Stock identification of Yukon River Chum Salmon using Microsatellite DNA Loci

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Abstract

Population structure and the application to genetic stock identification for chum salmon (Oncorhynchus keta) in the Yukon River was examined using microsatellite markers. Variation at 13 microsatellite loci (*Ots3, Oke3, Oki2, Oki100, One101, One102, One103, One104, One106, One111, One114*, Ssa419, and OtsG68) was surveyed for approximately 1500 chum salmon from nine Yukon Territory populations and approximately 1900 chum salmon from 13 populations in Alaska. Genetic differentiation among eight populations analyzed, sampled in two or more years, was, on average, over three times greater than annual variation within these populations, indicative of relative stability of allele frequencies. Regional population structure was observed for the 23 populations surveyed.

In the analysis of simulated single-population mixtures, where the expected result was 100% allocation to the target population, the mean estimated stock composition over the 13 Alaskan populations evaluated was 83%, and 87% for nine Yukon Territory populations. For populations contained in four local geographic areas in Alaska and two local areas in the Yukon Territory, mean estimated stock composition was 91% correctly assigned to the local geographic area. In multi-population simulated mixtures, mean estimated stock compositions were generally within 3-4% of the specific population contribution, within 2% for the local geographic region (six regions, four in Alaska, two in the Yukon Territory), and within 1% for Alaska and Yukon Territory contributions. The results of the simulations suggest that microsatellite variation has the potential to provide reliable estimates of stock composition of Yukon River chum salmon.

Introduction

Chum salmon (*Oncorhynchus keta)* are widely distributed within the Yukon River drainage, spawning in tributaries ranging from the headwaters (for example, Teslin River, Yukon Territory) to near the mouth of the river (for example, Andreafsky River, Alaska). Management for conservation of biodiversity within the drainage requires knowledge of genetic variation among populations as well as population-specific information from fisheries. Effective management of fisheries within major drainages like the Yukon River generally requires that information on the harvesting and timing of specific populations be known, should managers wish to change exploitation rates on specific populations for conservation purposes. For example, the Canada/U.S. Yukon River Salmon Agreement established specific escapement targets and harvest sharing provisions for Canadian-origin chum salmon stocks. It is therefore important to develop a management system that allows managers to assess accurately the status of these stocks in fisheries throughout the drainage during the season so that management decisions can ensure that Treaty obligations are met. Accurate post-season run reconstructions are essential in evaluating whether management actions were consistent with meeting overall objectives and Treaty obligations. Run reconstructions are also important in monitoring the productivity of stocks and assessing the adequacy of current escapement targets and both pre-season and in-season run forecasting techniques. A suitable technique for identifying Canadian-origin chum salmon in lower river catches has not yet been found either for post-season analysis or for in-season use in fisheries management. Consequently, this makes managing to achieve Treaty obligations very difficult and it severely limits the assessment of factors influencing stock productivity, which appears to have fluctuated widely in recent years.

Stock identification of chum salmon migrating through the lower river is a continuing issue of management concern, and there is no effective way to provide estimates of stock composition in the detail required by fishery managers. Although allozyme-based methods of stock identification have proven useful in estimation of chum salmon stock composition in mixed-stock fisheries (Shaklee et al. 1999), and differentiation at allozyme loci occurs among Yukon River chum salmon (Beacham et al. 1988; Wilmot et al. 1994), the level of population discrimination available in the Yukon River is not yet sufficient for population-specific applications. Variation in microsatellite loci has been applied in other species requiring discrimination among salmonid populations within watersheds (Small et al. 1998; Beacham and Wood 1999; Beacham et al. 2001), and has been shown to be useful in stock discrimination in chinook salmon (Banks et al. 2000). Variation at microsatellite loci has been particularly useful for population-specific estimates of stock composition of Fraser River chinook salmon (Beacham et al. 2003), and would likely work equally well for both the summer and fall runs of Yukon River chum salmon.

In the present study, we survey variation at 13 microsatellite loci, provide information on allele size ranges and heterozygosity of the loci, and evaluate the utility of using microsatellite variation for stock identification of Yukon River chum salmon. This is accomplished by analysis of simulated mixtures containing chum salmon from only a single population for 22 populations in the baseline, as well as mixtures containing several populations in the drainage.

Methods

Collection of DNA samples and laboratory analysis

Tissue samples were collected from adult fish in chum salmon populations in the Yukon River drainage (Figure 1), and DNA extracted from the samples as described by Withler et al. (2000). For the survey of baseline populations, PCR products at 13 microsatellite loci: *Ots3* (Banks et al. 1999), *Oke3* (Buchholz et al. 1998), *Oki2* (Smith et al. 1998), *Oki100* (Miller et al. unpub), *One101, One102, One103, One104, One106, One111,* and *One114* (Olsen et al. 2000), Ssa419 (Cairney et al. 2000), and OtsG68 (Williamson et al. 2002) were size fractionated on denaturing polyacrylamide gels with the ABI 377 automated DNA sequencer. Allele sizes were determined with Genescan 3.1 and Genotyper 2.5 software (PE Biosystems, Foster City, CA). Allele frequency differences among populations were then compared.

Baseline populations

The baseline survey consisted of analysis of approximately 1500 chum salmon from nine Canadian populations and approximately 1900 chum salmon from 13 populations in Alaska (Table 1). Each population at each locus was tested for departure from Hardy-Weinberg equilibrium (HWE) using GDA (Lewis and Zaykin 2001). Annual samples within populations were tested separately, with 34 tests conducted at each locus. Critical significance levels for simultaneous tests were evaluated using sequential Bonferroni adjustment (Rice, 1989). F_{ST} estimates for each locus were calculated with GDA, and the standard deviation of the estimate for an individual locus was determined by jackknifing over populations and for all loci combined by bootstrapping over loci. Estimation of variance components of annual variation within populations was determined with GDA, with only those populations (Sheenjek, Chena, Salcha, Fishing Branch, Minto, Chandindu, Kluane, and Teslin) for which two or more years of sampling were available being included in the analyses. All annual samples available for a specific sample location were combined to estimate population allele frequencies, as was recommended by Waples (1990).

Estimation of stock composition

Genotypic frequencies were determined at each locus in each population and the statistical package for the analysis of mixtures software program (SPAM version 3.7, Ranala and Mountain correction to allele frequencies used) (Debevec et al. 2000) was used to estimate stock composition of each simulated mixture. Each locus was assumed to be in HWE, and expected genotypic frequencies were determined from the observed allele frequencies and used as model inputs. The Kluane Lake spawning population (12 fish sample) was not included in the baseline for stock identification analysis as the sample was considered too small for reliable estimation of allele frequencies.

Each baseline population was resampled with replacement in order to simulate random variation involved in the collection of the baseline samples before the estimation of stock composition of each simulated mixture. Simulated mixtures composed of chum salmon from different populations were examined in order to evaluate accuracy and precision of the estimated stock compositions. Simulated fishery samples, comprising only a single population of 150 fish, were generated by randomly resampling the baseline populations with replacement in each drainage. Estimated stock composition of a simulated mixture was then determined, and the whole process was repeated 100 times to estimate the mean and standard deviation of the individual stock composition estimates. Mixtures comprising only a single population illustrate the maximum bias expected in estimated stock compositions for that population. However, in practice, mixed-stock fishery samples will contain a range of populations, and estimated stock compositions from these mixtures may in fact be more reliable than those of single-population mixtures. Estimated stock compositions of simulated multi-population mixtures were also evaluated for a range of populations in the mixtures.

Results and Discussion

Variation within populations

All loci surveyed were polymorphic in all populations sampled. The number of observed alleles at each locus ranged from 10 to 84, with lower heterozygosity observed at those loci with fewer alleles (eg. *Oke3*) (Table 2). Heterozygosity varied both among loci and among the populations surveyed. Genotypic frequencies at each locus within sampling location and year generally conformed to those expected under Hardy-Weinberg equilibrium, with the exception of *One106* (Table 2). For that locus, upper allele "drop out" may have resulted in some underestimation of the number of heterozygotes. In order for a genetic-based method of stock identification to be applied successfully, there must be significant genetic differences among the populations that fishery mangers wish to separate. Significant genetic differentiation at the microsatellite loci was observed among the 23 chum salmon populations surveyed to date from the Yukon River drainage. The average Fst value over all loci was 0.016, indicative of only moderate differentiation among populations (Table 2).

Distribution of genetic variation

Gene diversity analysis of the 13 loci surveyed was used to determine the magnitude of annual variation within populations and of variation among eight salmon populations, with only populations having two or more years of sampling included in the analysis. The amount of variation contained within populations ranged from 96.6% (*Oke3*) to 99.1% (*One102*), with the average for microsatellite loci 97.2% (Table 3). The maximum range of sampling times was 10 years for each of the Fishing Branch River and the Teslin River populations, and 14 years for the Kluane River population. Genetic differentiation among the eight populations analyzed was, on average, over three times greater than annual variation within these populations. This stability of allele frequencies relative to population differentiation is a key characteristic of microsatellite loci (Beacham and Wood 1999; Tessier and Bernatchez 1999), and is in sharp contrast to other techniques such as scale pattern analysis, where annual variability in the scale patterns used in stock identification requires annual sampling of the baseline. Owing to the relative stability of the microsatellite allele frequencies, baseline samples collected in one year can be used to estimate stock compositions of samples collected in following years, or indeed in years previous to collection of the baseline samples. Annual stability of the characters used to discriminate among stocks is a key attribute of any technique used in stock identification, particularly if the baseline populations cover a wide geographic area.

Population structure

Regional structuring of population samples was observed in the survey. Most Yukon Territory populations were quite distinct from populations in Alaska. Three populations in the White River drainage, Kluane River, Kluane Lake, and Donjek River, were most similar to each other and clustered together in the dendrogram analysis (Figure 2). Mainstem spawning populations were similar to each other as well. In Alaska, summer-run populations were similar to each other (Andreafsky, Chulinak, and Koyukuk), as were Tanana River drainage populations. In the Porcupine drainage, the Sheenjek River population was distinct from the Fishing Branch River population, even though both are located in the Porcupine River drainage.

Simulated mixed-fishery samples

Results of classifying simulated single population mixtures for Yukon River chum salmon (150 chum salmon from each population) using Rannala and Mountain correction for small sample size are summarized in Table 4. The sum of allocations to the regional group is also indicated. For example, Andreafsky was defined as a lower river summer run, so the model estimated on average 85.4% allocation to Andreafsky, and 95.2% allocation to the lower river summer run populations. Andreafsky and Chulinak were summed to provide an estimate of lower river summers. Jim and Koyukuk (south fork) were summed to provide an estimate of Koyukuk River. Kantishna, Toklat, Delta, Chena, and Salcha were summed to estimate the Tanana River contribution, whereas Sheenjek and Black were summed to provide the United States portion of the Porcupine River drainage. All 13 populations in Alaska were summed to provide a United States (US) estimate. In Canada: the Kluane and Donjek allocations were summed to provide a White River drainage allocation; Pelly, Big Creek, Tatchun, and Minto were summed to provide a mainstem Yukon allocation; and all nine populations in the Yukon Territory were summed to provide an estimate of the Canadian allocation. Estimates to the individual population in the mixture sample are in bold.

In the analysis of single-population mixtures, where the expected result was 100% allocation to the target population, mean estimated stock composition over the 13 Alaskan populations evaluated was 83%, and 87% for nine Yukon Territory populations (Table 4). Within the regional reporting groups defined: lower river summer run (Andreafsky, Chulinak), Koyukuk River (Jim River, south fork Koyukuk), Tanana River (Kantishna, Toklat, Delta, Chena, Salcha), Alaska Porcupine River (Sheenjek, Black), White River (Kluane, Donjek), mainstem Yukon River (Pelly, Big Creek, Tatchun, Minto), higher accuracies of estimation were observed. For the 11 populations in Alaska contained in four local geographic areas, mean estimated stock composition was 91% correctly assigned to the local geographic area. For the two Yukon Territory local areas containing six populations, White River and mainstem Yukon River, mean estimated stock composition was 91% correctly assigned to the local geographic area. Individual populations particularly well estimated (allocation in excess of 90% in the simulations) included Chulinak River, Kluane River, and Teslin River, and many of the allocations to specific populations were in the 85%-90% range (Table 4).

As noted previously, mixtures comprising only a single population illustrate the maximum bias expected in estimated stock compositions for that population. In actual applications, mixed-stock fishery samples will contain a range of populations, and estimated stock compositions from these mixtures may in fact be more reliable than those of single-population mixtures. Four multi-population mixtures were evaluated to assess accuracy and precision of estimated stock compositions that one may expect to occur in actual applications. Classification results (percentages for True (T), Estimated (Est), and standard deviations (SD)) by population and region for Yukon River chum salmon for four simulated mixtures of 150 chum salmon from each population using Rannala and Mountain correction for small sample size are summarized in Table 5. The sum of allocations to the regional group is also indicated. In the first simulation, 10% of the sample was derived from the lower river summer run populations, 10% from the Koyukuk River, 20% from the Tanana River, and 20% from the United States portion of the Porcupine River drainage, totaling 60% American portion of the first mixture. Mean estimated stock compositions were usually within 3-4% of the specific population contribution, within 2% for the local geographic region (six regions, four in Alaska, two in the Yukon Territory), and within 1% for Alaska and Yukon Territory contributions (Table 5).

The second simulated mixture was composed entirely of Yukon Territory origin populations: Canadian mainstem Yukon River populations comprised 30% of the mixture (10% Pelly, 10% Big Creek, 10% Minto), and the mean estimate of the mainstem contribution was 27.2%. The results indicated that Canadian-origin chum salmon should be readily identifiable in mixed-stock fisheries. In particular, the Fishing Branch River population was distinguished from Alaskan-origin populations in the Porcupine River drainage, and distinguished from Canadian mainstem spawning populations.

The third simulated mixture was centered on fall-run populations in the upper portion of the Yukon River drainage in Alaska, with representation from three Canadian populations from areas difficult to differentiate with allozymes. Canadian mainstem-spawning populations, as well as the Fishing Branch population, were well differentiated from populations in Alaska (Table 5).

The final simulated mixture evaluated was weighted heavily towards Alaskan-origin populations, with 20% of the mixture from lower river summer-run populations, 20% from the Koyukuk River, 40% from the Tanana River drainage, with the final 20% from Canadian populations. Estimated stock compositions were generally within 2% of the local geographic contribution, and within 1% for nation of origin. Generally, the results of the simulations suggest that microsatellite variation has the potential to provide reliable estimates of stock composition for regional groups of Yukon River chum salmon.

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Table 1. Chum salmon samples collected and analyzed from 23 populations in the Yukon River drainage. Sample sizes (N) are for years sampled.

Population	Years sampled	N	Total N
Canadian populations			
Fishing Branch	1987, 1994, 1997	95, 75, 161	331
Chandindu	1998, 2001	35, 20	55
Kluane (river)	1987, 1992, 2001	41, 100, 358	462
Kluane (lake spawners)	2002	12	12
Donjek	1994	72	72
Teslin	1992, 2002	100, 43	143
Mainstem@Pelly	1993	84	84
Mainstem@Big_Creek	1995	100	100
Mainstem@Minto	1989, 2002	100, 66	166
Mainstem@Tatchun	1987	75	75
U.S. populations			
Sheenjek	1987, 1988, 1989	108, 76, 79	263
Andreafsky	1987	61	61
Chulinak	1989	100	100
Delta	1990	80	80
Chena	1992, 1994	86, 100	186
Salcha	1994, 2001	100, 85	185
Toklat	1994	200	200

Kantishna	2001	161	161
Black	1995	95	95
Chandalar	2001	200	200
Jim	2002	159	159
Big Salt	2001	81	81
Koyukuk (south fork)	1996	92	92

Table 2. Number of alleles observed, expected heterozygosity (H_e), observed heterozygosity (H_o), number of significant Hardy-Weinberg equilibrium tests (HWE, N=34 tests), and F_{ST} among 23 chum salmon populations for 13 microsatellite loci. Standard deviations are in parentheses.

Locus	Alleles	H_e	H_o	HWE	F_{ST}
Oki2	20	0.76	0.76	2	0.028 (0.006)
Oke3	10	0.61	0.58	1	0.031 (0.010)
Oki100	23	0.81	0.81	0	0.016 (0.006)
Ots3	25	0.71	0.70	3	0.015 (0.004)
Otsg68	40	0.91	0.92	0	0.015 (0.004)
Ssa419	15	0.84	0.88	1	0.008 (0.002)
One101	39	0.85	0.83	2	0.018 (0.007)
One102	36	0.89	0.83	4	0.012 (0.003)
One103	35	0.85	0.87	0	0.017 (0.007)
One104	27	0.90	0.90	2	0.016 (0.005)
One106	47	0.95	0.84	8	0.008 (0.002)
One111	84	0.81	0.80	2	0.022 (0.009)
One114	38	0.88	0.89	0	0.006 (0.010)
All loci					0.016 (0.002)

Table 3. Hierarchical gene-diversity analysis of Sheenjek, Chena, Salcha, Fishing Branch, Minto, Chandindu, Kluane, and Teslin populations of chum salmon for 13 microsatellite. Populations and years within populations are outlined in Table 1.

Locus	Within Populations	Among years within populations	Among populations
Oki2	0.9720	0.0198	0.0082
Oke3	0.9661	0.0080	0.0259
One104	0.9805	0.0024	0.0171
Oki100	0.9770	0.0037	0.0193
Ots3	0.9772	0.0087	0.0110
Otsg68	0.9811	0.0013	0.0176
Ots103	0.9744	0.0044	0.0212
Ssa419	0.9903	0.0018	0.0079
One101	0.9650	0.0069	0.0212
One102	0.9906	0.0014	0.0080
One106	0.9900	0.0024	0.0076
One111	0.9675	0.0121	0.0204
One114	0.9848	0.0000	0.0152
All loci	0.9724	0.0051	0.0160

Table 4. Estimated (Est) percentage classifications, including standard deviations (SD), of known mixtures (T=100%) of Yukon River chum salmon populations using microsatellite markers.

	Simulation 1			Simulation 2			Simulation 3			Simulation 4			Simulation 5			Simulation 6		
Stock grouping	T	Est	SD	T	Est	SD	T	Est	SD	T	Est	SD	T	Est	SD	T	Est	SD
Andreafsky	100	**85.4**	4.1		2.1	1.8		0.1	0.4		0.4	0.7		0.0	0.1		0.0	0.1
Chulinak		9.8	3.4	100	**92.8**	3.2		0.4	0.6		2.4	1.6		0.2	0.4		0.1	0.2
Σ Summer (lower)	100	95.2	2.4	100	94.9	2.6		0.5	0.7		2.8	1.9		0.2	0.4		0.1	0.2
Jim		0.8	1.1		0.8	1.2	100	**85.4**	4.7		3.6	2.7		1.0	1.3		0.7	1.1
Koyukuk (south)		1.2	1.3		1.3	1.4		1.0	1.2	100	**77.0**	4.9		0.4	0.7		0.4	0.7
Σ Koyukuk River		2.0	1.7		2.1	1.9	100	86.4	4.5	100	80.6	4.8		1.4	1.5		1.3	1.4
Kantishna		0.1	0.2		0.3	0.5		0.9	1.2		0.6	1.0	100	**89.3**	4.0		4.0	2.8
Toklat		0.2	0.5		0.1	0.3		0.6	0.9		1.4	1.6		5.8	3.7	100	**87.7**	4.2
Delta		0.0	0.1		0.1	0.2		0.2	0.5		0.1	0.3		0.4	0.7		0.8	1.0
Chena		0.4	0.6		0.6	0.9		4.2	3.4		4.2	2.9		0.7	1.0		1.7	2.0
Salcha		0.7	0.9		0.5	0.7		2.2	2.1		4.4	3.0		0.3	0.6		1.2	1.4
Σ Tanana River		1.4	1.2		1.5	1.4		8.2	3.8		10.8	3.7	100	96.5	1.8	100	95.2	2.5
Sheenjek		0.2	0.4		0.3	0.6		1.3	1.5		1.4	1.7		0.4	0.8		0.9	1.2
Black		0.0	0.1		0.2	0.4		0.3	0.6		0.6	0.9		0.0	0.2		0.3	0.5
Σ Porcupine (US)		0.2	0.4		0.4	0.7		1.5	1.6		2.0	1.8		0.5	0.8		1.2	1.3
Chandalar		0.2	0.4		0.1	0.3		1.4	1.5		0.4	0.8		0.2	0.4		0.3	0.7
Big Salt		0.1	0.3		0.1	0.2		0.4	0.6		0.6	0.9		0.3	0.6		0.2	0.5
Σ US (all Alaska)	100	99.3	2.4	100	99.2	2.6	100	98.4	4.5	100	97.2	4.8	100	98.9	1.8	100	98.1	2.5
Fishing Branch		0.3	0.5		0.2	0.5		0.4	0.9		1.3	1.5		0.4	0.6		0.7	1.1
Chandindu		0.0	0.2		0.0	0.1		0.1	0.3		0.2	0.4		0.0	0.2		0.1	0.2
Kluane		0.1	0.3		0.1	0.2		0.1	0.2		0.1	0.3		0.2	0.2		0.1	0.2
Donjek		0.0	0.0		0.0	0.1		0.0	0.1		0.0	0.1		0.0	0.1		0.0	0.2
Σ White		0.1	0.3		0.1	0.2		0.1	0.2		0.1	0.3		0.1	0.2		0.1	0.3
Pelly		0.1	0.3		0.0	0.1		0.1	0.2		0.0	0.1		0.1	0.2		0.1	0.3
Big_Creek		0.1	0.2		0.1	0.3		0.3	0.6		0.5	0.7		0.2	0.5		0.4	0.7
Tatchun		0.1	0.4		0.1	0.3		0.1	0.2		0.2	0.4		0.1	0.2		0.1	0.3
Minto		0.2	0.4		0.2	0.3		0.5	0.9		0.6	1.0		0.2	0.5		0.4	0.6
Σ Mainstem		0.5	0.7		0.5	0.6		1.0	1.1		1.3	1.3		0.5	0.7		0.9	1.1
Teslin		0.0	0.1		0.1	0.2		0.1	0.2		0.1	0.3		0.1	0.2		0.1	0.3
Σ Canada		0.7	0.9		0.8	2.6		1.6	4.5		2.8	4.8		1.1	1.8		1.9	2.5

Table 4. Estimated (Est) percentage classifications, including standard deviations (SD), of known mixtures (T=100%) of Yukon River chum salmon populations using microsatellite markers.

	Simulation 1			Simulation 2			Simulation 3			Simulation 4			Simulation 5			Simulation 6		
Stock grouping	T	Est	SD	T	Est	SD	T	Est	SD	T	Est	SD	T	Est	SD	T	Est	SD
Andreafsky	100	**85.4**	4.1		2.1	1.8		0.1	0.4		0.4	0.7		0.0	0.1		0.0	0.1
Chulinak		9.8	3.4	100	**92.8**	3.2		0.4	0.6		2.4	1.6		0.2	0.4		0.1	0.2
Σ Summer (lower)	100	95.2	2.4	100	94.9	2.6		0.5	0.7		2.8	1.9		0.2	0.4		0.1	0.2
Jim		0.8	1.1		0.8	1.2	100	**85.4**	4.7		3.6	2.7		1.0	1.3		0.7	1.1
Koyukuk (south)		1.2	1.3		1.3	1.4		1.0	1.2	100	**77.0**	4.9		0.4	0.7		0.4	0.7
Σ Koyukuk River		2.0	1.7		2.1	1.9	100	86.4	4.5	100	80.6	4.8		1.4	1.5		1.3	1.4
Kantishna		0.1	0.2		0.3	0.5		0.9	1.2		0.6	1.0	100	**89.3**	4.0		4.0	2.8
Toklat		0.2	0.5		0.1	0.3		0.6	0.9		1.4	1.6		5.8	3.7	100	**87.7**	4.2
Delta		0.0	0.1		0.1	0.2		0.2	0.5		0.1	0.3		0.4	0.7		0.8	1.0
Chena		0.4	0.6		0.6	0.9		4.2	3.4		4.2	2.9		0.7	1.0		1.7	2.0
Salcha		0.7	0.9		0.5	0.7		2.2	2.1		4.4	3.0		0.3	0.6		1.2	1.4
Σ Tanana River		1.4	1.2		1.5	1.4		8.2	3.8		10.8	3.7	100	96.5	1.8	100	95.2	2.5
Sheenjek		0.2	0.4		0.3	0.6		1.3	1.5		1.4	1.7		0.4	0.8		0.9	1.2
Black		0.0	0.1		0.2	0.4		0.3	0.6		0.6	0.9		0.0	0.2		0.3	0.5
Σ Porcupine (US)		0.2	0.4		0.4	0.7		1.5	1.6		2.0	1.8		0.5	0.8		1.2	1.3
Chandalar		0.2	0.4		0.1	0.3		1.4	1.5		0.4	0.8		0.2	0.4		0.3	0.7
Big Salt		0.1	0.3		0.1	0.2		0.4	0.6		0.6	0.9		0.3	0.6		0.2	0.5
Σ US (all Alaska)	100	99.3	2.4	100	99.2	2.6	100	98.4	4.5	100	97.2	4.8	100	98.9	1.8	100	98.1	2.5
Fishing Branch		0.3	0.5		0.2	0.5		0.4	0.9		1.3	1.5		0.4	0.6		0.7	1.1
Chandindu		0.0	0.2		0.0	0.1		0.1	0.3		0.2	0.4		0.0	0.2		0.1	0.2
Kluane		0.1	0.3		0.1	0.2		0.1	0.2		0.1	0.3		0.2	0.2		0.1	0.2
Donjek		0.0	0.0		0.0	0.1		0.0	0.1		0.0	0.1		0.0	0.1		0.0	0.2
Σ White		0.1	0.3		0.1	0.2		0.1	0.2		0.1	0.3		0.1	0.2		0.1	0.3
Pelly		0.1	0.3		0.0	0.1		0.1	0.2		0.0	0.1		0.1	0.2		0.1	0.3
Big_Creek		0.1	0.2		0.1	0.3		0.3	0.6		0.5	0.7		0.2	0.5		0.4	0.7
Tatchun		0.1	0.4		0.1	0.3		0.1	0.2		0.2	0.4		0.1	0.2		0.1	0.3
Minto		0.2	0.4		0.2	0.3		0.5	0.9		0.6	1.0		0.2	0.5		0.4	0.6
Σ Mainstem		0.5	0.7		0.5	0.6		1.0	1.1		1.3	1.3		0.5	0.7		0.9	1.1
Teslin		0.0	0.1		0.1	0.2		0.1	0.2		0.1	0.3		0.1	0.2		0.1	0.3
Σ Canada		0.7	0.9		0.8	2.6		1.6	4.5		2.8	4.8		1.1	1.8		1.9	2.5

Table 4 (cont'd)

	Simulation 7			Simulation 8			Simulation 9			Simulation 10			Simulation 11			Simulation 12		
Stock grouping	T	Est	SD	T	Est	SD	T	Est	SD	T	Est	SD	T	Est	SD	T	Est	SD
Andreafsky		0.1	0.3		0.1	0.2		0.1	0.2		0.0	0.0		0.1	0.2		0.1	0.2
Chulinak		0.1	0.4		0.2	0.5		0.2	0.5		0.1	0.3		0.1	0.2		0.1	0.3
Σ Summer (lower)		0.2	0.5		0.2	0.6		0.3	0.5		0.1	0.3		0.1	0.3		0.2	0.4
Jim		1.1	1.3		1.9	2.1		1.8	2.1		0.4	0.7		0.7	1.0		1.9	1.9
Koyukuk (south)		0.3	0.5		0.7	1.2		0.9	1.2		0.3	0.6		0.6	1.0		0.2	0.4
Σ Koyukuk		1.4	1.5		2.6	2.5		2.7	2.4		0.7	0.7		1.3	1.4		2.1	1.9
Kantishna		1.7	1.8		0.6	1.0		0.4	0.7		0.3	0.6		0.3	0.7		0.2	0.5
Toklat		5.0	3.3		1.4	1.7		1.2	1.5		0.7	1.1		0.8	1.2		0.4	0.9
Delta	100	**86.5**	3.7		0.2	0.4		0.2	0.5		0.1	0.3		0.3	0.5		0.1	0.4
Chena		0.6	0.9	100	**82.2**	5.6		11.4	5.0		0.7	1.1		0.7	1.0		0.5	1.1
Salcha		0.5	0.9		9.7	5.0	100	**81.5**	5.6		0.5	0.9		0.6	1.0		0.3	0.5
Σ Tanana	100	94.3	2.4	100	94.1	3.0	100	94.7	2.9		2.2	1.9		2.6	2.0		1.6	1.7
Sheenjek		0.7	1.1		1.1	1.3		0.5	0.9	100	**86.5**	4.6		2.2	2.2		6.0	4.2
Black		0.4	0.7		0.2	0.4		0.2	0.6		0.4	0.9	100	**79.6**	5.5		1.0	1.2
Σ Porcupine (US)		1.0	1.2		1.2	1.4		0.8	1.0	100	86.9	4.6	100	81.8	5.3		7.0	4.2
Chandalar		0.5	0.8		0.3	0.5		0.2	0.5		1.5	1.9		1.5	1.8	100	**81.5**	4.9
Big Salt		0.2	0.3		0.2	0.5		0.2	0.6		0.5	0.9		0.4	0.7		0.3	0.6
Σ US	100	97.6	2.4	100	98.7	3.0	100	98.9	2.9	100	91.9	4.6	100	87.7	5.3	100	92.6	5.0
Fishing Branch		0.9	1.3		0.5	0.8		0.3	0.7		5.3	3.7		8.5	4.4		2.8	2.3
Chandindu		0.0	0.1		0.1	0.3		0.2	0.4		0.1	0.2		0.1	0.3		0.1	0.3
Kluane		0.2	0.3		0.1	0.2		0.0	0.1		0.1	0.2		0.2	0.4		0.2	0.4
Donjek		0.1	0.2		0.0	0.1		0.0	0.0		0.0	0.1		0.0	0.2		0.0	0.2
Σ White		0.2	0.4		0.1	0.2		0.1	0.2		0.1	0.2		0.2	0.4		0.2	0.4
Pelly		0.1	0.2		0.1	0.2		0.0	0.2		0.2	0.5		0.2	0.5		0.1	0.3
Big_Creek		0.4	0.7		0.2	0.4		0.2	0.4		0.9	1.3		1.1	1.5		1.3	1.6
Tatchun		0.2	0.4		0.1	0.3		0.1	0.2		0.3	0.7		0.7	0.9		0.3	0.6
Minto		0.4	0.6		0.2	0.5		0.3	0.6		1.4	1.7		1.4	1.7		2.3	2.3
Σ Mainstem		1.1	0.9		0.6	0.8		0.6	0.8		2.7	2.2		3.4	2.3		4.1	2.7
Teslin		0.2	0.4		0.1	0.3		0.0	0.1		0.1	0.3		0.1	0.2		0.3	0.5
Σ Canada		2.4	2.4		1.3	3.0		1.1	2.9		8.1	4.6		12.3	5.3		7.4	5.0

Table 4 (cont'd)

Stock grouping	Simulation 13			Simulation 14			Simulation 15			Simulation 16			Simulation 17			Simulation 18		
	T	Est	SD	T	Est	SD	T	Est	SD	T	Est	SD	T	Est	SD	T	Est	SD
Andreafsky		0.2	0.4		0.0	0.1		0.1	0.4		0.0	0.0		0.0	0.1		0.0	0.1
Chulinak		0.4	0.7		0.1	0.2		0.3	0.5		0.0	0.2		0.0	0.1		0.1	0.3
Σ Summer (lower)		0.6	0.8		0.1	0.2		0.4	0.6		0.0	0.2		0.0	0.1		0.1	0.3
Jim		3.7	2.6		0.1	0.4		1.0	1.4		0.0	0.1		0.1	0.3		0.4	0.7
Koyukuk (south)		2.1	2.0		0.2	0.4		0.6	1.0		0.0	0.2		0.1	0.2		0.1	0.3
Σ Koyukuk		5.8	2.9		0.3	0.5		1.6	1.7		0.0	0.2		0.2	0.3		0.5	0.7
Kantishna		0.8	1.1		0.2	0.4		0.2	0.5		0.0	0.1		0.0	0.1		0.3	0.6
Toklat		1.1	1.6		0.3	0.7		0.4	0.8		0.0	0.1		0.1	0.2		0.2	0.6
Delta		0.2	0.6		0.1	0.2		0.0	0.1		0.0	0.1		0.1	0.2		0.1	0.3
Chena		3.8	3.1		0.3	0.6		1.3	1.7		0.0	0.1		0.2	0.5		0.2	0.5
Salcha		2.4	2.6		0.2	0.6		1.2	1.5		0.0	0.1		0.1	0.3		0.3	0.6
Σ Tanana		8.4	4.2		1.0	1.1		3.2	2.3		0.0	0.3		0.4	0.6		1.2	1.2
Sheenjek		9.7	4.2		3.4	2.8		1.1	1.2		0.1	0.2		0.2	0.4		2.1	2.2
Black		0.5	0.7		0.9	1.3		0.6	0.8		0.1	0.3		0.1	0.3		0.6	0.9
Σ Porcupine (US)		10.2	4.2		4.3	3.0		1.6	1.4		0.1	0.4		0.3	0.5		2.7	2.3
Chandalar		1.5	1.8		0.7	1.2		0.4	0.8		0.0	0.1		0.3	0.6		0.6	0.8
Big Salt	100	**63.2**	6.4		0.2	0.4		0.4	0.5		0.0	0.1		0.1	0.3		0.2	0.4
Σ US	100	89.6	6.0		6.6	3.6		7.5	3.0		0.4	0.7		1.1	1.4		5.2	3.4
Fishing Branch		6.5	4.3	100	**89.7**	3.6		2.5	1.9		0.1	0.3		0.4	0.6		4.4	2.8
Chandindu		0.3	0.6		0.1	0.2	100	**87.6**	3.0		0.0	0.0		0.0	0.0		0.1	0.2
Kluane		0.2	0.5		0.2	0.4		0.1	0.4	100	**98.8**	1.2		12.4	3.6		0.6	0.8
Donjek		0.1	0.1		0.1	0.2		0.0	0.1		0.5	0.8	100	**85.5**	3.6		0.0	0.1
Σ White		0.3	0.5		0.3	0.4		0.1	0.4	100	99.3	0.7	100	97.9	1.3		0.6	0.8
Pelly		0.1	0.3		0.2	0.4		0.1	0.3		0.0	0.1		0.0	0.1	100	**80.6**	4.9
Big_Creek		0.9	1.3		1.1	1.5		0.5	0.9		0.1	0.2		0.2	0.5		3.0	2.4
Tatchun		0.2	0.5		0.4	0.7		0.1	0.3		0.0	0.1		0.2	0.3		0.7	0.9
Minto		1.8	1.9		1.5	1.8		1.3	1.5		0.0	0.1		0.1	0.3		5.2	3.4
Σ Mainstem		3.1	2.6		3.1	2.5		2.1	1.7		0.2	0.3		0.5	0.7	100	89.5	3.4
Teslin		0.2	0.3		0.2	0.4		0.2	0.5		0.0	0.0		0.0	0.2		0.3	0.5
Σ Canada		10.4	6.0	100	93.4	3.6		92.5	3.0		99.6	0.7		98.9	1.4	100	94.8	3.4

Table 4 (continued)

Stock grouping	Simulation 19			Simulation 20			Simulation 21			Simulation 22		
	T	Est	SD	T	Est	SD	T	Est	SD	T	Est	SD
Andreafsky		0.0	0.1		0.2	0.4		0.1	0.2		0.0	0.1
Chulinak		0.1	0.3		0.2	0.5		0.1	0.3		0.1	0.2
Σ Summer (lower)		0.2	0.3		0.4	0.6		0.2	0.5		0.1	0.3
Jim		0.8	1.0		0.4	0.6		0.5	0.9		0.2	0.4
Koyukuk (south)		0.2	0.5		0.2	0.5		0.3	0.5		0.1	0.3
Σ Koyukuk		1.4	1.4		0.6	0.6		0.8	1.1		0.3	0.5
Kantishna		0.3	0.5		0.1	0.2		0.2	0.5		0.2	0.4
Toklat		0.6	1.1		0.2	0.4		0.6	1.0		0.2	0.5
Delta		0.3	0.6		0.1	0.3		0.1	0.2		0.1	0.3
Chena		0.6	1.0		0.2	0.5		0.3	0.5		0.1	0.3
Salcha		0.4	0.7		0.2	0.6		0.3	0.6		0.1	0.3
Σ Tanana		2.1	1.9		0.8	0.9		1.4	1.3		0.7	0.8
Sheenjek		4.2	3.4		1.4	1.7		3.2	2.8		0.4	0.8
Black		1.1	1.4		1.0	1.3		0.6	1.0		0.1	0.2
Σ Porcupine (US)		5.3	3.7		2.4	2.2		3.8	2.9		0.4	0.9
Chandalar		1.4	1.7		0.8	1.1		1.8	2.1		0.5	0.7
Big Salt		0.4	0.7		0.2	0.5		0.2	0.5		0.1	0.2
Σ US		10.3	6.0		5.1	4.0		8.2	5.1		2.1	0.2
Fishing Branch		6.0	4.5		5.7	3.1		3.6	3.4		0.8	1.1
Chandindu		0.1	0.3		0.1	0.2		0.1	0.3		0.0	0.2
Kluane		0.3	0.4		0.3	0.5		0.1	0.2		0.0	0.1
Donjek		0.1	0.2		0.1	0.2		0.0	0.1		0.0	0.0
Σ White		0.3	0.5		0.3	0.6		0.1	0.3		0.0	0.1
Pelly		0.5	0.7		0.3	0.6		0.3	0.5		0.1	0.3
Big_Creek	100	**76.1**	6.4		1.8	2.0		1.9	1.9		0.5	0.9
Tatchun		0.6	0.9	100	**81.6**	4.9		1.1	1.3		0.2	0.4
Minto		5.6	3.7		4.8	3.2	100	**84.3**	5.4		1.1	1.1
Σ Mainstem	100	82.8	5.7	100	88.5	4.0		87.6	5.1		1.9	1.5
Teslin		0.4	0.9		0.4	0.8		0.5	0.7	100	**95.1**	2.1
Σ Canada	100	89.7	6.0	100	94.9	4.0	100	91.8	5.1	100	97.9	0.2

Table 5. Simulations (percentages for True (T), Estimated (Est), and standard deviations (SD)) by population and region for Yukon River chum salmon for four simulated mixtures of 150 chum salmon from each population using Rannala and Mountain correction for small sample size.

	Simulation 1			Simulation 2			Simulation 3			Simulation 4		
	TRUE	Est	SD	T	Est	SD	T	Est	SD	T	Est	SD
Andreafsky		0.4	0.6		0.0	0.2		0.1	0.2		0.6	0.8
Chulinak	10	9.4	2.6		0.1	0.3		0.1	0.4	20	17.9	3.7
Σ Summer (lower)	10	9.7	2.6		0.1	0.3		0.2	0.5	20	18.5	3.8
Jim		1.3	1.6		0.4	0.8		1.7	1.7	10	10.1	3.5
Koyukuk (south)	10	6.9	2.7		0.2	0.5		0.7	1.1	10	7.6	3.0
Σ Koyukuk	10	8.2	2.8		0.6	0.8		2.4	1.9	20	17.7	4.4
Kantishna		0.6	0.9		0.2	0.5	10	8.3	2.9		1.4	1.5
Toklat		1.8	2.0		0.6	0.9		2.5	2.5	20	16.7	4.3
Delta	20	15.7	3.5		0.1	0.4	10	7.5	2.3		0.3	0.6
Cheena		1.2	1.3		0.4	0.8	10	8.6	3.4		4.6	3.2
Salcha		0.9	1.2		0.4	0.7		1.7	1.8	20	16.8	4.3
Σ Tanana	20	20.2	4.0		1.7	1.6	30	28.6	4.5	40	39.8	5.1
Sheenjek	20	19.1	4.7		2.6	2.3	15	17.0	4.8		1.7	1.8
Black		0.9	1.3		0.5	0.9	5	3.5	2.0		0.4	0.7
Σ Porcupine (US)	20	20.0	4.8		3.1	2.5	20	20.5	5.3		2.1	1.8
Chandalar		0.9	1.5		0.7	1.0	15	11.9	3.6		0.7	1.2
Big Salt		0.3	0.6		0.2	0.6	5	2.1	1.5		0.4	0.7
Σ US	60	59.4	5.5		6.4	5.2	70	65.7	4.5	80	79.2	2.7
Fishing Branch	30	30.6	5.5	25	25.9	4.5	10	12.9	4.2	10	9.0	3.1
Chandindu		0.1	0.3	10	7.4	2.5		0.1	0.3		0.1	0.2
Kluane		0.1	0.3	20	19.5	3.2	10	10.2	2.8	10	9.9	2.7
Donjek		0.1	0.2		0.2	0.5		0.1	0.3		0.1	0.3
Σ White		0.2	0.4	20	19.8	3.1		10.3	2.8	10	10.0	2.7
Pelly		0.2	0.4	10	6.7	2.4		0.1	0.3		0.0	0.1
Big_Creek		1.1	1.7	10	8.4	3.1		1.0	1.3		0.7	1.0
Tatchun	10	5.9	2.6		0.3	0.7		0.4	0.8		0.3	0.5
Minto		2.1	2.2	10	11.8	4.1	10	9.2	3.6		0.7	1.1
Σ Mainstem	10	9.6	3.8	30	27.2	4.6	10	10.8	3.8		1.7	1.5
Teslin		0.2	0.5	15	13.4	3.6		0.2	0.6		0.1	0.3
Σ Canada	40	40.6	5.5	100	93.6	5.2	30	34.3	4.5		20.8	2.7

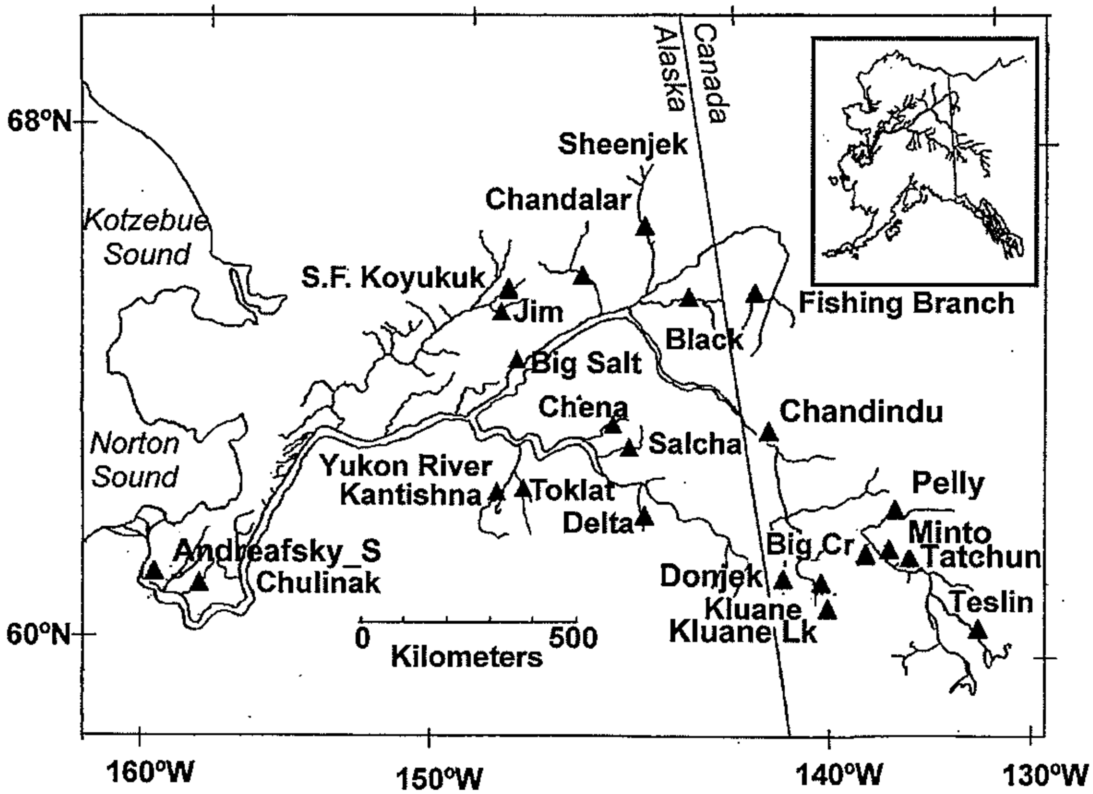

Figure 1. Locations of chum salmon populations sampled in the Yukon River drainage. Numbers and sampling years are indicated in Table 1.

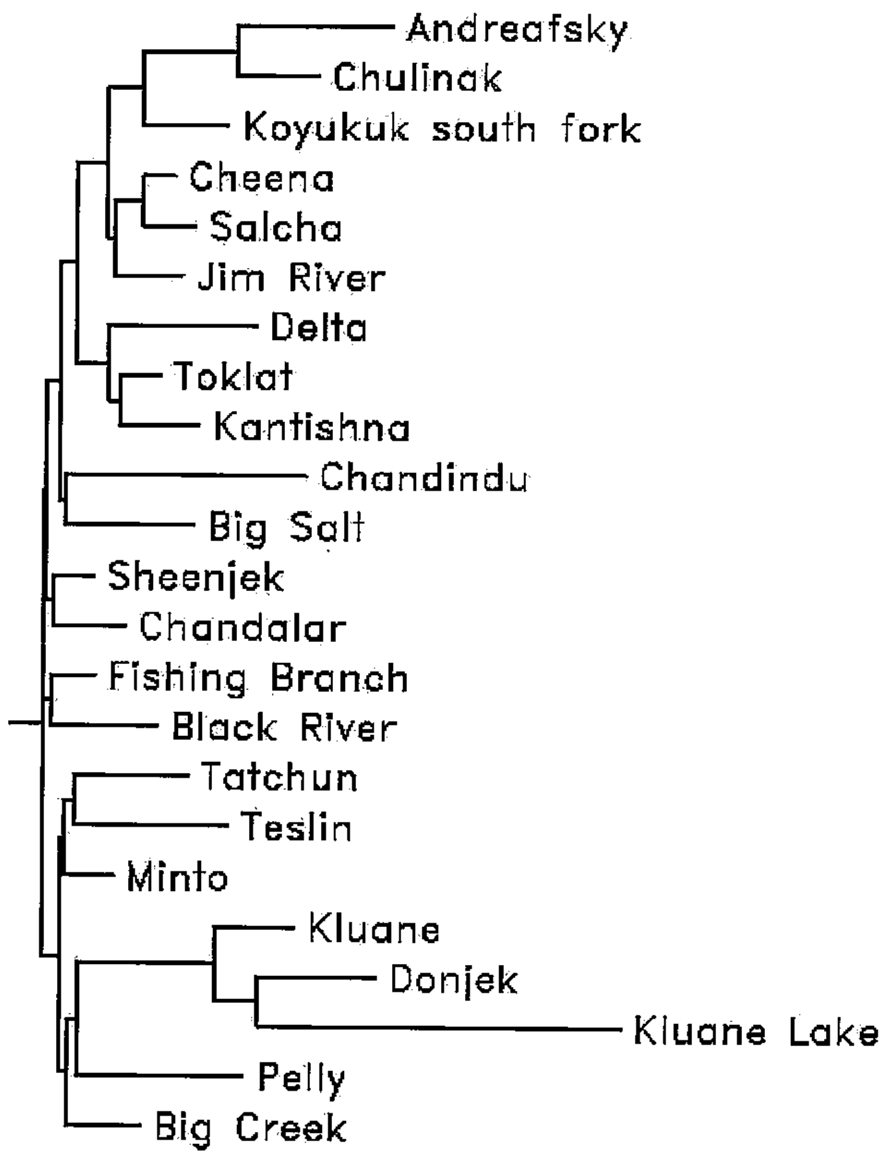

Figure 2. Neighbor-joining dendrogram based on Cavalli-Sforza and Edward's (1967) chord distance for 23 Yukon River chum salmon populations.