously.

TABLE 2.—Pairwise comparisons of population divergence based on allele frequencies (F_{ST}; below diagonal) and allele sizes (R_{ST}; above diagonal) among natural brook trout from four interconnected lakes (FF, RE, HA, and WE; see Table 1 for defintion of abbreviations), one isolated lake (ST), and the historical hatchery stocking source (HI). Pairwise F_{ST} values marked with an asterisk were significant ($P < 0.05$) after sequential Bonferroni correction.

Population	FF	RE	HA	WE	ST	HI
FF	—	0.010	−0.009	−0.002	0.238	0.033
RE	0.000	—	0.022	−0.004	0.143	0.092
HA	0.008	0.010	—	0.001	0.273	0.014
WE	0.009	0.011	0.000	—	0.195	0.042
ST	0.126*	0.111*	0.144*	0.122*	—	0.374
HI	0.050*	0.035*	0.048*	0.043*	0.113*	—

Simulations assumed random mating, a 1:1 sex ratio, free recombination among loci, a common mutation rate of 5×10^{-4} (Estoup and Angers 1998), a single-step mutation model, and nine allelic states per locus.

Census population (N_c) estimates used in the simulations were based on a published combined N_c estimate of 714 adults for Rence, Harry, and Welcome lakes (Quinn et al. 1994). Individual population estimates of 145, 174, and 395 adults for Rence, Harry, and Welcome lakes, respectively, were calculated based on surface areas of the three lakes (Table 1) and the assumption of constant brook trout density throughout the three waterbodies. The combined population estimate for Florence and Frank lakes (70 adults) was determined by using surface area (Table 1) and the density estimates for Rence, Harry, and Welcome lakes.

One-hundred replicates for each of three modeling scenarios were run to assess expected F_{ST} under different ratios of effective population size (N_e) to N_c and under different population sizes. The scenarios included (1) a 1:1 ratio of N_e:N_c using the mean population estimate from Quinn et al. (1994); (2) an N_e:N_c ratio of 0.4:1.0 using the lower 95% confidence limit of N_c; and (3) an N_e:N_c ratio of 0.4:1.0 using the upper 95% confidence limit of N_c. Based on findings for other salmonids, the first scenario was highly conservative since N_e in salmonids is often a small fraction of N_c (Waples 2004). The 0.4:1.0 N_e:N_c ratio is probably closer to the true ratio, as indicated by behavioral and genetic observations of variance in reproductive success for male and female lacustrine brook trout (Blanchfield et al. 2003).

Results

Genetic Diversity

All microsatellite loci sampled were moderately to highly polymorphic, with number of alleles per locus ranging from 4 (*SfoC38*) to 26 (*Sfo23*; Table A.1). Locus heterozygosity across populations ranged from 0.55 (*SfoC38*) to 0.89 (*Sfo23*; Table A.1). Six loci showed significant deviations ($P < 0.05$) from HWE expectations when tested across all populations; of these loci, one (*SfoC129*) remained significant after sequential Bonferroni correction for multiple tests. Significant deviations ($P < 0.05$) from HWE expectations were also noted in 14 of 66 tests when assessed within populations for each locus; two tests for *SfoC129* remained significant after correction for multiple tests. As mentioned above, *SfoC129* was excluded from all subsequent analyses due to the potential for bias from null alleles.

Allelic richness (N_A) estimates across all loci for populations from the Galipo lakes ranged from 7.4 to 8.4 (Table 1). In comparison with the Galipo lake populations, the estimated N_A of the natural population from Stringer Lake (outgroup) was much lower (5.4), while the estimated N_A for the historical stocking source (Hills Lake Hatchery) was comparable (7.5; Table 1). Inbreeding coefficient (F_{IS}) estimates ranged from −0.003 to 0.099 for the Galipo lake populations and were −0.043 and 0.070, respectively, for Stringer Lake and the Hills Lake Hatchery strain (Table 1).

Population-Based Differentiation

Brook trout populations from the four Galipo lakes exhibited low levels of divergence based on both F_{ST} (range = 0.000–0.011) and R_{ST} (range = −0.009 to 0.022; Table 2). In contrast, all pairwise F_{ST} comparisons between brook trout from the Galipo lakes and Stringer Lake were significant ($P < 0.05$); these pairwise F_{ST} estimates ranged from 0.111 to 0.144 (Table 2). Similarly, significant ($P < 0.05$) divergence was observed between brook trout from the Galipo lakes and the historical stocking source (Hills Lake Hatchery), with low but significant pairwise F_{ST} estimates ranging from 0.035 to 0.050 (Table 2).

Individual-Based Assignment Methods

The most probable number of populations present (K) within the data set was estimated without using a priori sampling site information in STRUCTURE (Pritchard et al. 2000) by estimating the mean $\log_e(\Pr[X \mid K])$ for models with values of K ranging

from 1 to 6. The resulting distribution of $\log_e(\Pr[X \mid K])$ across models was unimodal (Figure 2a). The rapid increase of $\log_e(\Pr[X \mid K])$ at K-values between 1 and 3 indicated that individuals from the outgroup (Stringer Lake) and the historical hatchery source (Hills Lake Hatchery) were clearly distinct from populations within the Galipo River watershed. The rate of increase in $\log_e(\Pr[X \mid K])$ began to decline at a K-value of 3, and the maximum mean $\log_e(\Pr[X \mid K])$ value occurred at a K-value of 5 (Figure 2a). Based on tradeoffs between $\log_e(\Pr[X \mid K])$ and proportional group membership coefficients (Q) for individual fish, explanatory power was greatest for a K-value of 3 (mean $Q_{\max} = 0.88$; Figure 2b). Increasing values of K failed to identify substructure within and among the Galipo lake populations (Figure 2c). Setting K at 6 to represent the sampled number of waterbodies or sources failed to increase resolution among sites and resulted in multiple low Q-values for brook trout from the Galipo River watershed (data not shown). Using sampling location information a priori to inform membership (updating allele frequencies of putative groups) similarly failed to increase resolution within the data set and resulted in more negative (higher improbability) values of $\log_e(\Pr[X \mid K])$ (data not shown).

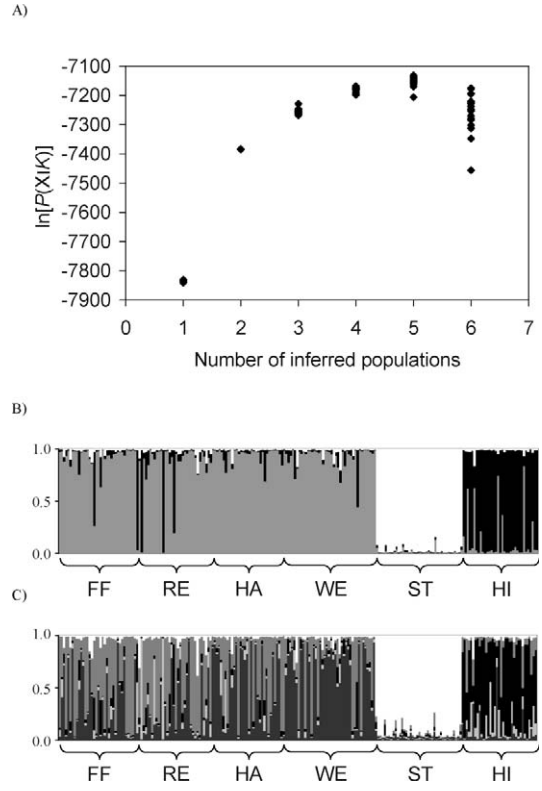

FIGURE 2.—**(a)** Estimated log probability, $\log_e(\Pr[X \mid K])$, provided by STRUCTURE (Pritchard et al. 2000) for models using K-values of 1–6 (K = number of inferred populations) when individual brook trout from Florence–Frank (FF), Rence (RE), Harry (HA), and Welcome (WE) lakes (Galipo River watershed), Stringer Lake (ST; outgroup), and the Hills Lake Hatchery strain (HI) were included. Also presented are STRUCTURE plots of estimated membership coefficients (Q) for individuals to K populations at **(b)** a K-value of 3 and **(c)** a K-value of 5. Each individual is represented by a vertical line that is partitioned into K segments (fractional Q-values between 0 and 1, which represent the individual's estimated membership fraction to each inferred population or genetic group).

Theoretical Population-Based Differentiation

Estimated F_{ST} among computer-simulated populations varied between the three models. Simulation scenarios 1 and 3 provided similar estimates of differentiation among populations, with mean F_{ST} estimates of 0.029 (range = 0.016–0.041) and 0.027 (range = 0.016–0.038), respectively (Table 3). In comparison, simulation scenario 2 provided much higher estimates of differentiation, with a mean F_{ST} of 0.113 (range = 0.068–0.161; Table 3). The F_{ST} and associated 95% confidence intervals for all three scenarios were significantly greater ($P < 0.01$) than the empirical F_{ST} values among populations from the Galipo lakes (Table 2) based on one-tailed t-tests of samples against a distribution (Sokal and Rohlf 1981).

Discussion

The results from this study clearly show that microgeographic genetic structure of brook trout did not correspond with separate lacustrine environments within the Galipo River watershed. Both indirect (F_{ST}) and direct (individual assignment) measures of gene flow supported the null hypothesis of no significant genetic structure among the Galipo lake populations studied, inferring substantial movement and gene flow. The genetic results are in agreement with tagging data indicating that brook trout are highly mobile within the study area (Norm Quinn, unpublished data) and augment those data by suggesting that movement has resulted in substantial gene flow. In combination, the genetic and tagging data suggest that brook trout within the study area represent a continuous population within multiple connected habitats rather than discrete lacustrine populations.

The simulations of predicted neutral divergence values (F_{ST} estimates) assuming no migration provided strong evidence that the observed contemporary divergence is significantly less than would be expected if the study lakes represented individual populations. It was important to test the simulated F_{ST} values because significant historical stocking within the study area

TABLE 3.—Predicted pairwise genetic differentiation index (F_{ST}) values for three brook trout population simulation scenarios. Scenario 1 used the mean census population size (N_c) and assumed a 1:1 ratio of effective population size (N_e) to N_c. Scenario 2 used the lower 95% confidence estimate of N_c and assumed a 0.4:1.0 ratio of N_e to N_c. Scenario 3 used the upper 95% confidence estimate of N_c and assumed a 0.4:1.0 ratio of N_e to N_c. Means (95% confidence intervals in parentheses) are F_{ST} values estimated from population data based on 100 simulation repetitions using EASYPOP (Balloux 1999). Population abbreviations are defined in Table 1.

Pairwise comparison	F_{ST} value from Table 2	Scenario 1	Scenario 2	Scenario 3
FF–RE	0.000	0.039 (0.037–0.040)	0.161 (0.154–0.168)	0.038 (0.036–0.040)
FF–HA	0.008	0.041 (0.039–0.043)	0.149 (0.142–0.156)	0.036 (0.034–0.038)
FF–WE	0.009	0.033 (0.031–0.034)	0.119 (0.113–0.124)	0.030 (0.029–0.032)
RE–HA	0.010	0.024 (0.023–0.025)	0.102 (0.097–0.107)	0.023 (0.022–0.025)
RE–WE	0.011	0.016 (0.016–0.017)	0.076 (0.072–0.079)	0.017 (0.017–0.018)
HA–WE	0.000	0.018 (0.017–0.019)	0.068 (0.064–0.071)	0.016 (0.015–0.017)
Mean	0.006	0.029	0.113	0.027

introduced the potential for genetic homogenization in the absence of natural gene flow (Waples 1995), which if not considered could falsely provide the impression that significant gene flow was occurring within the system. Use of simulated F_{ST} allowed us to estimate the impact of potential homogenization on divergence under the null hypothesis. The simulation scenarios were extremely conservative as we assumed complete initial homogenization among the four Galipo lake populations via their introduction from a shared hatchery source (Hills Lake Hatchery strain). Based on unpublished allozyme data indicating the presence of native genes within the system (C. C. Wilson et al., unpublished data), this approach should have significantly underestimated interpopulation divergence if populations were historically divergent as the result of reciprocal isolation since postglacial recolonization (e.g., Danzmann and Ihssen 1995). Secondly, the N_e used in the simulations assumed N_e:N_c ratios of 1.0 (scenario 1) and 0.4 (scenarios 2 and 3), which are high in comparison to values reported for other salmonids in the literature (Waples 2004), again providing a conservative estimate of expected divergence. Empirical measures of F_{ST} were well below all simulated F_{ST} estimates, providing strong evidence for substantial movement and gene flow within the watershed.

The modeling results were strongly supported by the individual-based analysis of genetic membership. In general, choosing the appropriate value of K when using STRUCTURE is difficult (Pritchard et al. 2000), particularly when gene flow among populations is high (Waples and Gaggiotti 2006). Pritchard et al. (2000) warned that solely using $\log_e(\Pr[X \mid K])$ to estimate the most appropriate value of K can lead to incorrect conclusions. They added that the smallest K that captures the major structure in the data is likely to be the most parsimonious. In our case, the K-value of 3 was the smallest K that captured the majority of genetic structure among the populations in the Galipo lakes, the outgroup population (Stringer Lake), and the historical stocking strain (Hills Lake Hatchery) and was therefore accepted as the most probable number of groups. However, despite the absence of stocking for eight generations, some individuals from the study lakes were assigned to the historical stocking strain as a result of model limitations and extensive historical stocking. These same factors similarly resulted in the assignment of some hatchery fish to the Galipo lakes group. In contrast, the K of 5 provided marginally better resolution of the three groups (Galipo lakes, hatchery, and outgroup) with very few misclassifications among groups but had lower mean proportional Q-values (artificial splitting) for individual fish within the Galipo lakes. Although the wild fish were not sampled during the spawning season, when maximum spatial segregation would be expected, the existence of multiple discrete gene pools within the Galipo lakes (if present) would have been detected by the STRUCTURE analysis. Instead, the homogeneous splitting of Q-values indicates artificial subdivision by the model condition that forced multiple populations (Figure 2c). It is worth noting that STRUCTURE is highly effective at detecting migrants (Pritchard et al. 2000) but has limited resolution under conditions of high gene flow (Waples and Gaggiotti 2006), as indicated by the low F_{ST} and R_{ST} values among the populations of the Galipo lakes (Table 2). In combination, the different models that were run suggest that (1) little genetic structure exists within the study lakes and (2) these lakes are genetically differentiated from the geographically isolated outgroup and the historical stocking strain despite substantial hatchery introgression from past stocking events.

Our evidence for significant movement of brook trout within the Galipo River watershed agrees with results of brook trout tagging within the watershed (Norm Quinn, unpublished data) and with the majority of ecological studies that have assessed microgeographic movements

of brook trout by use of tagging methods (Gowan and Fausch 1996; Adams et al. 2000, 2001; Curry et al. 2002; but see Adams and Hutchings 2003). These and other ecological studies have identified that brook trout are highly mobile and often move within watersheds (Josephson and Youngs 1996).

In contrast, our data appear to conflict with other genetic studies that have assessed genetic population structure of brook trout. Many studies have reported results that are consistent with strong microgeographic genetic structuring among populations within watersheds (Angers et al. 1995, 1999; Jones et al. 1996; Hébert et al. 2000; Castric et al. 2001; Adams and Hutchings 2003). In general, our study system was spatially restricted in comparison with the scales assessed in previous studies (Angers et al. 1995, 1999; Jones et al. 1996; Hébert et al. 2000; Castric et al. 2001). The relatively short length of the streams linking the four small waterbodies (680–1,500 m) may facilitate easy movement of individuals between habitat patches. In addition to the difference in scale, interpretive discrepancies between our findings and those from previous studies (Angers et al. 1995, 1999; Jones et al. 1996; Hébert et al. 2000; Castric et al. 2001) probably also reflect differences in analytical approaches.

Most published studies of lacustrine brook trout genetic structure have defined populations a priori by sampling location (Angers et al. 1995, 1999; Jones et al. 1996; Hébert et al. 2000; Castric et al. 2001; Adams and Hutchings 2003). Although this practice is common for studies that utilize population-based approaches, it may introduce biological inconsistencies and may have potentially misleading consequences for analysis of geographic structure and population divergence (Pritchard et al. 2000; Pearse and Crandall 2004). This is particularly true for small populations and for cases of active dispersal or movement among habitat patches (Pearse and Crandall 2004). Ecological and genetic studies, however, have shown that brook trout are highly mobile within watersheds (Gowan and Fausch 1996; Josephson and Youngs 1996; Adams et al. 2000, 2001) and that sampling locations alone may not correspond with genetic population membership (e.g., Rogers and Curry 2004). Accordingly, a priori definition of populations may not be appropriate for highly mobile species such as brook trout.

Inconsistencies arising from this historical reliance on predefined population membership may have been further exacerbated by the use of population-based approaches, such as D_A and F_{ST} estimates, to infer metapopulation structure. Pooling information from individual genotypes into assumed populations greatly reduces the resolving power of the available genetic data (Pritchard et al. 2000; Pearse and Crandall 2004). Valuable information is therefore discarded, and the resultant pairwise F_{ST} values are treated in subsequent cluster analyses as point estimates with no variance; as such, the rank order clustering distances may be supported by bootstrap tests even in the absence of strong interpopulation segregation. Individual-based approaches used by programs such as STRUCTURE circumvent such pitfalls by using variation from multiple levels to assess overall genetic structure (Pritchard et al. 2000; Pearse and Crandall 2004). This contradiction in data interpretation is exemplified by our population-based cluster analysis that showed strongly supported differentiation among the Galipo lake populations (Figure 3), whereas all other analyses indicated very little genetic structure or separation among these populations.

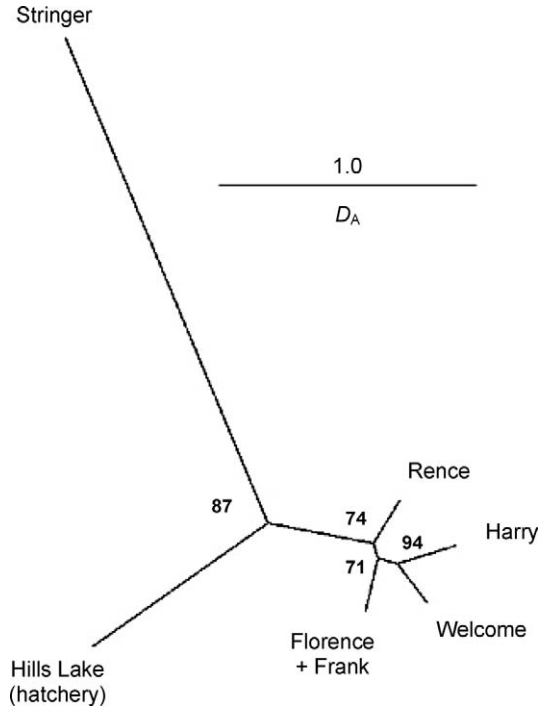

FIGURE 3.—Unrooted neighbor-joining dendrogram of genetic divergence among brook trout from Florence–Frank, Harry, Rence, and Welcome lakes (Galipo River watershed), Stringer Lake (outgroup), and the Hills Lake Hatchery strain based on Nei et al.'s (1983) genetic distance (D_A) estimated from 10 microsatellite loci. Bootstrap values are based on 1,000 permutations.

The causes of significant gene flow within the Galipo River watershed remain unknown. However, evidence exists that brook trout migrate within systems to gain access to suitable foraging opportunities (Gowan and Fausch 1996) and spawning areas

(Josephson and Youngs 1996); young-of-the-year brook trout are also known to disperse from spawning areas (Biro and Ridgway 1995). Movement of tagged adult brook trout among study lakes immediately prior to spawning (Norm Quinn, unpublished data) suggests that brook trout either are (1) returning to their natal spawning sites after moving between lakes in search of suitable habitat or feeding opportunities or (2) leaving their lake of origin in search of additional spawning opportunities.

The results presented here suggest that brook trout within the Galipo River watershed exhibit high rates of migration between interconnected lacustrine environments, resulting in the presence of a largely panmictic population. As the scale of the Galipo River watershed is comparable with the known vagility of brook trout (Scott and Crossman 1973; Gowan and Fausch 1996; Adams et al. 2000, 2001), these results have significant implications for both conservation and resource management. Identifying and understanding panmixia among populations in separate but interconnected habitats are extremely important for maximizing the persistence of populations and also for most efficiently meeting the goals of exploited species management (Smedbol and Wroblewski 2002). When compared with other studies pertaining to movement of brook trout, our results are in agreement with the majority of ecological studies and in disagreement with the majority of genetic studies. Our results also underscore the value of collecting and analyzing genetic data within an ecological context: analytical approaches should reflect the biology of species, with individual-based approaches (tagging, genetics, dispersal, and reproduction) complementing population-level comparisons. Although the results of some studies have suggested that lacustrine brook trout should be managed on a lake-by-lake basis (Adams and Hutchings 2003), our results indicate that in systems such as the one studied here, lacustrine brook trout management may be most effective if carried out at the watershed scale. In combination with previous studies, our work provides evidence that the appropriate scale for brook trout management within watersheds should reflect their biology in terms of movement and reproduction. This scale can best be determined by using both tagging and genetic data to quantify the degree of isolation or connectivity among habitat patches, thereby ensuring biologically appropriate management of populations and their habitats.

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Appendix: Brook Trout Allele Frequencies

Table A.1—Allele frequencies at each locus for brook trout from Ontario lakes (population abbreviations are defined in Table 1).

Locus and allele	Population					
	FF	RE	HA	WE	ST	HI
SfoD100						
209	0.07	0.07	0.05	0.00	0.20	0.13
213	0.04	0.01	0.06	0.05	0.00	0.23
217	0.36	0.37	0.45	0.40	0.31	0.03
221	0.17	0.17	0.15	0.27	0.05	0.33
225	0.22	0.14	0.08	0.16	0.14	0.04
229	0.03	0.07	0.03	0.03	0.00	0.00
233	0.04	0.03	0.09	0.02	0.01	0.06
237	0.07	0.11	0.09	0.03	0.29	0.10
241	0.00	0.01	0.00	0.03	0.00	0.07
273	0.00	0.00	0.00	0.00	0.00	0.01
SfoC113						
112	0.00	0.00	0.00	0.00	0.03	0.00
130	0.00	0.03	0.00	0.00	0.00	0.00
133	0.31	0.37	0.44	0.26	0.16	0.28
136	0.11	0.13	0.11	0.19	0.14	0.04

Table A.1.—Continued.

Locus and allele	Population					
	FF	RE	HA	WE	ST	HI
139	0.10	0.04	0.14	0.07	0.06	0.10
142	0.07	0.03	0.00	0.02	0.00	0.10
145	0.25	0.19	0.15	0.26	0.33	0.00
148	0.00	0.03	0.02	0.02	0.00	0.09
151	0.00	0.00	0.00	0.00	0.00	0.09
154	0.17	0.19	0.15	0.19	0.29	0.29
SfoC115						
218	0.00	0.00	0.00	0.01	0.00	0.00
232	0.00	0.00	0.00	0.00	0.00	0.07
234	0.00	0.00	0.00	0.01	0.21	0.00
240	0.03	0.04	0.00	0.01	0.13	0.01
242	0.18	0.21	0.20	0.17	0.05	0.04
244	0.00	0.00	0.02	0.02	0.05	0.00
246	0.32	0.26	0.12	0.14	0.25	0.09
248	0.04	0.11	0.02	0.02	0.24	0.06
250	0.00	0.00	0.15	0.16	0.00	0.00
252	0.00	0.01	0.02	0.01	0.00	0.00
254	0.00	0.00	0.00	0.00	0.00	0.04
300	0.00	0.03	0.00	0.00	0.00	0.00
304	0.00	0.00	0.00	0.00	0.00	0.09
308	0.17	0.19	0.26	0.26	0.00	0.30
312	0.08	0.04	0.08	0.05	0.05	0.23
316	0.00	0.00	0.00	0.00	0.00	0.04
322	0.03	0.01	0.00	0.01	0.00	0.00
334	0.04	0.03	0.05	0.08	0.00	0.00
340	0.11	0.06	0.11	0.03	0.03	0.03
SfoC129						
225	0.00	0.06	0.00	0.05	0.00	0.00
228	0.04	0.07	0.09	0.10	0.05	0.03
231	0.04	0.04	0.12	0.10	0.00	0.00
234	0.18	0.07	0.17	0.19	0.23	0.26
237	0.69	0.64	0.58	0.49	0.38	0.61
240	0.04	0.10	0.05	0.07	0.35	0.07
243	0.00	0.01	0.00	0.00	0.00	0.03
Sfo18						
168	0.07	0.04	0.06	0.01	0.00	0.00
172	0.04	0.07	0.05	0.08	0.00	0.19
174	0.00	0.00	0.00	0.00	0.00	0.01
176	0.39	0.21	0.47	0.38	0.16	0.15
178	0.04	0.09	0.05	0.12	0.01	0.01
180	0.01	0.03	0.02	0.08	0.00	0.09
182	0.33	0.34	0.21	0.17	0.49	0.35
184	0.06	0.07	0.05	0.05	0.10	0.01
186	0.04	0.01	0.05	0.00	0.05	0.04
188	0.01	0.06	0.05	0.01	0.00	0.04
190	0.00	0.00	0.00	0.00	0.00	0.01
192	0.00	0.00	0.00	0.00	0.00	0.07
224	0.00	0.00	0.00	0.01	0.03	0.00
226	0.00	0.07	0.02	0.08	0.16	0.00
Sfo23						
149	0.03	0.06	0.09	0.08	0.00	0.00
155	0.01	0.01	0.00	0.00	0.00	0.00
161	0.00	0.04	0.00	0.00	0.00	0.00
163	0.00	0.03	0.00	0.00	0.09	0.01
165	0.00	0.03	0.02	0.00	0.00	0.01
167	0.01	0.00	0.00	0.03	0.54	0.26
169	0.06	0.13	0.05	0.06	0.00	0.09
171	0.06	0.07	0.15	0.17	0.00	0.01
173	0.10	0.04	0.06	0.07	0.00	0.00
177	0.04	0.03	0.03	0.02	0.00	0.00
179	0.17	0.03	0.03	0.08	0.00	0.00
181	0.00	0.00	0.00	0.00	0.00	0.01
183	0.00	0.00	0.02	0.01	0.01	0.01
185	0.21	0.26	0.21	0.26	0.24	0.37
187	0.03	0.06	0.03	0.06	0.00	0.00
189	0.07	0.04	0.05	0.02	0.00	0.12
191	0.00	0.00	0.00	0.00	0.04	0.00
193	0.01	0.04	0.05	0.03	0.07	0.00

Table A.1.—Continued.

Locus and allele	Population					
	FF	RE	HA	WE	ST	HI
197	0.00	0.01	0.00	0.00	0.00	0.00
199	0.01	0.01	0.06	0.01	0.00	0.00
203	0.00	0.00	0.02	0.00	0.00	0.00
205	0.13	0.04	0.11	0.08	0.00	0.04
207	0.06	0.06	0.00	0.00	0.00	0.00
209	0.00	0.00	0.05	0.00	0.00	0.00
211	0.01	0.00	0.00	0.00	0.00	0.00
215	0.00	0.00	0.00	0.00	0.01	0.04
SfoC24						
114	0.01	0.03	0.02	0.00	0.25	0.00
117	0.29	0.33	0.18	0.27	0.41	0.31
120	0.69	0.57	0.71	0.66	0.10	0.41
123	0.00	0.07	0.09	0.07	0.24	0.26
183	0.00	0.00	0.00	0.00	0.00	0.01
SfoD28						
169	0.00	0.00	0.00	0.00	0.00	0.03
173	0.00	0.06	0.00	0.00	0.00	0.00
177	0.28	0.20	0.23	0.16	0.00	0.10
181	0.32	0.29	0.41	0.41	0.10	0.40
185	0.19	0.21	0.26	0.30	0.36	0.17
189	0.10	0.21	0.06	0.03	0.04	0.17
193	0.08	0.03	0.03	0.06	0.45	0.13
197	0.03	0.00	0.02	0.03	0.05	0.00
SfoC38						
143	0.13	0.11	0.08	0.05	0.01	0.20
146	0.51	0.51	0.64	0.61	0.86	0.59
149	0.31	0.24	0.26	0.26	0.13	0.13
152	0.06	0.13	0.03	0.08	0.00	0.09
SfoC88						
183	0.15	0.17	0.08	0.08	0.00	0.07
186	0.40	0.31	0.33	0.44	0.75	0.44
189	0.08	0.17	0.11	0.07	0.10	0.09
192	0.25	0.26	0.35	0.27	0.09	0.33
195	0.11	0.09	0.14	0.14	0.06	0.07
SfoB52						
195	0.00	0.00	0.00	0.00	0.21	0.00
203	0.03	0.04	0.05	0.05	0.00	0.04
207	0.04	0.06	0.02	0.05	0.00	0.09
211	0.01	0.04	0.14	0.10	0.00	0.01
215	0.35	0.34	0.24	0.21	0.35	0.16
219	0.11	0.19	0.17	0.15	0.00	0.21
223	0.01	0.01	0.02	0.03	0.03	0.04
225	0.22	0.16	0.24	0.26	0.00	0.29
227	0.11	0.06	0.00	0.09	0.01	0.03
231	0.10	0.09	0.14	0.05	0.00	0.11
235	0.01	0.01	0.00	0.00	0.40	0.01
237	0.00	0.00	0.00	0.01	0.00	0.00