Genetic population structure of broad whitefish, *Coregonus nasus*, from the Mackenzie River, Northwest Territories: implications for subsistence fishery management

Les N. Harris and Eric B. Taylor

Abstract: We assayed microsatellite DNA variation among 1013 broad whitefish, *Coregonus nasus*, from 36 localities within the lower Mackenzie River (Northwest Territories, Canada) to provide the first assessment of fine-scale population structuring of broad whitefish in this large system. Among sampling locations, averaged across all loci, the number of alleles ranged from 3.00 to 6.71 and heterozygosity averaged 0.54. Population subdivision was generally low, but significant ($\theta = 0.026$, $P < 0.05$), although pairwise comparisons indicated that overall significance was heavily influenced by comparisons between anadromous and lacustrine groups. Bayesian-based STRUCTURE analysis suggested that there are two main genetic groups within our study area: anadromous and lacustrine broad whitefish. A mixture analysis indicated that all populations contribute to the lower Mackenzie River subsistence fishery, yet catches were dominated by Peel River fish, highlighting the importance of this tributary. Our data also supported the idea that there are several units of conservation among Mackenzie River system broad whitefish populations and that management strategies should be implemented accordingly.

Résumé : Nous avons évalué la variation de l'ADN des microsatellites chez 1 013 corégones tschir, *Coregonus nasus*, de 36 sites sur le cours inférieur du Mackenzie (Territoires du Nord-Ouest, Canada) afin d'obtenir une première évaluation de la structure à échelle fine de la population de ces corégones dans ce grand réseau hydrographique. Pour l'ensemble des sites d'échantillonnage, le nombre moyen d'allèles pour tous les locus varie de 3,00 à 6,71 et l'hétérozygotie moyenne est de 0,54. La subdivision de la population est généralement faible, mais significative ($\theta = 0{,}026$, $P < 0{,}05$), bien que des comparaisons appariées indiquent que la signification statistique globale est fortement influencée par les comparaisons entre les groupes anadromes et lacustres. Une analyse STRUCTURE de type bayésien laisse croire qu'il y a deux groupes génétiques principaux dans notre région d'étude, les corégones tschir anadromes et les lacustres. Une analyse de mélange indique que toutes les populations contribuent à la pêche de subsistance dans le cours inférieur du Mackenzie, bien que les captures soient dominées par les poissons de la rivière Peel, ce qui souligne l'importance de ce tributaire. Nos données appuient aussi la proposition qu'il existe plusieurs unités de conservation au sein des populations de corégones tschir du réseau du Mackenzie et que les stratégies d'aménagement devraient en tenir compte.

[Traduit par la Rédaction]

Introduction

Determining the causes of genetic differentiation and the factors that promote variation between and within populations is fundamental for understanding adaptation and is, therefore, a primary goal of population and conservation genetics (e.g., Allendorf and Luikart 2007). Geographic, ecological, and behavioural factors can all contribute to differentiation among populations (Hedrick 2000) and it is apparent that populations of most, if not all, species show some level of genetic structuring or some degree of genetic differentiation among localities (Balloux and Lugon-Moulin 2002; Avise 2004). The extent of genetic structure among populations is ultimately the outcome of interactions among genetic drift, selection, migration, and mutation (Balloux and Lugon-Moulin 2002), which in turn are influenced by historical factors such as glaciation (Hewitt 1996; Bernatchez and Wilson 1998), contemporary factors such as landscape complexity (e.g., Costello et al. 2003; Taylor et al. 2003). and environmental factors such as salinity (McCairns and Bernatchez 2008).

Resolving genetic structure and quantifying genetic variation in high-latitude species that are potentially faced with global warming-induced environmental change is vital for

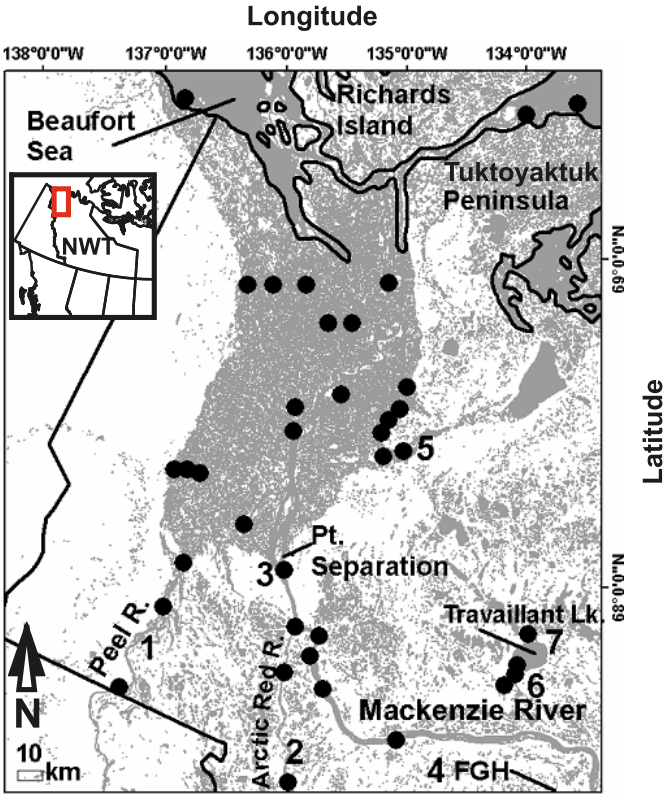
Received 29 May 2009. Accepted 22 February 2010. Published on the NRC Research Press Web site at cjfas.nrc.ca on 11 May 2010. J21223

Paper handled by Associate Editor Anti Vasemagi.

L.N. Harris[1,2] and E.B. Taylor. Department of Zoology and Native Fishes Research Group, University of British Columbia, 6270 University Boulevard, Vancouver, BC V6T 1Z4, Canada.

[1]Corresponding author (e-mail: Les.N.Harris@dfo-mpo.gc.ca).
[2]Present address: Fisheries and Oceans Canada, 501 University Crescent, Winnipeg, MB R3T 2N6, Canada.

Fig. 1. Map showing sampling locations throughout the Mackenzie River system. The inset shows the location in the Northwest Territories (NWT), Canada. Numbers correspond to spawning populations previously identified in the literature: Peel River (1), Arctic Red River (2), Point Separation (3), the Rampart Rapids near the town of Fort Good Hope (FGH) (4), Campbell Lake (5), Travaillant River North (6), and Travaillant River South (7). Note that Fort Good Hope is not shown on the map (located 200 km upstream on the Mackenzie River). Note also that the channels and lakes of Mackenzie Delta are too densely packed to show individually.



gaining perspectives on how such species may adapt and cope with these potential changes. One such species, the broad whitefish, *Coregonus nasus*, is distributed within the Holarctic region from western Russia to the Coppermine River in Nunavut, Canada, where it occurs as both freshwater resident and anadromous populations. The Mackenzie River basin is the largest watershed in Arctic Canada, includes Canada's longest river, and consists of at least six subbasins (Fig. 1) (Abdul Aziz and Burn 2006). This system contains a diverse array of freshwater habitats culminating with the Mackenzie River Delta at its lower reaches, a system of almost 50 000 lakes of varying sizes and depths (Emmerton et al. 2007). Within the Mackenzie River system, anadromous and adfluvial potamodromous (from herein referred to as lacustrine) broad whitefish are found as far upstream as the Rampart Rapids near the town of Fort Good Hope (Reist and Chang-Kue 1997; N. Millar, L.N. Harris, and K. Howland, unpublished data). Spawning areas of anadromous populations have been identified using radiotelemetry and include several locations on the Mackenzie River mainstem (Fort Good Hope and Point Separation just upstream of the Mackenzie River Delta) and at least one upstream location in both the Peel and Arctic Red rivers (Chang-Kue and Jessop 1997; Reist and Chang-Kue 1997) (Fig. 1). The current understanding is that broad whitefish spawn at these areas in the fall and that young-of-the-year fish are carried to the outer Mackenzie River Delta and the near shore environments of the Beaufort Sea during the spring freshet (Reist and Chang-Kue 1997). The majority of young-of-the-year fish are swept eastward along the Tuktoyuktuk Peninsula or Richards Island by prevailing currents. They subsequently migrate into the productive freshwater lakes of these systems to feed after they become ice-free (Bond and Erickson 1985; Reist and Chang-Kue 1997). Upon sexual maturity, fish move to the outer Mackenzie River Delta or lakes of the outer delta systems before migrating to the aforementioned spawning locations in the fall (Chang-Kue and Jessop 1997; Reist and Chang-Kue 1997).

Mackenzie River system lacustrine populations of broad whitefish also exist in Travaillant Lake (Fig. 1) located 400 km upstream from the Beaufort Sea, which is connected to the mainstem Mackenzie River by the 70 km long Travaillant River. Little information is available, however, regarding possible spawning areas of broad whitefish in this system. Stable isotope analysis had suggested that these fish are transient visitors to the lake that have assimilated a significant fraction of their sulphur from food sources outside the lake (Hesslein et al. 1991). By contrast, comparisons of genetic variation (allozyme variation), life history vital rates, morphology, and habitat use suggested that Travaillant Lake broad whitefish are distinct from those in the Mackenzie River (Reist 1997; Chudobiak et al. 2002; Tallman et al. 2002). Most recently, radiotelemetry studies have shown that Travaillant Lake broad whitefish do not leave this system and therefore represent a truly lacustrine population (N. Millar, L.N. Harris, and K. Howland, unpublished data).

Several hypotheses can be put forth concerning the degree of genetic differentiation and the number of discrete genetic populations within the Mackenzie River system. If broad whitefish exhibit natal philopatry, it is probable that a number of discrete populations exist (Hendry et al. 2004). These populations would be differentiated due to reduced gene flow, with drift and possibly selection both promoting divergence. If homing in broad whitefish is imprecise, then the homogenizing effects of gene flow would lessen the degree of differentiation among putative populations and (or) fewer genetic populations are expected to exist. A lack of interpopulation differentiation in another Mackenzie River coregonine (Arctic cisco, *Coregonus autumnalis*) has recently been observed (J.L. Nielsen, Alaska Science Center, US Geological Survey, 4210 University Drive, Anchorage, Alaska, personal communication (2008)), yet it is not uncommon for genetic structuring to occur over very short geographic scales in other salmonids (e.g., Angers and Bernatchez 1998). Additionally, if Travaillant Lake populations are strictly lacustrine, then gene flow should be limited between this population and adjacent anadromous populations that should be reflected in significant genetic differentiation between them.

Anadromous populations of broad whitefish in the Mackenzie River system are also exploited during summer and autumn subsistence and, periodically, commercial fisheries (Treble 1996), but the relative contributions of these popula-

tions to the Mackenzie River based fisheries are unknown. Several broad whitefish populations migrate through the Mackenzie River Delta at any given time during the autumn fishery (Reist and Chang-Kue 1997), and consequently, any of them are potentially vulnerable to harvest across three different aboriginal land claim settlement areas within the region. Although physical tagging studies have had some limited success in determining catch composition of this harvest (Babaluk et al. 1997), molecular techniques have never been used to assess contributions of populations to this mixed-stock fishery despite the power of their application in other fisheries (e.g., Beacham et al. 2005).

Extensive research has been conducted on broad whitefish from the Mackenzie River system to address questions concerning their biology (Treble and Reist 1997), morphology (Chudobiak et al. 2002), life history variation (Chudobiak 1995; Tallman et al. 2002), and specific habitat requirements (Chang-Kue and Jessop 1997). Very little research, however, exists regarding genetic variation within and among these broad whitefish populations and their relative contributions to fisheries. Here, we sought to fill these important knowledge gaps and to provide valuable information to inform conservation planning.

Within this context, our study has three objectives. The first objective was to assay microsatellite DNA variation to determine the scale at which genetic structuring occurs in the Mackenzie River system, especially among anadromous populations. If homing to natal sites is high and straying is low, we expected to find several genetically differentiated populations in this system. Our second objective was to assess genetic diversity in known lacustrine (Travaillant Lake) populations of broad whitefish and to test for their genetic distinctiveness from known anadromous populations. Finally, we wanted to elucidate the relative contributions of the different broad whitefish populations to the Mackenzie River based subsistence fishery.

Materials and methods

Sample collection

Samples were collected in October and November 2003 and 2004 using gill nets to coincide with spawning time from six areas previously identified as important spawning locations: two locations along the mainstem Mackenzie River, the Peel and Arctic Red Rivers, and two locations in the Travaillant Lake system (Table 1; Fig. 1). Samples from mature and maturing fish were also collected from Campbell Lake, a lake approximately 10 km in length on the east side of the Mackenzie River Delta, where uncertainties remain regarding whether fish in this lake represent a discrete spawning population. Mixed-stock fishery samples were also collected mostly by local fishermen in subsistence fishing areas through which several populations are known to migrate (Table 1; Fig. 1).

Microsatellite DNA

Fin clips or muscle tissue was preserved in 95% ethanol and DNA was isolated from approximately 5 mg of tissue using Qiagen DNA extraction kits. Seven microsatellite loci were included in this study and included six that were developed specifically for lake whitefish, *Coregonus clupeaformis* (*Cocl-Lav4*, *Cocl-Lav6*, *Cocl-Lav8*, *Cocl-Lav10*, *Cocl-Lav18*, and *Cocl-27*; Rogers et al. 2004; Table 2), and one developed for Chinook salmon, *Oncorhynchus tshawytscha* (*Ots103*; Small et al. 1998; Table 2). Polymerase chain reaction (PCR) protocols were as described in Rogers et al. (2004) for the *Cocl-Lav* primers and Small et al. (1998) for *Ots103*, with slight modifications described in Harris and Taylor (2010). Each PCR was performed in a 10 μL volume with 1 μL of genomic DNA, 0.2 μmol/L of the fluorescently labelled forward primer, 0.5 μmol/L of the unlabelled reverse primer, 10 mmol/L dNTP, 1 μL of reaction buffer (New England Biolabs), and 0.1 U of *Taq* polymerase (New England Biolabs). PCR products were visualized on a Beckman-Coulter CEQ 8000 automated sequencer where alleles were scored by eye.

Genetic analysis

Basic descriptive statistics of microsatellite variation, including number of alleles (N_A), expected heterozygosity (H_E), and observed heterozygosity (H_O), were calculated using TFPGA version 1.3 (Miller 1997) and allelic richness (A_R, calculated using the rarefaction method; El Mousadik and Petit 1996) was calculated using FSTAT version 2.9.3.2 (Goudet 2002). Differences in A_R and multilocus H_E between populations from Mackenzie River system and Travaillant Lake were assessed using the permutation approach in FSTAT. The program HP-RARE (Kalinowski 2005) was used for the detection of genetic variation unique to specific sampling locations or areas (when sampling locations were combined) accounting for differences in sample size (private allelic richness (N_P)). For this analysis, we organized our samples into three groups: Mackenzie River system baseline populations (those that contribute fish to the mixed-stock fishery), Mackenzie River system fishery samples, and samples collected in the Travaillant Lake system. We rarefied to the minimal size of 412 alleles for each group.

Tests for deviations from Hardy–Weinberg equilibrium of observed genotypes were performed using GENEPOP version 3.4 (Raymond and Rousset 2003) for each locus–population combination using an exact test in which two-tailed P values were estimated using a Markov chain method of Guo and Thompson (1992). GENEPOP was also used to test for genotypic linkage disequilibrium for all combinations of locus pairs within sampling locations using a Markov chain method and to test for population differentiation between all pairs of populations (refer to Table 1; Fig. 1) over all loci combined using log-likelihood (G) based exact tests (Goudet et al. 1996) with default values. The results from all tests were compared with both a nominal alpha of 0.05 and an adjusted alpha using the sequential Bonferroni procedure (Rice 1989). We also used POWSIM (Ryman and Palm 2006) to investigate the power of our microsatellite DNA assays and the log-likelihood (G) based exact tests to resolve differences between localities across a range of effective population size (N_E) values and generations of drift under a model of complete isolation.

Spatial genetic structure was calculated at the population level by estimating F_{ST} (θ) (Weir and Cockerham 1984) and R_{ST} (Slatkin 1995) to measure the extent of genetic differentiation between populations. Pairwise F_{ST} and R_{ST} values were calculated using FSTAT version 2.9.3.2 (Goudet 2002)

Table 1. Broad whitefish sampling locations, sample sizes (N), and microsatellite diversity showing the average number of alleles per locus (N_A), number of private alleles (N_P), allelic richness (A_R), observed heterozygosity (H_O), and expected heterozygosity (H_E).

Region/sampling location	Location	N	N_A	N_P	A_R	H_O	H_E
Peel River (1)							
Scrapper Hill	67°15′N, 134°53′W	99	6.00	1	3.75	0.54	0.58
F. Koe Camp	67°27′N, 134°52′W	30	4.14	0	3.48	0.55	0.58
Road River	66°52′N, 135°00′W	60	5.29	2	3.67	0.54	0.57
Arctic Red River (2)	66°58′N, 133°16′W	35	5.14	1	3.54	0.55	0.62
Mackenzie River Delta							
East channel, Inuvik (2003)	68°20′N, 133°24′W	33	5.14	2	3.70	0.58	0.57
East channel, Inuvik (2004)	68°20′N, 133°24′W	11	3.00	0	2.89	0.47	0.54
East channel, W. Simon Camp	68°14′N, 133°49′W	17	4.00	0	3.45	0.51	0.52
West channel, Destruction City (2004)	67°44′N, 135°22′W	20	4.29	0	3.61	0.44	0.56
West channel, Destruction City (2005)	67°44′N, 135°22′W	19	4.00	0	3.37	0.52	0.56
West channel, Rat River (2004)	67°45′N, 135°07′W	25	4.57	0	3.60	0.55	0.53
West channel, Rat River (2005)	67°45′N, 135°07′W	32	4.29	0	3.39	0.52	0.55
C. Allen Camp	68°40′N, 134°20′W	30	4.86	2	3.81	0.57	0.55
B. Day Camp	68°18′N, 134°12′W	30	5.14	1	3.69	0.55	0.58
Napoiak Channel	68°35′N, 134°53′W	11	4.00	0	3.93	0.54	0.58
J. Firth Samples	68°13′N, 134°31′W	30	4.86	1	3.69	0.56	0.52
J. Maring Samples	68°06′N, 134°30′W	30	4.57	0	3.56	0.60	0.53
E. Lennie Camp	68°29′N, 134°33′W	30	4.43	1	3.28	0.53	0.49
Bassook	67°44′N, 134°38′W	27	3.71	0	2.92	0.57	0.52
Cuttoff	67°38′N, 134°38′W	28	4.57	0	3.67	0.57	0.57
Point Separation (3)	67°35′N, 134°04′W	23	4.43	0	3.68	0.48	0.57
Campbell Lake	68°12′N, 133°27′W	29	4.71	1	3.58	0.57	0.58
Tuktoyuktuk Harbour	69°22′N, 133°38′W	95	5.14	0	2.95	0.50	0.46
Mackenzie River Proper							
Mouth of Arctic Red River	67°26′N, 133°44′W	12	3.00	0	2.96	0.44	0.50
Tree River	67°26′N, 132°31′W	16	4.29	0	3.72	0.58	0.54
Fort Good Hope (4)	66°39′N, 129°25′W	34	5.14	0	3.65	0.57	0.56
Travaillant Lake System							
Travaillant Lake (2003)	67°40′N, 131°53′W	21	3.57	1	3.25	0.49	0.51
Travaillant Lake (2004)	67°40′N, 131°53′W	20	4.29	0	3.38	0.44	0.46
Travaillant Lake (2005)	67°40′N, 131°53′W	32	3.71	0	2.94	0.46	0.44
Travaillant River south (2003) (6)	67°36′N, 131°51′W	30	3.71	0	2.94	0.46	0.44
Travaillant River south (2004) (6)	67°36′N, 131°51′W	20	3.57	0	2.98	0.44	0.46
Travaillant River south (2005) (6)	67°36′N, 131°51′W	19	3.86	0	3.16	0.42	0.44
Travaillant River north (2004) (7)	67°45′N, 131°51′W	35	4.14	1	3.05	0.49	0.49
Travaillant River north (2005) (7)	67°45′N, 131°51′W	30	3.57	0	2.91	0.50	0.47

Note: Numbers following sample locations refer to baseline populations used in our mixed-stock assessment (refer to Fig. 1). Those without numbers are fishery (mixture) samples.

Table 2. Above diagonal: genetic differentiation among pairs of populations (ns, nonsignificant; asterisks, significant, Bonferroni-corrected minimum alpha 0.00238); below diagonal: pairwise F_{ST} (θ) comparisons among all pairs of populations.

Population	1	2	3	4	5	6	7
1	—	ns	ns	ns	ns	*	*
2	0.0092	—	ns	ns	ns	*	*
3	0.0187	0.0365	—	ns	ns	*	*
4	0.0052	0.0200	0.0002	—	ns	*	*
5	0.0024	0.0058	0.0255	0.0112	—	*	*
6	0.0418	0.0431	0.0487	0.0339	0.0602	—	ns
7	0.0376	0.0306	0.0492	0.0302	0.0393	0.0051	—

Note: Underlined values represent comparisons that are not significant ($P > 0.05$) based on the permutation process. 1, Peel River; 2, Arctic Red River; 3, Point Separation; 4, Mackenzie River at Fort Good Hope; 5, Campbell Lake; 6, Travaillant Lake south; 7, Travaillant Lake north.

with the significance of these estimates calculated using 1000 permutations in Arlequin version 3.1 (Excoffier et al. 2005). Global population differentiation across all populations, including 95% intervals and significance assessed with jackknife and bootstrap procedures, was also estimated using θ calculated in FSTAT. The program SPAGeDi (Hardy and Vekemans 2002) was used to determine if allele size significantly contributed to population differentiation, in which case R_{ST}, instead of F_{ST}, would be a better estimator of differentiation (allele permutation test with 20 000 permutations).

Genetic distances were estimated using the pairwise chord distance (D_{CE}) of Cavalli-Sforza and Edwards (1967), which has been shown to estimate tree topologies well in very closely related populations where drift is the prime factor driving divergence and because it is free of assumptions regarding modes of molecular evolution (Takezaki and Nei 1996). PHYLIP version 3.5 (Felsenstein 1993) was used to calculate D_{CE} and the corresponding genetic distance matrix was used to construct an unrooted neighbour-joining (NJ) tree to visualize, using the DRAWTREE module, genetic relationships among populations and sampling localities.

To further detect patterns of genetic differentiation between samples, a factorial correspondence analysis (FCA) of the microsatellite genotype data was conducted with the program Genetix version 4.05.02 (Belkhir et al. 2004). This was used to find the best linear combination of allele frequencies at different microsatellite loci that best describe variation between individual observations (e.g., Taylor et al. 2007).

To estimate the most likely number of populations in the Mackenzie River and Travaillant Lake systems, we conducted an analysis of population divergence assuming no particular structure a priori. We used the Bayesian model based clustering algorithm implemented by the STRUCTURE software (Pritchard et al. 2000) to assess the level of population subdivision within a set of collections without any a priori designation of populations. This analysis uses a likelihood approach to find the most likely number of K populations (i.e., the K value with the highest log-likelihood score) that are most consistent with the observed microsatellite allele frequency data. The analysis estimates the minimum number of populations in the total data set that minimizes departures from Hardy–Weinburg equilibrium and linkage equilibrium; deviations from such equilibria are typically found when mixtures of genetically divergent populations are analyzed as a composite. The STRUCTURE analysis was conducted using a burn-in period of 10 000 replications with subsequent analysis continuing for a further 10 000 MCMC replications (longer burn-in and replication runs produced identical results). For each value of K (from 1 to the most likely number of populations plus 2 in our study; cf. Evanno et al. 2005) that was assessed, we conducted 20 independent iterations to check for variability of obtained log-likelihood values (Pritchard et al. 2000). We ran the analysis under the correlated allele frequencies option because (*i*) previous tests of population differentiation suggested that the Mackenzie River system broad whitefish populations are not highly differentiated from each other and (*ii*) this option improves assignment of individuals in closely related populations (Pritchard et al. 2000). Default values implemented in STRUCTURE were selected for all other model parameters. Upon generation of the log probability given the data ($\Pr(X|K)$) (eq. 12 in Pritchard et al. 2000), where applicable, the posterior probability of K was calculated as suggested in the STRUCTURE manual.

Finally, a conditional maximum likelihood approach (Millar 1987) as implemented in the genetic stock identification program ONCOR (Kalinowski et al. 2007) was used to estimate the stock composition of populations (Peel River, Arctic Red River, Point Separation, and Fort Good Hope; Reist and Chang-Kue 1997) that contribute fish to those caught during subsistence fisheries in the lower Mackenzie River system. Mixture proportions (including 95% confidence intervals) for the fishery were estimated by bootstrapping baseline (as per Rannala and Mountain 1997) and fishery (mixture) samples 1000 times. Next, our data were subjected to two kinds of simulations to assess the accuracy of our mixture analysis. First, the original mixture proportions were used to perform realistic fishery simulations by randomly sampling 1000 fish from the fishery. To assess how differences in baseline population sizes may potentially impact our mixed-stock estimates, the realistic simulations were performed first with the empirical baseline population sizes and then with simulated baseline population sizes of 50, 100, and 500. For analyses involving empirical baseline population sizes, mixture genotypes were simulated as per Anderson et al. (2008) and when nonempirical baseline population sizes were used, mixture genotypes were simulated following Kalinowski et al. (2007). Each realistic fishery analysis was simulated 1000 times. Samples collected at the same location over multiple years (e.g., Peel River) were tested for deviations from Hardy–Weinburg equilibrium. Where no deviations were detected, samples were combined to increase fishery sample sizes for the ONCOR analysis. Second, to further assess the accuracy of our genetic stock identification estimates, fishery samples were simulated (N = 500 and data were bootstrapped 5000 times) in which all of the individuals in the fishery sample are from the same baseline population. Using these data, mixture proportions for all baseline populations contributing to the simulated mixtures were then estimated. Sample size effects on our estimates were assessed by performing simulations initially with our empirical baseline sample size and then using simulated baseline sample sizes of 50, 100, and 500 fish.

Results

Intrapopulation genetic variation

A total of 1013 samples were collected from 36 localities (Table 1; Fig. 1) and genotyped across seven microsatellite loci, all of which were polymorphic. The N_A detected ranged from 5 (*Cocl-Lav27*) to 21 (Cocl-Lav8) and H_E ranged from 0.41 (*Cocl-Lav27*) and 0.66 (*Ots103*). Within sampling locations, N_A averaged across all loci ranged from 3.0 in the east channel of Mackenzie Delta to 6.1 in the Peel River (Table 1). The overall mean A_R based on a minimum sample size of nine diploid individuals) was 3.4 and varied from 2.9 in the east channel of the Mackenzie Delta to 3.9 in the Napoiak channel in the Mackenzie River Delta (Table 1). Mean H_E was 0.54, ranging from 0.43 in a Travaillant River South sample to 0.58 in the Napoiak channel

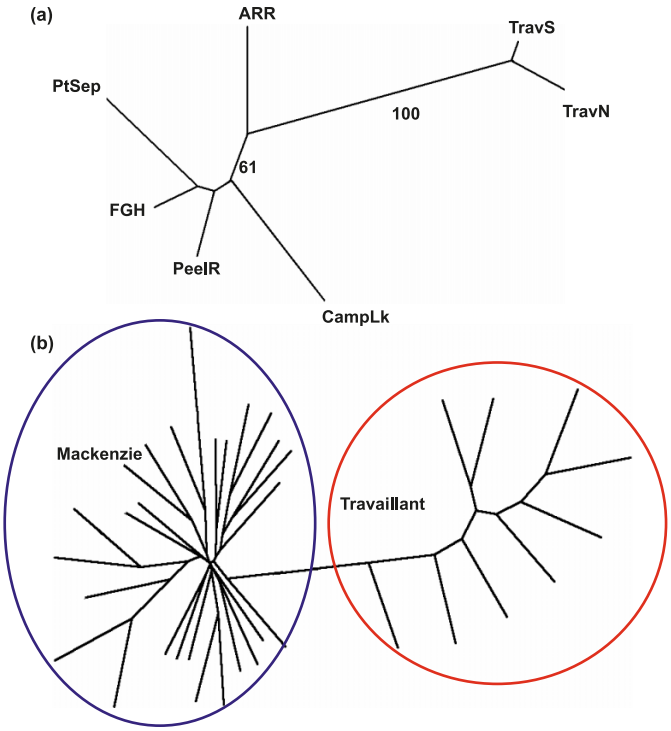


Fig. 2. Neighbour-joining tree based on Cavalli-Sforza and Edwards (1967) chord distances for broad whitefish populations surveyed in this study. Only a priori designated populations based on (*a*) previous literature and (*b*) all sample sites in the Mackenzie River system. Bootstrap values greater than 50% are shown. Circles show the geographic regions. PeelR, Peel River; ARR, Arctic Red River; PtSep, Point Separation; FGH, Mackenzie River at Fort Good Hope; CampLk, Campbell Lake; TravS, Travaillant Lake south; TravN, Travaillant Lake north.

sample (Table 1). The Travaillant Lake system had significantly lower H_E (0.47 compared with 0.54) and A_R (2.5 compared with 2.7) compared with the Mackenzie River system ($P < 0.001$). Over all loci, genetic variation unique to groups was quite low with private allelic richness (N_P) ranging from 0.40 (Travaillant Lake system) to 0.95 (Mackenzie River system baseline populations, data not shown).

Prior to Bonferroni adjustments, conformation to Hardy–Weinberg equilibrium was rejected in 33 of 224 tests ($P < 0.05$), 22 of which involved deficits of heterozygotes. Comparisons using the sequential Bonferroni correction (minimum adjusted alpha = 0.0002) showed that four tests were significant, two of which occurred in a sample collected from Tuktoyuktuk Harbour and the other two significant departures were from samples collected from one sampling location in the Mackenzie River Delta. Significant genotypic linkage disequilibrium was detected in 33 of 672 tests ($P < 0.05$), but after sequential Bonferroni corrections for multiple comparisons (minimum adjusted alpha = 0.00007), only one case of genotypic disequilibrium was found in a sample from the Tuktoyuktuk Harbour and the loci *Cocl-Lav8* and *Ots103*.

Population divergence and genetic structure

Log-likelihood (*G*) based exact tests of population differentiation indicated that the two main regions included in this study (i.e., Mackenzie River system and Travaillant Lake system) are significantly differentiated from each other ($P < 0.05$). Fourteen of 21 comparisons of differentiation between population pairs were significant ($P < 0.05$), but after sequential Bonferroni corrections of alpha (minimum adjusted alpha = 0.00238), this was reduced to eight pairwise comparisons (Table 2). None of the anadromous Mackenzie River populations were differentiated from each other (including the sample collected from Campbell Lake) using exact tests, but all were differentiated from both Travaillant Lake system populations ($P < 0.00238$) (Table 2). The two Travaillant Lake populations were not differentiated from each other ($P = 0.153$). Simulations using POWSIM indicated that our data provided >95% power to detect genetic differentiation at the observed level of F_{ST} (~0.01) within the Mackenzie River system (i.e., a true $F_{ST} = 0.01$ would result in detection of genetic differentiation using *G* tests with the range of loci that we used >95% of the time).

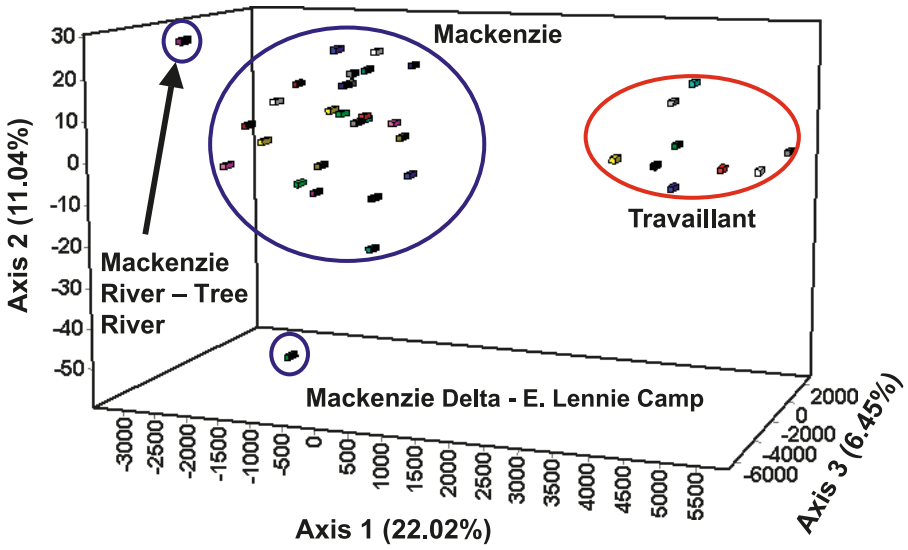
Allele size contributed significantly to population differentiation in only 14 of the 496 possible comparisons across loci and populations (results from SPAGeDi), and therefore, only F_{ST}, instead of R_{ST}, values are considered further. Values of F_{ST} (θ) ranged from 0.001 (*Cocl-Lav4*) to 0.072 (*Cocl-Lav6*) and the overall level of population subdivision based on average pairwise estimates was low ($\theta = 0.026$, 95% confidence interval = 0.010–0.045) among all localities. Among localities, pairwise F_{ST} values ranged from 0.0002 (between Point Separation and Fort Good Hope) to 0.0492 (between the Travaillant River South and Campbell Lake) (Table 2). Differences in θ were not substantial, but the comparisons were statistically significant in 14 of the 21 comparisons ($P < 0.05$) (Table 2) prior to sequential Bonferroni corrections and in 12 of 14 comparisons after adjustments were made (minimum adjusted alpha = 0.00238). Samples from the Travaillant Lake system were, however, always significantly different than samples from the anadromous Mackenzie River populations.

A clear genetic discontinuity was observed between anadromous populations and those sampled from Travaillant Lake as shown in the NJ tree with 100% bootstrap support (Fig. 2). When all sampling locations were included (i.e., those from mixed-stock fisheries), the major population clusters of Travaillant Lake and all other Mackenzie River samples were also clearly evident (Fig. 2).

Genetic differentiation among all samples, as summarized by FCA (Fig. 3), also revealed a strong geographical pattern of genetic variation. Similar to the results of the NJ dendogram, two distinct groupings were resolved showing the distinct genetic composition of Travaillant Lake and Mackenzie River system populations. In this analysis, when all sample sites were compared in both systems, there was no overlap between any samples and no intermediates between the two. There were, however, two outliers in the Mackenzie River samples that grouped apart from the other fish sampled from the Mackenzie River (Fig. 3). These included one location in the Mackenzie Delta at "E. Lennie's fish camp" and one location on the Mackenzie River proper at the mouth of the Tree River.

The STRUCTURE results revealed that that the most likely number of distinct genetic groups in the Mackenzie River system is two (mean –ln likelihood over the 20

Fig. 3. Results of the factorial correspondence analysis showing differentiation between Travaillant Lake system and Mackenzie River system broad whitefish.



runs = –14531.3; Supplementary Table S1).[3] This is consistent with the NJ tree and also the results of the FCA, which all show that there are at least two distinct clusters in this system. When Mackenzie River and Travaillant Lake samples were compared separately, the most likely number of populations within each system was one in both cases (K = 1, mean –ln likelihood over 20 runs = –11 619.4 and –2600.0 respectively; Supplementary Table S1). Similarly, when the Peel River and the Arctic Red River were analyzed by themselves, in both cases, the most likely number of populations in these rivers was one (K = 1 with the mean –ln likelihood over the 20 runs = –2665.2 and –3612.2, respectively, Supplementary Table S1). In all cases, the posterior probability of the most likely K value was 1.0 and any K value greater than or less than the most likely value had a posterior probability of 0.0 (Supplementary Table S1).

Mixed-stock analysis

The mixture analysis revealed that all baseline populations contribute to the Mackenzie Delta and Mackenzie River subsistence fishery and that there is variation in the contributions to the fishery depending on where fish are being exploited. When all fishery samples from the Mackenzie River were combined, the Peel River (including when all sampling locations were pooled given that no departures from Hardy–Weinberg equilibrium were found in the pooled sample) was estimated to be the largest contributor to the fishery (65.4% ± 3.4% SD) followed by the Arctic Red River (16.6 ± 2.3%), Fort Good Hope (10.6 ± 2.4%), and finally Point Separation (5.8 ± 1.7%) (Table 3). The results of the realistic fishery simulations were based on the estimated empirical mixture proportions of 0.554, 0.251, 0.157, and 0.0383 for the Peel River, Arctic Red River, Fort Good Hope, and Point Separation, respectively. There was, however, considerable variation in contributions to fisheries depending on harvest locations, but for the most part, the Peel River typically contributed the most in all cases (Table 3). For instance, the Peel River still contributed the most to fisheries in the east channel, west channel, and main channel of the Mackenzie Delta and the mainstem Mackenzie River when sampling locations in each region were combined; Peel River contributions were 66.9% ± 3.4%, 69.3% ± 3.2%, 65.9% ± 3.3%, and 76.9% ± 4.6%, respectively. The Point Separation source population often contributed the least to fisheries (Table 3). Variation in baseline sample sizes affected the point estimates of fishery contributions, but even at simulated baseline sample sizes of 500 fish for each population, the Peel River sample still was estimated as contributing the most to the fishery and Point Separation the least (Table 3).

Simulated mixtures (i.e., 100% of each baseline population examined in turn) were used to assess the accuracy and power of our mixture estimates and also indicated that increasing baseline sample sizes would increase the power of our analysis (data not shown). For example, a baseline sample size of 100 resulted in 77%, 89%, 88%, and 79% mixture estimations for the baseline populations Peel River, Arctic Red River, Point Separation, and Fort Good Hope, respectively, compared with 65%, 80%, 82%, and 70% when only 50 fish comprised each baseline sample.

Discussion

Genetic variability within and between populations

To our knowledge, this study represents the first genetic assessment of population structure within a large and complex river system in whitefish. Measures of genetic diversity resolved in the present study were similar to those reported in other studies of coregonines (e.g., Rogers et al. 2004) and remarkably less diverse than others (e.g., Säisä et al. 2008). As predicted, marked differences in genetic diversity were observed between lacustrine (Campbell Lake was not included in this group given its close affinity to anadromous populations) and anadromous populations of broad whitefish, a trend that has been previously documented in a vari-

[3] Supplementary data for this article are available on the journal Web site (http://cjfas.nrc.ca).

Table 3. Results of the genetic mixture analysis generated in ONCOR (Kalinowski et al. 2007) showing the estimated percent contribu- fisheries from various geographic locations from the lower Mackenzie River and Mackenzie River Delta.

	Peel River				Arctic Red River			
	50	100	500	E (189)	50	100	500	E (35)
All Mackenzie samples	42.0 (7.9)	46.1 (6.7)	52.8 (4.7)	65.4 (3.4)	26.0 (5.6)	26.2 (4.6)	25.5 (3.3)	16.6 (2.3)
Beaufort Sea[a]	26.7 (7.5)	26.6 (5.6)	27.6 (3.9)	48.2 (3.2)	57.2 (7.0)	61.9 (5.2)	66.8 (3.4)	39.4 (2.8)
East Channel[b]	42.8 (7.7)	47.7 (6.6)	55.8 (4.6)	66.9 (3.4)	21.8 (5.6)	21.1 (4.4)	19.2 (3.1)	13.6 (2.2)
West Channel[b]	45.4 (8.4)	50.3 (6.7)	57.2 (4.7)	69.3 (3.2)	12.2 (4.5)	9.7 (3.8)	6.6 (2.5)	6.8 (1.9)
Middle Channel[b]	42.2 (7.8)	46.1 (6.6)	51.4 (4.6)	65.9 (3.3)	21.3 (5.4)	20.3 (4.2)	19.3 (3.1)	13.2 (2.1)
Mackenzie River[c]	53.8 (8.7)	61.7 (6.9)	72.2 (4.5)	76.9 (3.1)	9.1 (4.7)	6.1 (3.5)	1.8 (1.8)	4.5 (1.8)

Note: The values represent the mean estimated percent contributions (±1 SD) estimated from realistic fishery simulations under a variety of simulated
[a]Includes samples from several locations in the Tuktoyuktuk Harbour.
[b]Indicates the different channels of the Mackenzie River Delta.
[c]Includes all Mackenzie River sampling sites upstream of the Arctic Red River.

ety of fish species including other salmonids (Ward et al. 1994; DeWoody and Avise 2000; Tonteri et al. 2007). Greater genetic variation in anadromous fish can likely be explained by larger evolutionarily effective population sizes of marine and anadromous fish species (Ward et al. 1994). Populations of freshwater fishes can be limited to particular drainages over short to moderate evolutionary time and therefore often exhibit lower effective populations sizes compared with marine or anadromous populations (DeWoody and Avise 2000).

Historical factors have also likely contributed to the observed differences in genetic variation. For instance, demographic events, such as bottlenecks or founder events associated with postglacial dispersal from Beringia (the key glacial refuge for broad whitefish; Harris and Taylor 2010), have probably affected recently derived freshwater populations more than their presumably anadromous/marine ancestors (Hewitt 1996; Bernatchez and Wilson 1998; Harris and Taylor 2010). Furthermore, populations near the periphery of a species' range (such as those in the Travaillant Lake system) were probably colonized later in deglaciation and typically show reduced genetic diversity associated with chance founder events and bottlenecks (Ibrahim et al. 1996). The lower genetic diversity may be the result of a small number of founding individuals with drift acting to lower genetic diversity in these populations that have been isolated from anadromous Mackenzie River populations for some time (Lesica and Allendorf 1995; Tonteri et al. 2007). Indeed, the lack of private alleles in the lacustrine broad whitefish from Travaillant Lake suggests that this population was founded from a small number of anadromous source populations after recolonization of the Mackenzie River system. This trend has been observed in many north-temperate fish species (e.g., Castric and Bernatchez 2003) and is not surprising given the glacial history of the area, which has provided many opportunities for postglacial dispersal into previously unoccupied habitats (Bernatchez and Wilson 1998; Rempel and Smith 1998).

Of special interest was the concordance among the STRUCTURE, genic differentiation, unrooted NJ tree, and FCAs that all suggested that lacustrine Travaillant Lake populations are highly differentiated from anadromous Mackenzie River populations. This is likely a result of the lake-resident life history of Travaillant Lake fish, which has presumably isolated them from their Mackenzie River populations for many generations. In addition to contemporary life history differences, historical factors, such as timing of postglacial colonization and refugial origin, could also contribute to genetic differentiation. For example, it is hypothesized that distinct postglacial origins of anadromous and lacustrine populations of Arctic char, *Salvelinus alpinus*, may explain why these populations are highly differentiated from one another (Bernatchez et al. 1998). Furthermore, secondary contact of distinct glacial races is not uncommon when examining the evolutionary history of north-temperate fishes (Wilson and Hebert 1998; Lu et al. 2001; Turgeon and Bernatchez 2001). Given the geological history of the area, the current North American distribution, and lack of alleles unique to lacustrine broad whitefish, separate glacial refugia are unlikely for broad whitefish (Harris and Taylor 2010). Secondary contact between lake whitefish lineages, however, has likely occurred in the Mackenzie River system, but this species survived in at least five glacial refugia (Bernatchez and Dodson 1991). In general, populations of broad whitefish in the Mackenzie River likely have a common origin from anadromous colonizers that dispersed postglacially from Beringia (Harris and Taylor 2010). This phenomenon, that is lacustrine populations founded from anadromous populations, has been suggested for several other salmonid species (see review by Behnke 1972; King et al. 2001).

Virtually all analyses showed that Travaillant Lake fish form a genetic cluster that is divergent from the anadromous Mackenzie River populations. Several studies have also found significant differences between these two groups of fish using a variety of methods. For example, Tallman et al. (2002) found that anadromous broad whitefish had greater reproductive investment (fecundity) and a greater age-at-maturity in comparison with lacustrine populations, although growth appeared to be similar among populations. Chudobiak et al. (2002) found that anadromous populations from the Arctic Red River and lacustrine populations from the Travaillant Lake differed morphologically and Reist (1997) provided the first insights that lacustrine Travaillant Lake fish and anadromous Mackenzie River fish are genetically divergent groups of populations based on allozymes. Furthermore, although broad whitefish can migrate upwards of 800 km (Babaluk et al. 1997; Chang-Kue and Jessop 1997), radiotelemetry studies have reported a lack of movement of broad whitefish between these two systems (Chang-Kue and Jessop 1997; M. Vangerwen-Toyne, Fisheries and Oceans

tions of source populations of broad whitefish to fish captured during summer and fall subsistence

Mackenzie River at Point Separation				Mackenzie River at the town of Fort Good Hope			
50	100	500	E (23)	50	100	500	E (34)
9.0 (3.9)	6.9 (3.1)	4.5 (2.2)	7.4 (1.9)	23.0 (6.6)	20.8 (5.7)	17.2 (3.9)	10.6 (2.4)
5.6 (3.5)	3.3 (2.4)	1.1 (1.2)	6.4 (1.8)	10.4 (5.2)	8.2 (3.7)	4.6 (2.5)	5.9 (2.1)
16.0 (4.5)	14.9 (3.6)	14.1 (2.7)	10.8 (2.0)	19.4 (6.5)	16.2 (5.2)	10.8 (3.5)	8.7 (2.5)
11.0 (4.2)	9.5 (3.3)	7.3 (2.8)	9.1 (1.8)	31.4 (7.6)	30.6 (6.0)	28.9 (4.5)	14.7 (2.6)
7.4 (3.8)	5.4 (2.8)	2.5 (1.8)	7.1 (1.9)	29.0 (7.0)	28.1 (5.7)	26.8 (4.3)	13.7 (2.5)
6.6 (4.1)	4.1 (2.9)	1.1 (1.4)	5.8 (1.7)	30.1 (7.6)	28.2 (6.4)	24.8 (4.5)	12.9 (2.6)

population sizes including the empirical baseline sizes (E).

Canada, Freshwater Institute, 501 University Crescent, Winnipeg, Manitoba, personal communication (2009)).

Perhaps more surprisingly, we found a lack of strong interpopulation genetic differentiation among anadromous populations in the Mackenzie River system despite previous work that suggested that there are probably several reproductively isolated populations within the system (Reist 1997; Reist and Chang-Kue 1997). Some of our pairwise estimates of F_{ST} were, however, significant (although very low). Comparisons of microsatellite DNA variation between Arctic cisco populations from the Coleville River and from the Mackenzie River system also revealed a general lack of strong differentiation despite the large distance between the two systems (J.L. Nielsen, Alaska Science Center, US Geological Survey, 4210 University Drive, Anchorage, Alaska, personal communication (2008)). By contrast, numerous studies have shown differentiation among fish populations in rivers separated by very short distances (e.g., Koskinen et al. 2001; Whiteley et al. 2004; Neville et al. 2006), but a lack of strong differentiation among some marine (Hutchings et al. 2007) and anadromous fish populations (McLean et al. 1999) is not unprecedented.

Several hypotheses may explain the low levels of genetic differentiation in the Mackenzie River system. First, homing behaviour may be imprecise, resulting in some straying between populations and thus limited reproductive isolation. Natal homing has evolved in several groups of fishes, typified by salmonids, and promotes fine-scale genetic structuring in these fishes (Hendry et al. 2004; Rich et al. 2006). Because anadromous fish often exhibit natal philopatry, fish populations typified by this life history often show genetic differentiation and subdivided population structure between freshwater spawning tributaries. In some cases, however, selection may favour straying if population sizes or spawning habitat quality are typically variable (Hendry et al. 2004; Esteve 2005) or when the risk of inbreeding is high (Hendry et al. 2004). In such cases, population structure is less well developed. For instance, Neville et al. (2006) showed that a lack of fine-scale homing in Chinook salmon resulted in a lack of genetic structuring in an Idaho river system. Pascual et al. (1995) reported straying rates as high as 41.6% in hatchery Chinook salmon (cf. Hendry and Stearns 2004). In the anadromous eulachon, *Thaleichthys pacificus*, Mclean et al. (1999) also found little genetic differentiation among populations from distinct freshwater locations throughout their range and suggested that this was the result of a high degree of straying among watersheds. The iteroparous coastal cutthroat trout, *Oncorhynchus clarkii clarkii*, has a life history more similar to that of the broad whitefish and straying rates can be as high as 35% (Michael 1989; cf. Hendry and Stearns 2004).

Broad whitefish may have a high degree of straying if they do not spend enough time in their freshwater natal streams to imprint effectively. For example, young-of-the-year are carried to nearshore marine environments and eventually to coastal lakes in the Tuktoyuktuk Peninsula during the spring freshet (Reist and Chang-Kue 1997). As such, imprinting may be to this nearshore environment or these coastal lakes rather than to the spawning locality per se. Similarly, pink salmon, *Oncorhynchus gorbuscha*, have a tendency to stray more than other species of Pacific salmon, possibly due to their short freshwater residency, which results in a reduced opportunity for imprinting (Hendry et al. 2004). Although there is a wealth of knowledge on the straying rates of salmonids (reviewed by Hendry et al. 2004), empirical and experimental data on the degree of straying of coregonines are lacking. Initial evidence of straying was provided by Babaluk et al. (1997) who found that a broad whitefish tagged in the west channel of the Mackenzie River Delta was recaptured the following year migrating up the east channel of the delta. Further work, however, is needed to determine if straying is the main cause of the lack of differentiation in this system.

Second, a lack of genetic differentiation in the Mackenzie River system may be due to historical factors having left a pronounced signature of past evolutionary processes. For example, the lack of differentiation may be evidence that this is a recently colonized area in which there was extensive historical gene flow between founding populations or one that has recently been colonized by a single founding panmictic population (and thus perhaps not enough evolutionary time has passed to promote divergence). If broad whitefish were isolated in a single refugium during the last Pleistocene glaciation, as appears to be the case (Harris and Taylor 2010), then they have had approximately 12 000 years to diverge into discrete populations (Lindsay and McPhail 1986; Pielou 1991), which may not have been long enough for distinct broad whitefish populations to form, at least when assessed with the loci used in this study. Estoup and Angers (1998) suggested that 2000 generations since population founding is needed to promote significant differentiation at microsatellite DNA loci via mutation. As the Mackenzie

River area has been subject to postglacial colonization for about 12 000 years, there likely has been only about 1700 generations for discrete populations to evolve given that broad whitefish first mature at approximately 7 years of age (Bond 1982). Consequently, it is likely that drift has been the predominate factor driving differentiation at microsatellite DNA loci — an inference supported by our SPAGeDi analyses.

Finally, N_E in this system may be extremely large such that the effects of genetic drift have been negligible in promoting differentiation among populations given the relatively short time since founding. Unfortunately, to our knowledge, no direct estimates of population size have yet been conducted, data that would greatly add to the understanding of the lack of differentiation in this system. Thera (1998), however, incorporated various expert opinions on abundance and estimated spawning population sizes for anadromous broad whitefish in the lower Mackenzie River at somewhere between 1 040 000 and 7 300 000 fish. Assuming an N_E to census size ratio of 0.2 (Waples 2002), a mid-range estimate of census spawning population size split across the six major suspected spawning areas, 1700 generations since founding, and the assemblage of microsatellite DNA alleles that we observed, the model of complete isolation employed in POWSIM generates an expected F_{ST} of 0.007. This expected F_{ST} under the complete isolation model is about one half of what we observed among the anadromous populations (~0.013), which suggests that perhaps N_E within populations is somewhat lower and more variable but also that it might not be necessary to invoke considerable contemporary gene flow among Mackenzie River anadromous broad whitefish populations as an explanation for the observed low levels of genetic differentiation. Given, however, tagging-based inferences of movement between localities (Babaluk et al. 1997), it is more reasonable to conclude that low differentiation among anadromous components of the Mackenzie River assemblage of broad whitefish results from the combined effects of some contemporary gene flow, large effective population sizes, and relatively recent postglacial colonization of the area.

Mixture analysis

Results of the mixture analysis indicated that all populations contribute to the subsistence fishery, although the catch is dominated by fish from the Peel River. In addition, when sample size effects of baseline populations were tested using realistic fishery simulations, we consistently found a high contribution of Peel River fish. However, because there was some variation in proportional contributions depending on simulated baseline population sizes, it seems clear that increasing empirical baseline sizes would increase the accuracy of mixture analyses. Despite some variability in point estimates of mixture proportions, we consistently found that the Peel River system contributed the most to mixtures over all and when the analyses were conducted on specific regions (e.g., east channel and eastern Mackenzie Delta verses west channel and western Mackenzie Delta). The Peel River system is the first major river system broad whitefish encounter during upstream spawning migrations, so it is perhaps not surprising that it would contribute the most. In a study in which 113 broad whitefish were tagged near the town of Aklavik (~90 km downstream from the mouth of the Peel River), four fish were recaptured, two of which were in the Peel River (Babaluk et al. 1997). The following year, 1225 broad whitefish were tagged at Horseshoe Bend, and although the majority of these fish were recaptured at the tagging location, fish were also recaptured in the Peel River, the Arctic Red River, and at the spawning location near Fort Good Hope (Babaluk et al. 1997), again suggesting that more than one population contributes to the fishery and that straying among populations exists in this system. Radiotelemetry studies have suggested that Point Separation is an important spawning location for broad whitefish in this system (Chang-Kue and Jessop 1997), a result not apparent from our genetic study. It has been suggested, however, that disturbance to fish associated with the extensive gill-netting at Point Separation at the time of the radiotelemetry studies may have induced premature spawning, giving the false impression that this area is an important spawning location (R. Tallman, Fisheries and Oceans Canada, Freshwater Institute, 501 University Crescent, Winnipeg, Manitoba, personal communication (2009)).

A large majority of broad whitefish captured upstream in the Mackenzie River (e.g., at Tree River) were estimated to have been composed of fish from the Peel River, yet we expected that most of these fish would be assigned to the next downstream spawning population at Fort Good Hope. Given the energetic requirements of migration, it is unlikely that broad whitefish would migrate that far upstream of the Peel River and then migrate back to that system to spawn. Instead, it is possible that there may be a riverine population in the Mackenzie River system that uses the Peel River to spawn. There is no confirmation of the existence of this life history in the area, although riverine forms have been known in Russia for some time (Berg 1962). J.A. Babaluk and J.D. Reist (Fisheries and Oceans Canada, Freshwater Institute, 501 University Crescent, Winnipeg, Manitoba, unpublished data) assessed strontium levels in broad whitefish otoliths throughout the Mackenzie River system and found that some fish inhabiting the Peel River appeared to be a completely freshwater form. It is unknown if those fish were Peel River residents or a Mackenzie River resident form that migrates to the Peel River during spawning season. Regardless, our mixture results are consistent with the suggestion by J.A. Babaluk and J.D. Reist (unpublished data) of the existence of a riverine freshwater-resident form and suggest that there may be a higher level of life history complexity in this system than previously appreciated.

Conservation implications

The results of our study have several implications for the conservation and management of Mackenzie River system broad whitefish. First is the clear genetic distinction observed between anadromous and lacustrine broad whitefish. These genetic data are consistent with previous morphological (Chudobiak et al. 2002), life history (Tallman et al. 2002), stable isotope (Hesslein et al. 1991), and allozyme data (Reist 1997). In combination, these data argue that there are two distinct units of conservation below the species level (e.g., potential "designatable units"; COSEWIC 2005) that should be considered important in terms of management: (*i*) anadromous populations of the Mackenzie River

and its tributaries and (*ii*) lacustrine populations from the Travaillant Lake system.

Although, based on our microsatellite data, it appears that these two groups have not been isolated from each other for an evolutionarily long time period, it is possible that unique local adaptations may have evolved in each, which would warrant their separate conservation status. For example, Travaillant Lake populations are probably adapted to live solely within freshwater, and these populations are at the periphery of their range in the Mackenzie River system. If postglacial colonization is still occurring in this system, locally adapted traits such as those associated with a solely freshwater lifestyle may be extremely important for colonization and persistence within novel freshwater environments. Peripheral populations are often the most genetically divergent and they may harbour distinct traits important for adaptation to changing environments or new conditions (Lesica and Allendorf 1995; Taylor et al. 2003). Newly formed lakes within the Mackenzie River system may represent such novel environments for colonizing anadromous whitefish. Furthermore, the results of our study emphasize the importance of considering life history variation when developing conservation strategies. Travaillant Lake fish are reproductively isolated from anadromous Mackenzie populations, and because this limits the possibility for new genetic diversity via gene flow, it is expected that these lacustrine populations may be more vulnerable to extinction following a population crash (Tonteri et al. 2007). As such, high conservation status should be given to populations that exhibit this life history, at least in the Mackenzie River system.

Alternatively, our analyses suggest that all anadromous populations in the Mackenzie River system could be managed as one unit, at least genetically. Ideally, all populations should be treated as independent management units, maintaining maximum genetic and phenotypic diversity, thereby preserving local adaptive diversity. We recognize, however, that this is not always possible given limited management resources in many situations. Consequently, in the absence of other data (e.g., morphological, ecological, physiological, etc.), anadromous populations of the Mackenzie River system appear to represent a single unit of management. If all anadromous populations are taken to be equal with respect to conservation, then priority for protection should be given to those that are particularly threatened by human impact (Bernatchez 2005). This may mean protecting those populations most harvested during subsistence fisheries (i.e., the Peel River), those that may contain unique life history variants (i.e., the potential riverine subpopulations of the Peel River), or those most likely to be impacted by oil and gas exploration and development (i.e., populations in closest proximity to construction of the potential Mackenzie Valley pipeline).

Major mixed-stock broad whitefish subsistence fisheries exist in the Beaufort Sea, the Mackenzie River Delta, and the Mackenzie River, which cover three different aboriginal land claim settlement areas (Inuvialuit, Gwich'in, and Sahtu). The results of mixture analysis in our study bring up several important management considerations. First, even though all populations contribute to subsistence fisheries of the Mackenzie Delta and Mackenzie River, our data indicate that the fishery is dominated for the most part by Peel River fish. In the absence of any empirical estimates of population size, our data suggest that it may be very important to define and protect critical habitats, such as those used for spawning, in the Peel River system. Second, because our results showed that contributions to the subsistence fishery are variable depending on the harvest location within this system (i.e., east, west, or main channel), different management regimes may be required depending on the fishing area. Because this subsistence fishery spans three land claims, coordination among the comanagement boards within these regions is a necessity for effective management of the species. Third, the results of the mixed-stock analysis have provided evidence that there may be a riverine life history form of broad whitefish present in this system that, if corroborated, would be an extremely rare phenomenon in this area. Conservation of such populations may be important, as they could represent a distinct evolutionary lineage separate from lacustrine and anadromous populations of the system and (or) they may have evolved locally adapted traits important for a riverine life history. Ideally, future radiotelemetry or otolith microchemistry studies can provide more insight into the possibility of this in the Mackenzie River system, which will help guide specific management decisions. Overall, our data provide a more complete understanding of a hitherto enigmatic species across a vast riverscape — information that will be useful in future management and conservation decisions.

Acknowledgements

We extend thanks to the many Gwich'in and Inuvialuit harvesters who kindly provided samples. Namely, we would like to thank W. Simon, J. Maring, J. Firth, C. Allen, E. Lennie, J. Carmichael, D. Andre, T. Kendo, S. Blake, F. Blake Sr., B. Wilson, R. Andre, and G. Niditchie. We also want to thank K. Howland, M. Vangerwen-Toyne, E. Hiebert, P. Cott, R. Tallman, D. Pittman, C. Wenghofer, and L. Harwood, all with Fisheries and Oceans Canada, and N. Millar (Gwich'in Renewable Resource Board) for either assistance in the field or providing archived samples of broad whitefish. We also thank the Taylor laboratory, A. Gerstein, and three anonymous reviewers for comments on this manuscript. Funding for this research was provided by the Gwich'in Renewable Resource Board, the Fisheries Joint Management Committee, Fisheries and Oceans Canada, Indian and Northern Affairs Canada, and a Natural Sciences and Engineering Research Council of Canada Discovery Grant awarded to E.B.T. Logistical support was provided by the Polar Continental Shelf Project.

References

Abdul Aziz, O.I., and Burn, D.H. 2006. Trends and variability in the hydrological regime of the Mackenzie River Basin. J. Hydrol. (Amst.), **319**(1–4): 282–294. doi:10.1016/j.jhydrol.2005.06.039.

Allendorf, F.W., and Luikart, G. 2007 Conservation and the genetics of populations. Blackwell Publications, Oxford, U.K.

Anderson, E.C., Waples, R.S., and Kalinowski, S.T. 2008. An improved method for predicting the accuracy of genetic stock identification. Can. J. Fish. Aquat. Sci. **65**(7): 1475–1486. doi:10.1139/F08-049.

Angers, B., and Bernatchez, L. 1998. Combined use of SMM and

non-SMM methods to infer fine structure and evolutionary history of closely related brook charr (*Salvelinus fontinalis*, Salmonidae) populations from microsatellites. Mol. Biol. Evol. **15**: 143–159.

Avise, J.C. 2004. Molecular markers, natural history, and evolution. 2nd ed. Sinauer, Sunderland, Mass.

Babaluk, J.A., Wastle, R.J., and Treble, M.A. 1997. Broad whitefish t-bar anchor tagging in the Mackenzie River Delta, NT, 1992–1993. *In* The Proceedings of the Broad Whitefish Workshop: the Biology, Traditional Knowledge and Scientific Management of Broad Whitefish (*Coregonus nasus* (Pallus)) in the Lower Mackenzie River. *Edited by* R.F. Tallman and J.D. Reist. Can. Tech. Rep. Fish. Aquat. Sci. No. 2193. pp. 107–116.

Balloux, F., and Lugon-Moulin, N. 2002. The estimation of population differentiation with microsatellite markers. Mol. Ecol. **11**(2): 155–165. doi:10.1046/j.0962-1083.2001.01436.x.

Beacham, T.D., Candy, J.R., McIntosh, B., MacConnachie, C., Tabata, A., Miller, K.M., and Withler, R.E. 2005. DNA-level variation of sockeye salmon in Southeast Alaska and the Nass and Skeena rivers, British Columbia, with applications to stock identification. N. Am. J. Fish. Manag. **25**(3): 763–776. doi:10.1577/M04-080.1.

Behnke, R.J. 1972. The systematics of salmonid fishes of recently glaciated lakes. J. Fish. Res. Board Can. **29**: 639–671.

Belkhir, K., Borsa, P., Chikhi, L., Raufaste, N., and Bonhomme, F. 2004. Genetix 4.05, logiciel sous windows TM pour la génétique des populations, Version 4.05. Laboratoire Génome, Populations, Interactions, CNRS UMR 5000, Université de Montpellier II, Montpellier, France.

Berg, L.S. 1962. Freshwater fishes of the USSR and adjacent countries. 4th ed. Israel Program for Scientific Translations, Jerusalem.

Bernatchez, L. 2005. On the role of natural selection in promoting population divergence in whitefish (*Coregonus* sp.): relevance for population management in the Great Lakes. *In* Proceedings of a Workshop on the Dynamics of Lake Whitefish (*Coregonus clupeaformis*) and the Amphipod Diporeia in the Great Lakes. Gt. Lakes Fish. Comm. Tech. Rep. No. 66. pp. 21–46.

Bernatchez, L., and Dodson, J.J. 1991. Phylogeographic structure in mitochondrial-DNA of the lake whitefish (*Coregonus clupeaformis*) and its relation to Pleistocene glaciations. Evolution, **45**(4): 1016–1035. doi:10.2307/2409706.

Bernatchez, L., and Wilson, C.C. 1998. Comparative phylogeography of Nearctic and Palearctic fishes. Mol. Ecol. **7**(4): 431–452. doi:10.1046/j.1365-294x.1998.00319.x.

Bernatchez, L., Dempson, J.B., and Martin, S. 1998. Microsatellite gene diversity analysis in anadromous arctic char, *Salvelinus alpinus*, from Labrador, Canada. Can. J. Fish. Aquat. Sci. **55**(5): 1264–1272. doi:10.1139/cjfas-55-5-1264.

Bond, W.A. 1982. A study of the fishery resources of Tuktoyaktuk Harbour, southern Beaufort Sea coast, with special reference to life histories of anadromous coregonids. Can. Tech. Rep. Fish. Aquat. Sci. No. 1119. pp. 1–90.

Bond, W.A., and Erickson, R.N. 1985. Life history studies of anadromous coregonid fishes in two freshwater lake systems on the Tuktoyaktuk Peninsula, Northwest Territories. Can. Tech. Rep. Fish. Aquat. Sci. No. 1336. pp. 1–61.

Castric, V., and Bernatchez, L. 2003. The rise and fall of isolation by distance in the anadromous brook charr (*Salvelinus fontinalis* Mitchill). Genetics, **163**(3): 983–996. PMID:12663537.

Cavalli-Sforza, L.L., and Edwards, A.W.F. 1967. Phylogenetic analysis. Models and estimation procedures. Am. J. Hum. Genet. **19**(3 Pt. 1): 233–257. PMID:6026583.

Chang-Kue, K.T.J., and Jessop, E.F. 1997. Broad whitefish radio tagging studies in the lower Mackenzie River and adjacent coastal region, 1982–1993. *In* The Proceedings of the Broad Whitefish Workshop: the Biology, Traditional Knowledge and Scientific Management of Broad Whitefish (*Coregonus nasus* (Pallus)) in the Lower Mackenzie River. *Edited by* R.F. Tallman and J.D. Reist. Can. Tech. Rep. Fish. Aquat. Sci. No. 2193. pp. 117–146.

Chudobiak, D.H. 1995. An examination of lacustrine and estuarine populations of Mackenzie broad whitefish (*Coregonus nasus* Pallus): the role of migration and commercial exploitation on life history variation. M.Sc. thesis, Department of Zoology, University of Manitoba, Winnipeg, Man.

Chudobiak, D.H., Abrahams, M.V., and Tallman, R.F. 2002. Variation in the morphology of two populations of Arctic broad whitefish, *Coregonus nasus* (Pallas), in the Mackenzie River. Arch. Hydrobiol. **57**(Special Issue): 291–305.

COSEWIC. 2005. Guidelines for recognizing designatable units below the species level. Committee on the Status of Endangered Wildlife in Canada, Ottawa, Ont. Available at www.cosewic.gc.ca/eng/sct2/sct2_5_e.cfm [accessed 14 July 2008].

Costello, A.B., Down, T.E., Pollard, S.M., Pacas, C.J., and Taylor, E.B. 2003. The influence of history and contemporary stream hydrology on the evolution of genetic diversity within species: an examination of microsatellite DNA variation in bull trout, *Salvelinus confluentus* (Pisces: Salmonidae). Evolution, **57**(2): 328–344. PMID:12683529.

DeWoody, J.A., and Avise, J.C. 2000. Microsatellite variation in marine, freshwater and anadromous fishes compared with other animals. J. Fish Biol. **56**(3): 461–473. doi:10.1111/j.1095-8649.2000.tb00748.x.

El Mousadik, A., and Petit, R.J. 1996. High level of genetic differentiation for allelic richness among populations of the argan tree [*Argania spinosa* (L.) Skeels] endemic to Morocco. Theor. Appl. Genet. **92**(7): 832–839. doi:10.1007/BF00221895.

Emmerton, C.A., Lesack, L.F.W., and Marsh, P. 2007. Lake abundance, potential water storage, and habitat distribution in the Mackenzie River Delta, western Canadian Arctic. Water Resour. Res. **43**(5): W05419. doi:10.1029/2006WR005139.

Esteve, M. 2005. Observations of spawning behaviour in Salmoninae: *Salmo*, *Oncorhynchus* and *Salvelinus*. Rev. Fish Biol. Fish. **15**(1–2): 1–21. doi:10.1007/s11160-005-7434-7.

Estoup, A., and Angers, B. 1998. Microsatellites and minisatellites for molecular ecology: theoretical and empirical considerations. *In* Advances in molecular ecology. *Edited by* G. Carvalho. IOS Press, Amsterdam, The Netherlands. pp. 55–86.

Evanno, G., Regnaut, S., and Goudet, J. 2005. Detecting the number of clusters of individuals using the software STRUCTURE: a simulation study. Mol. Ecol. **14**(8): 2611–2620. doi:10.1111/j.1365-294X.2005.02553.x. PMID:15969739.

Excoffier, L., Laval, G., and Schneider, S. 2005. Arlequin. Version 3.0. An integrated software package for population genetics data analysis. Evol. Bioinform. **1**: 47–50.

Felsenstein, J. 1993. PHYLIP (Phylogeny Inference Package) user manual. Department of Genetics, University of Washington, Seattle, Wash.

Goudet, J. 2002. FSTAT: a program to estimate and test gene diversities and fixation indices. Version 2.9.3.2. Available at www2.unil.ch/popgen/softwares/fstat.htm.

Goudet, J., Raymond, M., de Meeüs, T., and Rousset, F. 1996. Testing differentiation in diploid populations. Genetics, **144**(4): 1933–1940. PMID:8978076.

Guo, S.W., and Thompson, E.A. 1992. Performing the exact test of Hardy–Weinberg proportion for multiple alleles. Biometrics, **48**: 361–372. PMID:1637966.

Hardy, O.J., and Vekemans, X. 2002. SPAGeDi: a versatile compu-

ter program to analyse spatial genetic structure at the individual or population levels. Mol. Ecol. Notes, **2**(4): 618–620. doi:10.1046/j.1471-8286.2002.00305.x.

Harris, L.N., and Taylor, E.B. 2010. Pleistocene glaciations and contemporary genetic diversity in a Beringian fish, the broad whitefish, *Coregonus nasus* (Pallas): inferences from microsatellite DNA variation. J. Evol. Biol. **23**(1): 72–86. doi:10.1111/j.1420-9101.2009.01858.x. PMID:19925592.

Hedrick, P.W. 2000. Genetics of populations. 2nd ed. Jones and Bartlett Publishers, Boston, Mass.

Hendry, A.P., and Stearns, S.C. (*Editors*). 2004. Evolution illuminated: salmon and their relatives. Oxford University Press, Oxford, U.K.

Hendry, A.P., Castric, V., Kinnison, M.T., and Quinn, T.P. 2004. The evolution of philopatry and dispersal: homing versus straying in salmonids. *In* Evolution illuminated: salmon and their relatives. *Edited by* A.P. Hendry and S.C. Stearns. Oxford University Press, Oxford, U.K. pp. 52–91.

Hesslein, R.H., Capel, M.J., Fox, D.E., and Hallard, K.A. 1991. Stable isotopes of sulfur, carbon and nitrogen as indicators of trophic levels and fish migration in the lower Mackenzie River basin, Canada. Can. J. Fish. Aquat. Sci. **48**(11): 2258–2265. doi:10.1139/f91-265.

Hewitt, G.M. 1996. Some genetic consequences of ice ages, and their role in divergence and speciation. Biol. J. Linn. Soc. **58**: 247–276.

Hutchings, J.A., Swain, D.P., Rowe, S., Eddington, J.D., Puvanendran, V., and Brown, J.A. 2007. Genetic variation in life-history reaction norms in a marine fish. Proc. R. Soc. Lond. B Biol. Sci. **274**(1619): 1693–1699. doi:10.1098/rspb.2007.0263.

Ibrahim, K.M., Nichols, R.A., and Hewitt, G.M. 1996. Spatial patterns of genetic variation generated by different forms of dispersal during range expansion. Heredity, **77**(3): 282–291. doi:10.1038/hdy.1996.142.

Kalinowski, S.T. 2005. HP-RARE 1.0: a computer program for performing rarefaction on measures of allelic richness. Mol. Ecol. Notes, **5**(1): 187–189. doi:10.1111/j.1471-8286.2004.00845.x.

Kalinowski, S.T., Manlove, K.R., and Taper, M.L. 2007. ONCOR a computer program for genetic stock identification. Montana State University, Bozeman, Mont. Available at www.montana.edu/kalinowski/Software/ONCOR.htm

King, T.L., Kalinowski, S.T., Schill, W.B., Spidle, A.P., and Lubinski, B.A. 2001. Population structure of Atlantic salmon (*Salmo salar* L.): a range-wide perspective from microsatellite DNA variation. Mol. Ecol. **10**(4): 807–821. doi:10.1046/j.1365-294X.2001.01231.x. PMID:11348491.

Koskinen, M.T., Piironen, J., and Primmer, C.R. 2001. Interpopulation genetic divergence in European grayling (*Thymallus thymallus*, Salmonidae) at a microgeographic scale: implications for conservation. Conserv. Genet. **2**(2): 133–143. doi:10.1023/A:1011814528664.

Lesica, P., and Allendorf, F.W. 1995. When are peripheral populations valuable for conservation? Conserv. Biol. **9**(4): 753–760. doi:10.1046/j.1523-1739.1995.09040753.x.

Lindsay, C.C., and McPhail, D.J. 1986. Zoogeography of fishes of the Yukon and Mackenzie basins. *In* The zoogeography of North American freshwater fishes. *Edited by* C.H. Hocutt and E.O. Wiley. John Wiley & Sons, New York. pp. 639–674.

Lu, G., Basley, D.J., and Bernatchez, L. 2001. Contrasting patterns of mitochondrial DNA and microsatellite introgressive hybridization between lineages of lake whitefish (*Coregonus clupeaformis*); relevance for speciation. Mol. Ecol. **10**(4): 965–985. doi:10.1046/j.1365-294X.2001.01252.x. PMID:11348504.

McCairns, R.J.S., and Bernatchez, L. 2008. Landscape genetic analyses reveal cryptic population structure and putative selection gradients in a large-scale estuarine environment. Mol. Ecol. **17**(17): 3901–3916. doi:10.1111/j.1365-294X.2008.03884.x. PMID:18662229.

McLean, J.E., Hay, D.E., and Taylor, E.B. 1999. Marine population structure in an anadromous fish: life-history influences patterns of mitochondrial DNA variation in the eulachon, *Thaleichthys pacificus*. Mol. Ecol. **8**(Suppl. 1): S143–S158. doi:10.1046/j.1365-294X.1999.00818.x. PMID:10703557.

Michael, J.H., Jr. 1989. Life history of anadromous coastal cutthroat trout in Snow and Salmon creeks, Jefferson County, Washington, with implications for management. Calif. Fish Game, **75**: 188–203.

Millar, R.B. 1987. Maximum likelihood estimation of mixed stock fishery composition. Can. J. Fish. Aquat. Sci. **44**(3): 583–590. doi:10.1139/f87-071.

Miller, M.P. 1997. Tools for population genetic analysis. Version 1.3. Department of Biological Sciences, Northern Arizona University, Flagstaff, Ariz.

Neville, H.M., Isaak, D.J., Dunham, J.B., Thurow, R.F., and Rieman, B.E. 2006. Fine-scale natal homing and localized movement as shaped by sex and spawning habitat in Chinook salmon: insights from spatial autocorrelation analysis of individual genotypes. Mol. Ecol. **15**(14): 4589–4602. doi:10.1111/j.1365-294X.2006.03082.x. PMID:17107485.

Pascual, M.A., Quinn, T.P., and Fuss, H. 1995. Factors affecting the homing of fall chinook salmon from Columbia River hatcheries. Trans. Am. Fish. Soc. **124**(3): 308–320. doi:10.1577/1548-8659(1995)124<0308:FATHOF>2.3.CO;2.

Pielou, E.C. 1991. After the ice age: the return of life to glaciated North America. University of Chicago Press, Chicago, Ill.

Pritchard, J.K., Stephens, M., and Donnelly, P. 2000. Inference of population structure using multilocus genotype data. Genetics, **155**(2): 945–959. PMID:10835412.

Rannala, B., and Mountain, J.L. 1997. Detecting immigration by using multilocus genotypes. Proc. Natl. Acad. Sci. U.S.A. **94**(17): 9197–9201. doi:10.1073/pnas.94.17.9197. PMID:9256459.

Raymond, M., and Rousset, F. 2003. GENEPOP 3.4, an updated version of GENEPOP V.1.2 (1995): population genetics software for exact tests and ecumenicism. J. Hered. **86**: 248–249.

Reist, J.D. 1997. Stock structure and life history types of broad whitefish in the lower Mackenzie River basin — a summary of research. *In* The Proceedings of the Broad Whitefish Workshop: the Biology, Traditional Knowledge and Scientific Management of Broad Whitefish (*Coregonus nasus* (Pallus)) in the Lower Mackenzie River. *Edited by* R.F. Tallman and J.D. Reist. Can. Tech. Rep. Fish. Aquat. Sci. No. 2193. pp. 85–96.

Reist, J.D., and Chang-Kue, K.T.J. 1997 The life history and habitat usage of broad whitefish in the lower Mackenzie River basin. *In* The Proceedings of the Broad Whitefish Workshop: the Biology, Traditional Knowledge and Scientific Management of Broad Whitefish (*Coregonus nasus* (Pallus)) in the Lower Mackenzie River. *Edited by* R.F. Tallman and J.D. Reist. Can. Tech. Rep. Fish. Aquat. Sci. No. 2193. pp. 63–74.

Rempel, L.L., and Smith, D.G. 1998. Postglacial fish dispersal from the Mississippi refuge to the Mackenzie River basin. Can. J. Fish. Aquat. Sci. **55**(4): 893–899. doi:10.1139/cjfas-55-4-893.

Rice, W.R. 1989. Analyzing tables of statistical tests. Evolution, **43**(1): 223–225. doi:10.2307/2409177.

Rich, H.B.J., Jr., Carlson, S.M., Chasco, B.M., Briggs, K.C., and Quinn, T.P. 2006. Movements of male sockeye salmon, *Oncorhynchus nerka*, on spawning grounds: the effects of in-stream residency, density, and body size. Anim. Behav. **71**(4): 971–981. doi:10.1016/j.anbehav.2005.10.004.

Rogers, S.M., Marchand, M.H., and Bernatchez, L. 2004. Isolation, characterization and cross-salmonid amplification of 31 microsatellite loci in the lake whitefish (*Coregonus clupeaformis*, Mitchill). Mol. Ecol. Notes, **4**(1): 89–92. doi:10.1046/j.1471-8286.2003.00578.x.

Ryman, N., and Palm, S. 2006. POWSIM: a computer program for assessing statistical power when testing for genetic differentiation. Mol. Ecol. Notes, **6**(3): 600–602. doi:10.1111/j.1471-8286.2006.01378.x.

Säisä, M., Rönn, J., Aho, T., Björklund, M., Pasanen, P., and Koljonen, M.-L. 2008. Genetic differentiation among European whitefish ecotypes based on microsatellite data. Hereditas, **145**(2): 69–83. doi:10.1111/j.0018-0661.2008.02050.x. PMID:18503709.

Slatkin, M. 1995. A measure of population subdivision based on microsatellite allele frequencies. Genetics, **139**(1): 457–462. PMID:7705646.

Small, M.P., Beacham, T.D., Withler, R.E., and Nelson, J. 1998. Discriminating coho salmon (*Oncorhynchus kisutch*) populations within the Fraser River, British Columbia. Mol. Ecol. **7**(2): 141–155. doi:10.1046/j.1365-294x.1998.00324.x.

Takezaki, N., and Nei, M. 1996. Genetic distances and reconstruction of phylogenetic trees from microsatellite DNA. Genetics, **144**(1): 389–399. PMID:8878702.

Tallman, R.F., Abrahams, M.V., and Chudobiak, D.H. 2002. Migration and life history alternatives in a high latitude species, the broad whitefish, *Coregonus nasus* Pallus. Ecol. Freshwat. Fish, **11**(2): 101–111. doi:10.1034/j.1600-0633.2002.00001.x.

Taylor, E.B., Stamford, M.D., and Baxter, J.S. 2003. Population subdivision in westslope cutthroat trout (*Oncorhynchus clarki lewisi*) at the northern periphery of its range: evolutionary inferences and conservation implications. Mol. Ecol. **12**(10): 2609–2622. doi:10.1046/j.1365-294X.2003.01937.x. PMID:12969465.

Taylor, E.B., Tamkee, P., Sterling, G., and Hughson, W. 2007. Microsatellite DNA analysis of rainbow trout (*Oncorhynchus mykiss*) from western Alberta, Canada: native status and evolutionary distinctiveness of "Athabasca" rainbow trout. Conserv. Genet. **8**(1): 1–15. doi:10.1007/s10592-006-9142-9.

Thera, T. 1998. A quantitative life-cycle model to identify research priorities and test management strategies for the Mackenzie River broad whitefish (*Coregonus nasus* Pallus). Ph.D. thesis, Department of Zoology, University of Manitoba, Winnipeg, Man.

Tonteri, A., Veselov, A.J., Titov, S., Lumme, J., and Primmer, C.R. 2007. The effect of migratory behaviour on genetic diversity and population divergence: a comparison of anadromous and freshwater Atlantic salmon *Salmo salar*. J. Fish Biol. **70**(sc): 381–398. doi:10.1111/j.1095-8649.2007.01519.x.

Treble, M.A. 1996. Broad whitefish (*Coregonus nasus*) of the lower Mackenzie River: biological characteristics, commercial and subsistence harvest trends, and management issues. MNRM Practicum, University of Manitoba, Winnipeg, Man.

Treble, M.A., and Reist, J.D. 1997. Lower Mackenzie River broad whitefish: central delta biological characteristics (1984–1989), commercial and subsistence harvest trends (1955–1993), and local management issues. *In* The Proceedings of the Broad Whitefish Workshop: the Biology, Traditional Knowledge and Scientific Management of Broad Whitefish (*Coregonus nasus* (Pallus)) in the Lower Mackenzie River. *Edited by* R.F. Tallman and J.D. Reist. Can. Tech. Rep. Fish. Aquat. Sci. No. 2193. pp. 5–22.

Turgeon, J., and Bernatchez, L. 2001. Clinal variation at microsatellite loci reveals historical secondary intergradation between glacial races of *Coregonus artedi* (Teleostei: Coregoninae). Evolution, **55**(11): 2274–2286. PMID:11794787.

Waples, R.S. 2002. Definition and estimation of effective population size in the conservation of endangered species. *In* Population viability analysis. *Edited by* S.R. Beissinger and D.R. McCullough. University of Chicago Press, Chicago, Ill. pp. 147–168.

Ward, R.D., Woodwark, M., and Skibinski, D.O.F. 1994. A comparison of genetic diversity levels in marine, freshwater, and anadromous fishes. J. Fish Biol. **44**(2): 213–232. doi:10.1111/j.1095-8649.1994.tb01200.x.

Weir, B.S., and Cockerham, C.C. 1984. Estimating *F*-statistics for the analysis of population structure. Evolution, **38**(6): 1358–1370. doi:10.2307/2408641.

Whiteley, A.R., Spruell, P., and Allendorf, F.W. 2004. Ecological and life history characteristics predict population genetic divergence of two salmonids in the same landscape. Mol. Ecol. **13**(12): 3675–3688. doi:10.1111/j.1365-294X.2004.02365.x. PMID:15548282.

Wilson, C.C., and Hebert, P.D.N. 1998. Phylogeography and postglacial dispersal of lake trout, *Salvelinus namaycush*, in North America. Can. J. Fish. Aquat. Sci. **55**(4): 1010–1024. doi:10.1139/cjfas-55-4-1010.