Gene flow increases temporal stability of Chinook salmon (Oncorhynchus tshawytscha) populations in the Upper Fraser River, British Columbia, Canada

Ryan P. Walter, Tutku Aykanat, David W. Kelly, J. Mark Shrimpton, and Daniel D. Heath

Abstract: Temporal instability in population genetic structure has significant implications for management and conservation decisions. Here, we evaluate temporal stability in five populations of Chinook salmon (Oncorhynchus tshawytscha) from the Upper Fraser River, British Columbia, Canada, based on estimates of temporal allelic variance and effective population size ($N_e$) at 11 microsatellite loci. Significant temporal variation in allele frequencies was found within individual populations sampled at 5- to 12-year intervals. Removal of migrant fish or correcting for migrants resulted in higher allelic variance or reduced $N_e$. Populations with higher levels of temporally consistent gene flow show reduced temporal allelic variance (i.e., reduced genetic drift) and higher $N_e$. This study is an important empirical example of the effect of gene flow on genetic stability and $N_e$. In salmonids, low straying levels may have evolved to favor local adaptation; however, we show that even such low levels of gene flow can elevate effective population sizes and preserve genetic variability. This study highlights the importance of considering gene flow acting to temporally stabilize populations, particularly small ones, and should migration be interrupted, $N_e$ levels may decline with no obvious change in census population sizes.

Résumé : L’instabilité temporelle de la structure génétique de la population a des conséquences importantes pour les décisions reliées à la gestion et la conservation. Nous examinons ici la stabilité temporelle de cinq populations de saumons chinook (Oncorhynchus tshawytscha) du Fraser supérieur, Colombie-Britannique, Canada, d’après des estimations de la variance allélique temporelle et de la taille effective de la population ($N_e$) à 11 locus microsatellites. Il existe une variation temporelle significative de la fréquence des allèles dans les populations individuelles échantillonnées à des intervalles de 5–12 ans. Le retrait des poissons migrateurs ou l’addition d’une correction pour tenir compte des migrateurs entraîne une variance allélique plus élevée ou une $N_e$ réduite. Les populations qui possèdent des niveaux plus élevés de flux génique stable dans le temps ont une variance allélique temporelle réduite (donc une dérive génétique réduite) et une $N_e$ plus élevée. Notre étude constitue un exemple empirique important de l’effet du flux génique sur la stabilité génétique et sur $N_e$. Chez les salmonidés, les degrés faibles d’errance ont peut-être évolué pour améliorer l’adaptation locale; nous montrons, cependant, que même de tels niveaux faibles de flux génique peuvent faire augmenter la taille des populations effectives et préserver la variabilité génétique. Notre travail souligne l’importance de tenir compte du flux génique qui peut entraîner la stabilisation temporelle des populations, particulièrement de celles de petite taille; si la migration était interrompue, les valeurs de $N_e$ pourraient decliner sans changement évident dans la taille des populations recensées.

[Traduit par la Rédaction]

Introduction

Analyses of population genetic structure using microsatellite markers have widespread application in evolutionary and conservation biology. Those applications include the identification of populations of specific conservation concern, such as those severely bottlenecked or otherwise displaying reduced genetic diversity. However, the supposition of little or no recent genetic change (i.e., genetic stability) can be misleading as allele frequencies may fluctuate temporally as a consequence of variation in factors such as effective population size ($N_e$), species range and dispersal, and life history. For example, random drift based genetic change may confound conservation-based analyses testing for changes in genetic composition resulting from anthropogenic or environmental effects on population processes (Heath et al. 2002). Temporal genetic samples are available for a number of aquatic species because of their high abundance in nature and the availability of archived material. This is especially true of commercially important fish species, including cod.
(Ruzzante et al. 1997; Poulsen et al. 2006), sea basses (Rhodes et al. 2004), and various salmonids (Østergaard et al. 2003; Palm et al. 2003; Jensen et al. 2005). Among salmonids, there is no consistent pattern of genetic stability, as some studies have reported stable genetic structure and composition (Tessier and Bernatchez 1999; Hansen et al. 2002; Heath et al. 2002), and others have reported genetic instability (Østergaard et al. 2003; Palm et al. 2003; Jensen et al. 2005). As more studies are published with estimates of temporal genetic change, the potential for identifying the factors affecting temporal stability will likely increase.

Previous work in salmonids has demonstrated that, theoretically, significant variation in spatial and temporal genetic structure may result from interactions between drift and local adaptation (Elo 1993; Adkinson 1995). Although variation at gene loci is driven by selection, mutation, drift, and gene flow, small populations will encounter elevated drift effects and may appear to be less stable over time due to stochastic effects alone. This elevated variance may be tempered by intermittent gene flow serving to inflate local $N_e$ (Slatkin 1985). For example, gene flow between life history stages within a single river has been shown to have a stabilizing effect on $N_e$ (Araki et al. 2007). Alternatively, episodic gene flow among genetically divergent populations may artificially inflate allele frequency variance, increasing apparent genetic instability and leading to low estimates of $N_e$. With this in mind, relatively small populations that experience gene flow are ideal models in which to assess factors that affect temporal genetic stability, as genetic drift is likely to be high and the effect of gene flow is likely to be profound.

Pacific salmonids are particularly useful species in which to examine the relationship between gene flow and genetic stability as high levels of natal philopatry result in low rates of straying (Altukhov et al. 2000). The resulting limited gene flow among even geographically close populations often leads to differentiation via genetic drift and local adaptation (Taylor 1991; Quinn 1993; Heath et al. 2006). Indeed, a number of studies using microsatellite loci show particularly high levels of genetic structure in salmonid populations (e.g., Taylor 1995; Nielsen et al. 1997).

We use an historical microsatellite marker data set (1978–1998) from Shrimpton and Heath (2003) to test novel hypotheses concerning the temporal stability of allele frequencies in five populations of Chinook salmon (*Oncorhynchus tshawytscha*) in the Upper Fraser River, British Columbia, Canada. Chinook salmon were sampled at approximately 10-year intervals from the late 1970s to the late 1990s, and those samples proved useful for the determination of $N_e$ (Shrimpton and Heath 2003). Here, we first quantify temporal changes in genetic structure and allele frequency distribution to test the hypothesis that populations are temporally stable. We then examine the relationship between migration and temporal stability to test the hypothesis that gene flow through time reduces temporal allelic variance and raises $N_e$, thereby lending to increased population viability in the long term.

**Materials and methods**

**Study areas**

The five study populations for which microsatellite geno-

**Statistical analysis**

The 11 microsatellite loci used here had high levels of variation in the Chinook salmon populations examined, and nine tests out of 154 showed significant deviation from Hardy–Weinberg equilibrium, but without a consistent pattern. To test for differences in allele frequency distribution among sampling years and populations, we performed pairwise exact tests using TFGPA 1.3 (Miller 1997; 1000 dememorization steps, 20,000 permutations; Raymond and Rousset 1995). To quantify genetic divergence among populations and sampling years, we calculated pairwise $F_{ST}$ (Weir and Cockerham 1984) and estimated significance with 10,000 permutations using MSA software (Dieringer and Schlötterer 2003). We applied Bonferroni correction to maintain an experiment-wide $α$ level of 0.05 for all pairwise comparisons. Principal coordinates analysis (PCoA, covariance-standardized) was performed on the pairwise matrix of $F_{ST}$ values in GENALEX 6.1 (Peakall and Smouse 2006) to show relationships among samples.

To partition allele frequency variance among populations, among sampling years within populations, and among individuals, we performed a hierarchical analysis of molecular variance (AMOVA; Excoffier et al. 1992) using ARLEQUIN software (Schneider et al. 2000). Significance values of the variance components were obtained using 10,000 permutations.

To quantify the degree of temporal allelic variation within each population, we estimated the standardized allele variance ($\bar{F}$; Waples 1989) and effective population size ($N_e$; Waples 1989) using $N_e$ ESTIMATOR (Peel et al. 2004). Estimates of $N_e$ were corrected for overlapping generations by multiplying $N_e$ estimates by mean generation times (Shrimpton and Heath 2003). Both estimates were calculated for each pairwise temporal comparison within populations.

To determine the influence of migration on temporal stability we identified first-generation migrants based on population exclusion methods in GENECLASS 2.0 (Piry et al. 2004) using the Bayesian method (Rannala and Mountain 1997) and the likelihood ratio of $L_{\text{home}}$ to $L_{\text{max}}$ (Puetkau et
Monte-Carlo resampling was performed with 10,000 simulated individuals at an assignment threshold $P$ value of 0.05. We compared $D_{LR}$ values and $F_{ST}$ estimates among populations to determine whether detection of migrants is possible (Paetkau et al. 2004). We then recalculated allelic variance ($\overline{F}$) and moments-based $N_e$ in all populations with the identified migrants removed. To determine whether a reduction in sample size resulted in a change in $\overline{F}$ following removal of migrants, we randomly removed individuals (equal numbers as the identified migrants) from each temporal sample in 10 replicates and then recalculated $\overline{F}$ (Appendix A, Fig. A1).

To further illustrate the influence of migration on temporal stability, we also calculated $N_e$ via two methods using the maximum-likelihood approach of Wang and Whitlock (2003) in the software MNE 2.0. $N_e$ is inversely proportional to drift and, hence, temporal allelic variance. To determine the effect of migrant fish on $N_e$, we first estimated $N_e$ assuming “closed” populations on the original data set and then reran the analysis following removal of the migrants identified by GENECLASS. Next, we estimated $N_e$ allowing migration (e.g., “open” model) between focal populations ($T_1$, $T_2$, and $T_3$ for Nechako, Stuart, Bowron, and Dome; $T_1$ and $T_2$ for Willow) and a source population. Source populations consisted of pooled genotypes from all samples and time periods except the focal population, a technique that is suggested to be robust (Wang and Whitlock 2003). Generation times of 1 were used for temporal samples separated by 5 years, 2 for 8, 10, and 12 years, and 4 for 20 years. $N_e$ estimates were corrected for overlapping generations using the mean generation times as in Shrimpton and Heath (2003). We then compared estimates of all three $N_e$ estimates and their respective $N_e$–$N_c$ ratios to see whether trends were consistent across methods.

To determine directionality of gene flow among populations, we obtained estimates of migration rate ($m$) using BAYESASS 1.2 software (Wilson and Rannala 2003). Runs were performed allowing migration among samples in three temporally relevant groupings: (i) N-78, S-80, B-80, and W-80; (ii) N-88, S-88, B-88, and D-86; and (iii) N-98, S-98, B-98, and D-96. Estimates of $m$ were taken from averages of three replicate runs of $5 \times 10^7$ iterations, with $3 \times 10^7$ burn-in runs and five subsequent replicate runs of $3 \times 10^7$ to identify convergence among runs.

**Results**

Exact tests revealed significant differentiation in population genetic structure for all pairwise comparisons ($P < 0.001$) following Bonferroni correction. All pairwise $F_{ST}$ estimates were significant following Bonferroni correction with only four exceptions, only one of which was a spatial comparison (Table 1). The MDS plot of genetic differentiation among populations illustrates the magnitude of temporal variation for some populations compared with others (Fig. 2). For example, the proximity of data points for temporal samples from the Nechako and Stuart populations compared with those of the Dome or Bowron populations. The AMOVA showed significant genetic differentiation.
among sampling years, within populations (1.63%, $P < 0.001$), and among populations (1.21%, $P < 0.005$).

Of the 590 individuals in the data set, 76, or roughly 13%, were identified as migrants based on GENECLASS analysis, with Dome Creek harbouring the highest number of identified migrants and the Stuart showing the fewest (Appendix A, Table A1). $D_{LR}$ and $F_{ST}$ measurements from pairwise population comparisons showed that sufficient discriminatory power was available to detect migrants (Table 1; Appendix A, Table A1). The subsequent exclusion of migrant individuals from our samples amounted to removal of an average of five individuals per site study wide, resulting in the retention of approximately 87% of all individuals across all samples (Appendix A, Table A1). Following removal of migrants, the average sample size was 37 individuals per site. As predicted, increases in allelic variance were noted for all populations for all temporal samples following removal of migrants (Fig. 3). As predicted, increases in allelic variance were noted for all populations even after removal of migrants (Fig. 3a). Moments-based estimates of $N_e$ showed similar results in that $N_e$ decreased in all populations except the early comparison from the Bowron (Fig. 3b). Recalculation of $F$ following random removal of individuals from each temporal sample (numbers equal to the number of migrants identified) did not yield changes in $F$ comparable with those following migrant removal, thus the effect of removing migrants is not a result of the reduction in sample size (Fig. A1).

Calculations of $N_e$ using the Wang and Whitlock (2003) methods showed consistently higher $N_e$ when migrants were included in the samples (Fig. 4a). As $N_e$ estimates are less sensitive to sample sizes, the use of $N_e$ and its subsequent decrease following migrant removal exemplifies the stabilizing effect of the migrants across the study system, independent of sample size effects. Furthermore, the estimates of $N_e$ using the “open” model were comparable with those using the “closed” model with migrants removed (Figs. 4a, 4b). Comparison of $N_e$-$N_e$ ratios shows that this pattern is evident independent of census population size (Fig. 4b).

Estimation of migration rates from BAYESASS showed mean migration rates across all sampling periods of 0.032 for Nechako, 0.099 for Bowron, and 0.064 for Stuart. Migration rates estimates for the Dome 1986–1988 suggested a possible local optimum trap in BAYESASS at 0.33 migration rate, most likely due to a violation of the assumption of <1/3 migrants (Wilson and Rannala 2003; Austin et al. 2004; Hansen et al. 2007). Work by both Faubet et al. (2007) and Palstra et al. (2007) demonstrates the limitations of BAYESASS for estimating recent migration rates; therefore the following migration estimates should be interpreted with caution. BAYESASS indicated asymmetrical gene flow (i.e., non-overlap of confidence intervals) from the Nechako into the Stuart in the temporal sampling period 1978–1988 (Table 2). However, all other migration rates appeared to be bidirectional because of overlap in confidence intervals, despite some suggestion of asymmetrical migration again from Nechako into the Stuart for the 1998 samples (Table 2). For the populations and temporal periods in which BAYESASS was able to reliably estimate migration, both Dome (0.0106) and Nechako (1978, 0.0133; 1998, 0.0229) showed that the lowest incoming rates were smaller. Across all time periods, the Bowron received the most migrants, and within the 1986–1988 sampling period, the Dome appeared to be a

<table>
<thead>
<tr>
<th>Population</th>
<th>Nechako</th>
<th>Dome</th>
<th>Willow</th>
<th>Stuart</th>
</tr>
</thead>
<tbody>
<tr>
<td>N-78</td>
<td>N-88</td>
<td>N-88</td>
<td>N-88</td>
<td>N-88</td>
</tr>
<tr>
<td>B-88</td>
<td>B-86</td>
<td>B-91</td>
<td>B-96</td>
<td>B-80</td>
</tr>
<tr>
<td>S-98</td>
<td>S-98</td>
<td>S-88</td>
<td>S-88</td>
<td>S-88</td>
</tr>
</tbody>
</table>

Table 1. Pairwise $F$ for spatiotemporal comparisons of five populations of Chinook salmon (Oncorhynchus tshawytscha) from the Upper Fraser River.

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source of migrants for both the Nechako and Bowron populations (Table 2).

**Discussion**

Temporal instability in allele frequency distribution was found for all populations of Chinook salmon sampled from tributaries to the Upper Fraser River, with the overall magnitude of temporal within-population variation exceeding that of among-population variation. The level of stability of some populations (Nechako, Stuart) is consistently higher than that of others (Willow, Dome, Bowron). The temporal predictability of genetic structure among populations varied from nearly wholly consistent to essentially random, which may explain some of the inconsistencies among previous temporal studies of genetic structure in salmonids. Earlier work has reported both stable (Tessier and Bernatchez 1999; Hansen et al. 2002; Heath et al. 2002) and unstable (Laikre et al. 2002; Østergaard et al. 2003; Jensen et al. 2005) population genetic composition and structure in salmonids. Our results indicate that genetic stability clearly varies among populations of Chinook salmon, even within the restricted geographical range of the Upper Fraser River.

Three possibilities may account for the variability in population genetic stability among the geographically close Chinook salmon populations of the Upper Fraser River. First, within-season variation in the genetic composition of the spawning run coupled with changes in the sampling time could drive temporal instability. Fillatre et al. (2003) showed that comparisons of early- and late-run sockeye salmon (*Oncorhynchus nerka*) accounted for twice the genetic variation observed among years within the same river. However, we know of no records of multiple spawning run structure for Chinook in our study populations but cannot exclude the possibility of within-run temporal variation, as samples were not collected for specific periods within the annual yearly spawning runs. A second source of variation in temporal instability may stem from differential survival or reproductive success among populations. This point is typically well illustrated by comparing \( N_e \) with \( N_c \). Although the decoupling of \( N_e \) and \( N_c \) was shown for these populations by Shrimpton and Heath (2003) and is also observed in other salmonids (Araki et al. 2007; Fraser et al. 2007b), our estimates of \( N_c \) show the persistence of these patterns, despite any buffering effects that gene flow appears to confer. Although this decoupling may suggest that differential
survival and reproduction appears independent of gene flow, the consistent declines in \(N_e\) for each population following migrant removal or correction further demonstrate that gene flow is the third possibility driving temporal variation in these populations.

Generally, gene flow is expected to be stabilizing if the rate is constant in magnitude, time, and source (Wang and Whitlock 2003). Our analyses provide empirical evidence that variation in gene flow is likely driving the differences in temporal genetic stability among our sampled populations. Although we conclude that gene flow appears to confer stability for some populations, the relationship between temporal stability, gene flow, and neutral genetic differentiation is perhaps more complex as the effects of gene flow on genetic stability clearly depend not only on the source, but also on the genetic stability of the source population itself.

Philopatry in salmon may have evolved to match locally adapted fish with sites exhibiting similarities in habitat or spawning areas (e.g., Stuart and Nechako), suggesting that genetic stability of a recipient population likely depends on the drift-based variance of the source population. The Nechako and Stuart populations exhibited the greatest temporal stability, but the Stuart shows that migration rates from outside are nearly 10-fold higher than in the Nechako. The source of migrants for the Stuart is consistently the Nechako over the study period, itself a temporally stable system. Such patterns of gene flow are likely the result of straying among the geographically close Upper Fraser River Chinook salmon populations, as individuals may find it more difficult to distinguish between proximal natal and non-natal sites (Hendry et al. 2004). This dispersal or straying may not reflect individual “choice” (Hendry et al. 2004) as abiotic factors such as environmental perturbation possibly affect straying rates and patterns (e.g., controlled water discharge in the Nechako River may influence straying into the adjacent Stuart River). Furthermore, both habitat degradation and population declines have been noted for these populations (Shrimpton and Heath 2003), which likely impedes assessment of natural or original connectivity patterns (Palstra et al. 2007).

Recent work in salmonids has used patterns of asymmetrical gene flow from large into small populations as evidence for density-dependent dispersal (Fraser et al. 2004; Hansen et al. 2007). This pattern is not observed for our populations; however, directionality of gene flow has been shown to be primarily determined by the temporal scale over which migration was being estimated (Palstra et al. 2007). As we are restricted to estimating gene flow indirectly from point samples between rivers at different times, it is likely that we have not sampled all source populations and our estimates of specific directional migration rates between populations should be interpreted with caution. The migration rates estimated in BAYESASS further illustrate the complexity of the relationship between gene flow and stability as high migration rates estimated for Bowron 1978 do not translate into higher \(N_e\) estimates. This trend is also illustrated by the slight increase in \(N_e\) “open” estimates for the Bowron following removal of migrants using both moments-based and Wang and Whitlock’s methods. Nonetheless, the effect of correcting for migration on our estimates of \(\hat{F}\) and \(N_e\) consistently demonstrates the temporally stabilizing potential of gene flow.

A number of studies show gene flow induced genetic stability in other species, perhaps hinting at the generality of this effect. Dispersal (and subsequent gene flow) has been credited for the high temporal genetic stability of coyote populations despite aggressive removal efforts (Williams et al. 2003). Studies in insects have also found temporal stability to consistent gene flow (loxdale and Brookes 1990; Bourguet et al. 2000). For species exhibiting metapopulation-type structuring, such as cod (\(Gadus morhua\)), high migration rates buffer against bottlenecks through inflating \(N_e\), as evidenced by drastic reductions in census sizes but no corresponding changes in \(N_e\) (Ruzzante et al. 1997; Poulsen et al. 2006).

This study provides a valuable assessment of Wang and Whitlock’s (2003) “open” model for estimating \(N_e\). This model simulates migration between potential source populations and the focal populations at given time periods,
thereby $N_c$ estimates using the “open” model should resemble those of the “closed” model following migrant removal. For Atlantic salmon, Fraser et al. (2007a) identified $N_c$ “open” estimates that more closely reflected biological reality than higher $N_c$ “closed” estimates in populations that were known to have experienced bottlenecks. Fraser et al. (2007a) and Palstra and Ruzzante (2008) further suggest that $N_c$ “open” estimates may be generally biased downwards and $N_c$ “closed” estimates biased upwards. Palstra and Ruzzante (2008) observed upward biases of $N_c$ under $N_c$ “closed” conditions in 94% of their salmonid estimates, signifying that relatively continuous gene flow reduces drift. In this study, the congruence of the $N_c$ “open” estimates to those of the $N_c$ “closed” with migrants removed emphasizes this point that $N_c$ is augmented in Chinook salmon populations and that these populations are not as isolated as previously believed.

The effect of gene flow on genetic stability has implications for the management and ecology of Chinook salmon. First, the implicit assumption that straying in Pacific salmon is rare (and of little ecological relevance for long-term population viability) should be re-evaluated. As is well known, populations with low $N_c$ must be accorded high conservation priority; however, this study shows that even populations with moderately high $N_c$ may be unexpectedly at risk if migrant source populations are impacted. The results of this study thus emphasize the importance of nearby source populations, particularly those that are genetically stable, as they affect local population stability and help to maintain connectivity and long-term population viability. Hence, the definition of management and conservation units should consider temporal stability (and thus $N_c$) as an important population parameter as it reflects both within-population factors and among-population gene flow (Fraser et al. 2007a).

The results of this study are consistent with the hypothesis that populations experiencing regular gene flow may be buffered from temporal genetic variation, resulting in elevated estimates of $N_c$. From a management perspective, these findings emphasize the value of temporal genetic screening of populations for defining genetic relationships among populations and highlight the importance of gene flow in stabilizing both small and larger populations. As isolation increases genetic instability, isolated populations should be of high management priority. Furthermore, source populations within this system are also of high priority as they contribute to the genetic diversity of receiving populations. Given the range of temporal stability among our study populations, it is clear that no assumptions can be made concerning temporal genetic stability among even geographically close populations of a single species, much less across species.

**Acknowledgments**

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**Table 2.** Estimates of migration rates among populations and sampling dates using BAYESASS 1.3.

<table>
<thead>
<tr>
<th>Source</th>
<th>Into site:</th>
<th>W-80</th>
<th>B-80</th>
<th>S-80</th>
</tr>
</thead>
<tbody>
<tr>
<td>N-78</td>
<td>0.98667 (0.95996, 0.99936)</td>
<td>0.00498 (0.00002, 0.02667)</td>
<td>0.00571 (0.00004, 0.02531)</td>
<td>0.12467 (0.07421, 0.17297)</td>
</tr>
<tr>
<td>W-80</td>
<td>0.00320 (0.00001, 0.01523)</td>
<td><strong>0.97692 (0.92000, 0.99918)</strong></td>
<td>0.09765 (0.00309, 0.19019)</td>
<td>0.00404 (0.00003, 0.01744)</td>
</tr>
<tr>
<td>B-80</td>
<td>0.00333 (0.00001, 0.01653)</td>
<td>0.01026 (0.00002, 0.05605)</td>
<td><strong>0.88204 (0.79293, 0.98085)</strong></td>
<td>0.00582 (0.00005, 0.02283)</td>
</tr>
<tr>
<td>S-80</td>
<td>0.00680 (0.00002, 0.02814)</td>
<td>0.00783 (0.00002, 0.03767)</td>
<td>0.01460 (0.00010, 0.05931)</td>
<td><strong>0.86547 (0.81647, 0.91653)</strong></td>
</tr>
</tbody>
</table>

| $m$     | 0.01333 | 0.02308 | 0.11796 | 0.13453 |

<table>
<thead>
<tr>
<th>Source</th>
<th>Into site:</th>
<th>D-86</th>
<th>B-88</th>
<th>S-88</th>
</tr>
</thead>
<tbody>
<tr>
<td>N-88</td>
<td><strong>0.94075 (0.89629, 0.97518)</strong></td>
<td>0.00495 (0.00001, 0.02205)</td>
<td>0.00811 (0.00006, 0.03655)</td>
<td>0.01772 (0.00007, 0.06096)</td>
</tr>
<tr>
<td>D-86</td>
<td>0.04569 (0.01864, 0.08321)</td>
<td><strong>0.67707 (0.66702, 0.71099)</strong></td>
<td>0.11796 (0.05783, 0.22797)</td>
<td>0.00561 (0.00002, 0.02226)</td>
</tr>
<tr>
<td>B-88</td>
<td>0.00393 (0.00003, 0.01681)</td>
<td>0.31200 (0.26099, 0.32890)</td>
<td><strong>0.86736 (0.75720, 0.92552)</strong></td>
<td>0.00841 (0.00003, 0.03710)</td>
</tr>
<tr>
<td>S-88</td>
<td>0.00963 (0.00006, 0.03567)</td>
<td>0.00456 (0.00001, 0.02138)</td>
<td>0.00658 (0.00005, 0.03191)</td>
<td><strong>0.96827 (0.91673, 0.99855)</strong></td>
</tr>
</tbody>
</table>

| $m$     | 0.05925 | 0.32151 | 0.13264 | 0.03173 |

<table>
<thead>
<tr>
<th>Source</th>
<th>Into site:</th>
<th>D-96</th>
<th>B-98</th>
<th>S-98</th>
</tr>
</thead>
<tbody>
<tr>
<td>N-98</td>
<td><strong>0.97704 (0.93524, 0.99892)</strong></td>
<td>0.00261 (0.00001, 0.01369)</td>
<td>0.02060 (0.00008, 0.07173)</td>
<td>0.01729 (0.00007, 0.05531)</td>
</tr>
<tr>
<td>D-96</td>
<td>0.00588 (0.00003, 0.02642)</td>
<td><strong>0.98977 (0.96658, 0.99943)</strong></td>
<td>0.01231 (0.00006, 0.05270)</td>
<td>0.00529 (0.00001, 0.02513)</td>
</tr>
<tr>
<td>B-98</td>
<td>0.00987 (0.00005, 0.03472)</td>
<td>0.00290 (0.00001, 0.01494)</td>
<td><strong>0.95681 (0.88818, 0.99761)</strong></td>
<td>0.00399 (0.00001, 0.01835)</td>
</tr>
<tr>
<td>S-98</td>
<td>0.00721 (0.00002, 0.03490)</td>
<td>0.00472 (0.00003, 0.02106)</td>
<td>0.01027 (0.00004, 0.04566)</td>
<td><strong>0.97344 (0.93224, 0.99858)</strong></td>
</tr>
</tbody>
</table>

| $m$     | 0.02296 | 0.01023 | 0.04319 | 0.02656 |

**Note:** Bold values along the diagonal are the proportion of fish that were assigned to the site of capture and are thus non-migrant fish. Populations are designated by site codes (N, Nechako; W, Willow; B, Bowron; S, Stuart; D, Dome) and years (last two digits). Numbers in parentheses represent the 95% confidence limits. $m$, total migration rate into each population.
References


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Appendix A

Table A1 and Fig. A1 follow.
**Table A1.** Number of genotyped fish following removal of first-generation ($F_0$) migrants identified in each population by GENECLASS.

<table>
<thead>
<tr>
<th>Population</th>
<th>$n$</th>
<th>$F_0$ migrants</th>
<th>% migrants</th>
<th>Mean $D_{LR}$</th>
<th>$n$ without migrants</th>
</tr>
</thead>
<tbody>
<tr>
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**Note:** Population names follow as listed in the text; $n$, total number of genotyped fish per population; mean $D_{LR}$ measures genetic distance between focal population and all others.

**Fig. A1.** Comparison of $F$ estimates with migrants (open bars), removal of random individuals in equal proportion to detected migrants (shaded bars; 10 replicates, error bars represent standard deviation, SD), and removal of migrants detected by GENECLASS 2.0 (solid bars).