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United States And Canadian Chinook Salmon Populations In The Yukon River Can Be Segregated Based On Genetic Characteristics

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Abstract: Chinook salmon (*Oncorhynchus tshawytscha*) spawn throughout the Yukon River drainage, supporting fisheries in both the United States and Canada. To achieve management goals set under international agreements, it is vital to know the proportion of Canadian-origin Chinook salmon harvested in United States fisheries. Currently this proportion is estimated using scale pattern analysis, but this method has several weaknesses, including limited resolution and the necessity for annual sampling. We analyzed samples collected from representative spawning populations throughout the drainage and mixtures from inriver fisheries to investigate the utility of genetic stock identification for applications based on allozyme loci in the Yukon River. Populations demonstrated a strong association between genetic differences and geographic location and could be combined into 6 regional groups. Simulations showed that these regions could be identified in mixtures with a high degree of accuracy and precision.

INTRODUCTION

Chinook salmon (*Oncorhynchus tshawytscha*) return to spawn in their natal streams throughout the Yukon River drainage. For many stocks of Chinook salmon, this requires migrating thousands of kilometers upriver across the United States/Canada border to reach spawning sites in tributaries in the Yukon and British Columbia. Because these salmon enter freshwater in the United States, but spawn in Canada, fisheries that harvest Canadian stocks have been managed under various transboundary plans and interim agreements. These plans culminated in the signing of the Yukon River Salmon Agreement in 2002 as part of the Pacific Salmon Treaty under which recommendations are made to management agencies in Alaska and Canada to provide sufficient Chinook salmon for both fishery and escapement needs in Canada. To achieve management goals it is vital to know the proportion of Canadian-origin Chinook salmon harvested in United States fisheries.

Since 1996 the management goal for Canadian Chinook salmon in the Alaska portion of the river has been to provide for a minimum escapement of 28,000 and a harvest of approximately 18,000 Chinook salmon in the Canadian mainstem portion of the river. The United States/Canada border passage of Chinook salmon is estimated by tagging salmon captured in fishwheels near the border and recovering the tags further upstream in aboriginal and commercial fisheries. These estimates are complemented by a variety of other methods such as radio telemetry, a mark–recapture study at Rampart (river kilometer 763), sonar abundance estimation at Pilot Station (river kilometer 196), and aerial observation of spawning streams to provide an overview of the entire season.

The recent management history of Chinook salmon in the Yukon River provides a good example of how this process works in both high and low abundance years. Between 1989 and 1998, the average annual harvest was 156,000 Chinook salmon, but the abundance of Chinook salmon in the Yukon River began to decline in 1998, and by 2000 the run was the lowest on record. Beginning in 1998, Chinook salmon fisheries were restricted in response to low abundances, but goals for border passage in Canada were not met between 1998 and 2000. As a result, the Alaska Board of Fisheries declared Yukon River Chinook salmon to be a "stock of yield concern" in 2000 under the Sustainable Salmon Fisheries Policy (5 AAC 39.222).

Anticipating continued low abundance in 2001, commercial and sport fisheries for Chinook salmon

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were closed in the Alaska portion of the river. These closures, coupled with a larger than expected run, led to escapement goals being met for both countries, with a surplus in Canada of 20,000 Chinook salmon beyond subsistence and escapement needs. The mark–recapture study estimated that border passage into Canada was at record levels, yet aerial surveys of spawning grounds did not show similar indication of record escapement. The run in 2002 was similar, and escapement goals were met with 24,000 Chinook harvested in the Alaska commercial fisheries. Mark–recapture estimates showed 43,000 fish passing the border, and similar results were obtained from the radio telemetry study. Again, anticipating the need to curtail harvest, the commercial fishery was closed for the first half of the 2003 season. The run in 2003 was unexpectedly strong; 41,000 Chinook salmon were commercially harvested in Alaska, and more than 50,000 passed the border. Preliminary estimates indicated an excess escapement of 40,000 Chinook salmon.

The Alaska Department of Fish and Game (ADF&G) currently uses scale pattern analysis (SPA) to determine the age and stock composition of mixtures of Chinook salmon within the Yukon River. This analysis method uses scales collected annually from a set of reference populations representing three major stock groups: 1) Lower Yukon—Andreafsky, Anvik and Gisasa rivers, 2) Middle Yukon—Chena, Salcha, and Henshaw rivers, and 3) Upper Yukon—samples collected at fishwheels above the United States/Canada border. Estimates of stock contribution to area fisheries can be obtained by comparing patterns of scale growth for Chinook salmon sampled from the mixture with patterns observed in these representative populations. This method has shown acceptable levels of accuracy and precision, but it has several weaknesses: 1) the baseline must be sampled annually, 2) a limited set of populations represents the stock groups, and 3) stock-composition estimates require scales from salmon on the spawning grounds and are, therefore, only available post season (Lingnau 2000).

Genetic stock identification has been used in Chinook salmon fisheries across the species natural range (Washington and Columbia River—Utter et al. 1987; Shaklee et al. 1999; British Columbia—Beacham et al.1996; Southeast Alaska—Crane et al. 2000) and may prove useful for meeting management objectives in the Yukon River. Historic use of genetic stock identification has demonstrated the advantages of this technique for use in mixed-stock salmon fisheries including temporal stability of the baseline, more complete representation of populations in the baseline, and the timeliness of stock-composition estimates. Of course, the usefulness of genetic stock identification for any application is predicated on the level of quantifiable genetic differences among stocks or stock groups.

Previous studies of Chinook salmon in portions of the Yukon River drainage (Gharrett et al. 1987; Beacham et al. 1989) demonstrated significant genetic variation among some of the populations surveyed, but neither study attempted a comprehensive baseline. We analyzed samples collected from representative spawning populations throughout the drainage and mixtures of Chinook salmon from the lower Yukon River to investigate the utility of genetic stock identification for applications in the Yukon River. We report the investigation of genetic population structure based on information from allozyme loci and stock composition estimates of simulated and actual mixtures of Chinook salmon from the Yukon River.

METHODS

Sample Collection

The baseline genetic data were composed of Chinook salmon sampled from spawning aggregates in the major tributaries to the Yukon River (Table 1) as part of a larger study of Chinook and chum salmon populations in this drainage (Wilmot et al. 1992). Whenever possible, individuals were sampled on the spawning grounds, but as necessary were also collected from sonar and weir sites. Collections were made from some sites in more than one year to assess the temporal stability of allele frequencies. Sampling locations were selected based on two criteria: 1) access to spawning salmon in remote locations, and 2) preferential sampling from larger spawning populations. Target sample sizes were set at 75 individuals for collections of adults and 100 individuals for collections of juveniles. Samples were taken from four tissues (muscle, liver, eye and heart) from each salmon, placed in matching sets of individually labeled vials, and frozen prior to laboratory analysis.

Mixed-stock samples of adult Chinook salmon were collected from commercial and test fisheries on the lower Yukon River near Emmonak (District 1, below river kilometer 114) during the months of June and July from 1987 to 1990 and in 2002 and 2003 from the species apportionment fishery for the ADF&G sonar project at Pilot Station (river kilometer 196). Whenever possible, all Chinook salmon encountered in the test nets were sampled for genetic studies. Target sample size for commercially harvested Chinook salmon was set at 150 individuals per fishing period. Periods were

Table 1. Chinook salmon collections from the Yukon River. Populations are listed in order of geographical occurrence from the mouth of the Yukon River. The distances (river kilometers, RKm) from the mouth of the Yukon River to the confluence of each sampled tributary are included.

	Sample			
Population	Sizes	Years	Total	RKm
UNITED STATES				
Andreafsky River	100	1988	100	104
Anvik River	40, 60	1987, 1988	100	317
Nulato River				
North Fork	50	1988	50	483
South Fork	50	1988	50	483
Koyukuk Drainage				
Gisasa River	47, 91	1987, 1988	138	564
Henshaw River	87	1987	87	966
South Fork	112	1987	112	986
Jim River	79	1987	79	1026
Tanana Drainage				
Chena River	151, 98	1987, 1988	249	920
Salcha River	100	1988	100	965
CANADA				
Klondike River, North Fork	44, 50	1989, 1990	94	1320
McQuesten River	38, 200	1989, 1990	238	1455
Pelly River				
Ross River	14, 30	1988, 1989	44	1602
Blind Creek	150	1989	150	1575
Tatchun River	49, 29	1988, 1989	78	1530
Little Salmon Drainage				
Little Salmon River	35, 27	1988, 1989	62	1610
Bear Feed River	87	1989	87	1610
Big Salmon River	49, 77	1988, 1989	126	1621
Takhini Drainage				
Takhini River	26, 26	1988, 1990	52	1718
Stony River	121	1990	121	1718
Nisutlin River	71	1989	71	1788
TOTAL			2188	

usually opened twice a week throughout the summer. In some cases we used a smaller sample size rather than combine periods that were widely separated. Samples taken from District 1 commercial fisheries were comprised of four tissues (muscle, liver, eye and heart) from each salmon. Collections taken from Pilot Station in 2002 and 2003 consisted of only two tissues (muscle and fin). Additional collections were available from a radio telemetry project conducted on Yukon River Chinook salmon in 2002 and 2003 (Eiler et al. In press; John Eiler, NMFS Auke Bay Laboratory, personal communication), but the only tissue available was the axillary process.

Laboratory Analysis

Genetic data were collected in the form of individual genotypes inferred from phenotypes observed for 16 enzymes indicating variation at 22 enzyme-encoding loci (Table 2). This variation was assayed from protein extracts using horizontal starch gel electrophoresis as described by Aebersold et al. (1987) and Van Doornik et al. (1999). Loci and alleles used in this analysis follow protocols adopted for inclusion in the coastwide database for Chinook salmon (Teel et al. 1999). Not all loci could be resolved when only muscle and fin or only axillary process tissues were available. As a result, only 14 loci were used for the analysis of the Pilot Station mixed-stock collections, and 11 loci were used for the analysis of the radio telemetry samples. Enzyme nomenclature follows recommendations by the American Fisheries Society (Shaklee et al. 1990). Individual genotype data were summarized into allelic frequencies for all loci except for *sMEP-2**. The heterozygote phenotype at *sMEP-2** could not be consistently scored, so homozygous dominant and recessive phenotype frequencies were calculated for this locus by counting all potential heterozygous genotypes as homozygous dominant genotypes.

Table 2. Polymorphic allozyme loci assayed in Yukon River Chinook salmon populations and mixtures. All loci could be assayed when four tissues were present, but only a subset of the loci could be assayed when only muscle and fin (M/F) or axillary process (AX) tissues were available.

			Assay	
Enzyme	Enzyme Number	Locus	M/F	AX
Aspartate aminotransferase	2.6.1.1	*sAAT-3**		
		*sAAT-4**	X	
Adenosine deaminase	3.5.4.4	*ADA-1**	X	X
Aconitate hydratase	4.2.1.3	*sAH**	X	X
Alanine aminotransferase	2.6.1.2	*ALAT**	X	X
Glucose-6-phosphate isomerase	5.3.1.9	*GPI-B1**		
L-Iditol dehydrogenase	1.1.1.14	*IDDH-1**		
Isocitrate dehydrogenase (NADP+)	1.1.1.42	*sIDHP-1**	X	X
		*sIDHP-2**	X	X
L-lactate dehydrogenase	1.1.1.27	*LDH-B2**	X	X
Malate dehydrogenase	1.1.1.37	*sMDH-B1,2**	X	X
Malic enzyme (NADP+)	1.1.1.40	*sMEP-1**	X	
		*sMEP-2**	X	
Mannose-6-phosphate isomerase	5.3.1.8	*MPI**	X	X
Dipeptidase	3.4.-.-	*PEPA**	X	X
Tripeptide aminopeptidase	3.4.-.-	*PEPB-1**	X	X
Phosphoglucomutase	5.4.2.2	*PGM-1**		
Superoxide dismutase	1.15.1.1	*mSOD**		
		*sSOD-1**	X	X
Triosephosphate isomerase	5.3.1.1	*TPI-2**		
		*TPI-4**		

Population Structure Analysis

For each collection, the observed genotype distribution for each locus was tested against the proportions expected in a randomly mating and randomly sampled population (Hardy-Weinberg equilibrium) using a χ^2 goodness-of-fit test ($\alpha = 0.05$). To reduce the number of spurious significant tests caused by rare genotypes and sampling error (Type I error), two methods of pooling observed genotypes were used. The exact significance probabilities were calculated (analogous to Fisher's exact test) with a modification which pools genotypes into three classes when more than two alleles are observed. Loci not in Hardy-Weinberg proportions using this statistic were re-tested with the χ^2 test and genotypes were pooled if the expected number in any cell was less than four. One in 20 tests are expected to give "false positive" results in each population by chance alone, assuming that the loci studied are segregating independently.

For analysis of population structure, baseline data sets representing temporally and/or spatially stratified collections within river systems were compared using heterogeneity log-likelihood ratio statistics both pairwise and simultaneously among groups (G-test: Sokal and Rohlf 1995). Collections from the same site made at different times were pooled prior to all subsequent analyses based on recommendations by Waples (1990) that the aggregate of multi-year samples better represents populations with overlapping age structure than individual temporally-spaced samples.

Geographic and temporal patterns of genetic relatedness between baseline populations were examined using a measure of genetic distance (unbiased genetic distance; Nei 1978) using only the variable loci in the analysis. Cluster analysis of the genetic distance data was done using the unweighted pair-group method (UPGMA: Sneath and Sokal 1973), and the results were visualized as a dendrogram. The population structure observed in the dendrogram was examined using gene diversity analysis (Chakraborty et al. 1982) to quantify the level of genetic variability explained by the proposed structure.

Homogeneity of allelic frequencies among populations at each level of population grouping was tested using log-likelihood ratios summed over all loci (Seeb et al. 2000, modified from Weir 1990). Hierarchical levels were organized to test for homogeneity 1) between nations, 2) among regions within nations, and 3) among populations within a region. Comparison-wise significance levels were adjusted for multiple tests using a sequential Bonferroni adjustment (modified from Milliken and Johnson 1984 and Rice 1989) with the overall experiment-wise significance level set at $\alpha = 0.05$. This procedure first tested for differences at the top hierarchical level, the entire set of popula-

tions. If significant heterogeneity ($\alpha = 0.05$) exists at this level, then the significance of the between- and within-nation components of the heterogeneity were tested at an adjusted level ($\alpha = 0.05/2 = 0.025$). Significance within nations would lead to a sequentially adjusted test applied at the next level, with testing proceeding similarly through the hierarchy. If a test was not significant, all remaining lower levels were combined, and a final sequentially-adjusted multiple test of significance was performed.

Finally, a Mantel test of correlation (Hutchison and Templeton 1999) between genetic and geographic distances between pairs of populations was used to reveal a possible distance-related explanation for restricted gene flow. A lowess smoother (Chambers et al. 1983) was used to illustrate the trend of association in a plot of inter-population genetic and geographic distances.

All analyses were performed with user-defined functions in the S-plus analysis package (Insightful, Seattle, Washington).

Genetic Stock Identification

Relationships among populations indicated by the dendrogram were used in conjunction with geographical location to assign populations to the genetic/management groups used for reporting results of the mixed-stock analyses. The potential identifiability of these reporting groups was evaluated through simulations performed using the Statistical Package for Analyzing Mixtures (SPAM version 3.6, Debevec et al. 2000), which computes the most likely combination of populations that contribute to a given mixture. Simulations tested group identity by creating simulated mixtures ($N = 400$) composed entirely of the reporting group under study (each population in the reporting group contributes equally to the mixture) and observing the correct identification of this mixture by SPAM. The accuracy and precision of estimates of group identity were derived from the mean and 90% confidence interval of 1,000 simulations in which baseline and mixture genotypes were randomly generated from the baseline allele frequencies assuming Hardy-Weinberg equilibrium. For each simulation, contribution estimates were generated for all populations and summed to the regional level. The 1,000 estimates for a region were sorted from lowest to highest with the 51st and 950th values in the sequence taken respectively as the lower and upper bounds of the 90% confidence interval for that region. Reporting groups with correct mean estimates of 90% or better were considered highly identifiable in fishery.

Estimates of the stock contribution to the mixed-stock fisheries in the Yukon River were calculated for the collections taken from the processors and test net sites during the summers between 1987 and 1990 and from the Pilot Station sonar site in 2002 and 2003. Daily samples were combined to achieve minimum combined sample sizes of 150 individuals. Stock contributions of the defined reporting regions to the test fishery were estimated using SPAM by first calculating individual population estimates and then summing into reporting regions. Ninety percent confidence intervals for all regional contribution estimates were computed from 1,000 parametric bootstrap resamples of the baseline frequencies matched with nonparametric resamples of the mixture genotypes. For each set of estimates, individuals were removed from the analysis if the probability of their genotypes occurring in any of the baseline populations was near zero ($P < 1.0 \times 10^{-45}$). For these cases, the mixture estimates include an additional "unknown" group containing the proportion of the mixture composed of unexplainable genotypes.

RESULTS

Sample Collection

From 1987 to 1990, 2,188 individuals were sampled as part of 31 collections representing 21 different spawning populations (Table 1, Figure 1). Ten of the populations were from the United States portion of the Yukon River Drainage representing the major spawning populations from the lower and middle portions of the river. No samples were taken in United States waters of the Yukon River above the mouth of the Tanana River. The remaining collections were taken from populations located in the drainage above the Canada/United States border. Target samples sizes of 75 individuals from each population were achieved in most cases.

A total of 3,593 samples of adult Chinook salmon were collected from test fishery sites or fish processors in District 1 between 1987 and 1990 (1987: $N = 768$; 1988: $N = 891$; 1989: $N = 995$; 1990: $N = 939$). From the Pilot Station species apportionment fishery 405 Chinook salmon were sampled in 2002 and 587 in 2003 (excluding individuals caught in nets with 10.2-cm [4-in] or smaller mesh). In addition, samples were collected from 424 and 400 Chinook salmon as part of the radio telemetry project in 2002 and 2003, respectively. These salmon had been traced by means of the radio tags to their spawning grounds and were analyzed as a mixture of known composition to test the utility of genetic stock identification.

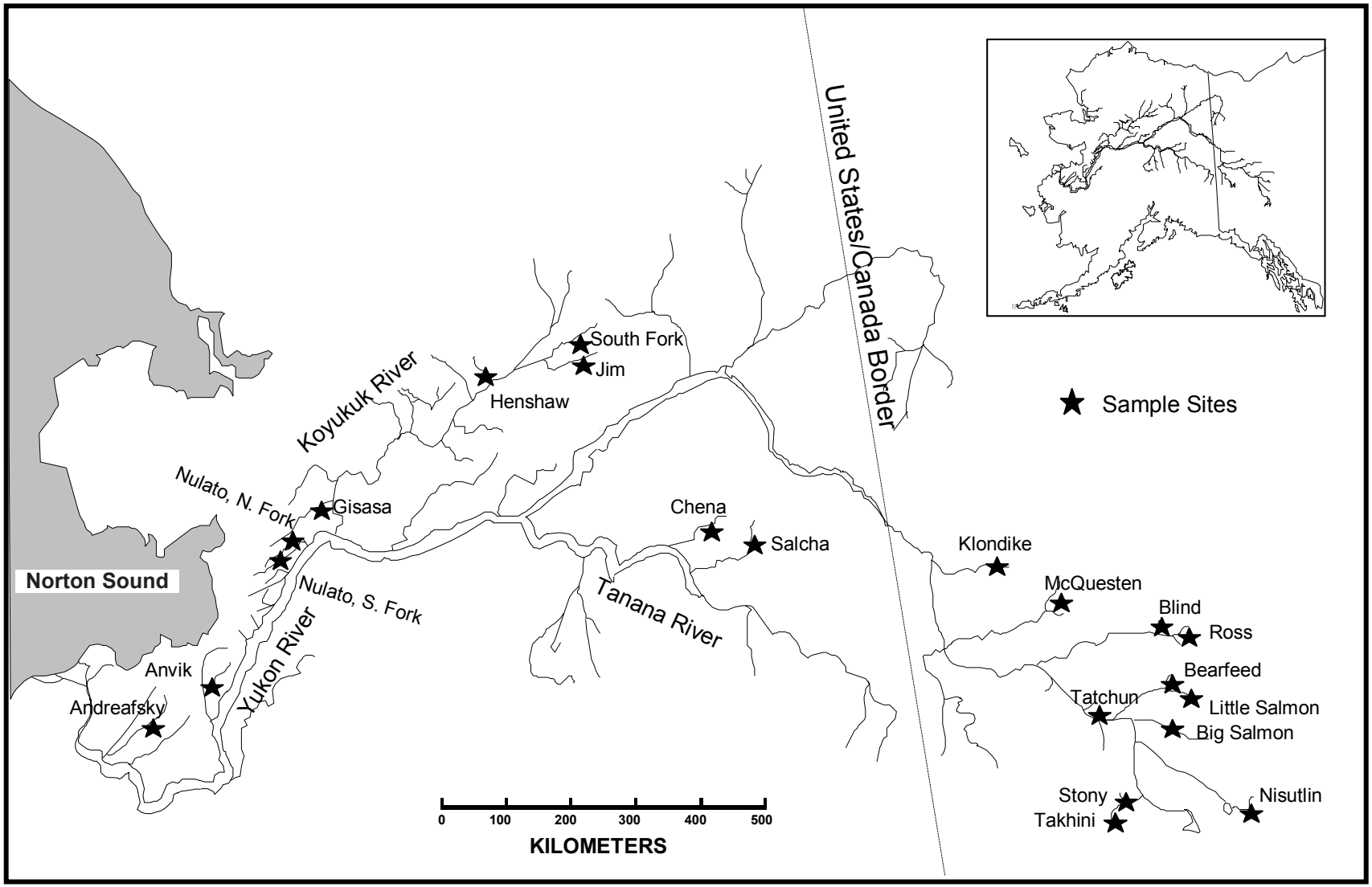

Figure 1. Collection sites for Chinook salmon from the Yukon River drainage.

Population Structure Analysis

Of the loci examined for departures from random mating (*sMEP-2* was treated as a non-segregating character) in the 31 collections, only 4 of 377 total tests were considered significantly different than expected ($\alpha = 0.05$).

Collections taken in multiple years from the same location were pooled for further analyses. Significant differences were found only between the collections from the Takhini River ($G = 17.4$, $df = 6$, $P < 0.01$). These collections were pooled with the Stony River collection for further analyses. Collections from Jim and Henshaw creeks were pooled to obtain a complete suite of loci; no significant differences were found between these collections at any of the loci tested. Finally, collections from the north and south forks of Nulato River were pooled to create a combined sample size of 100 individuals for this location. This resulted in a final baseline of 18 stocks (Appendix 1).

A dendrogram of genetic similarities was created using the genetic distances calculated between each pair of populations and the UPGMA clustering algorithm (Figure 2). This analysis identifies a distinction between Chinook populations of United States and Canadian origins. Within the United States populations two clusters are formed: a lower river group (below river kilometer 800) and a mid-river group (between river kilometer 800 and 1150). Within the Koyukuk River drainage, populations are split between these groups; the lower Koyukuk population, Gisasa River, clusters with the lower Yukon group; the upper river populations cluster with populations from the Tanana River. Within the main Canadian cluster, populations grouped geographically into four smaller regional clusters: populations near the United States/Canada border, the Pelly River drainage, Takhini River drainage, and the remaining upriver populations.

The gene diversity analysis estimated a total gene diversity of 0.101 (H_T) within the populations and an average population diversity of 0.095 (H_S). This analysis estimated that 1.0% of the total genetic diversity within these collections is associated with comparisons among populations within regional groups. An

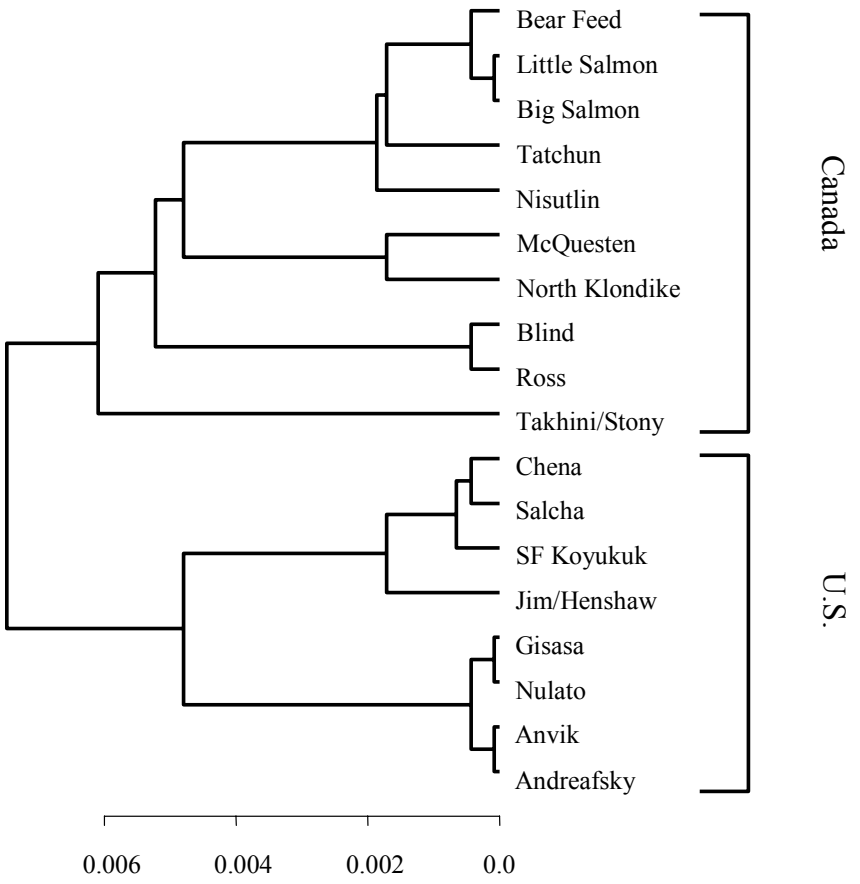

Figure 2. Dendrogram (UPGMA) based on Nei's (1972) genetic distance between populations of Yukon River Chinook salmon.

additional 1.9% of the diversity was accounted for by differences between regional groups within each nation and 1.5% between nations. The remaining 95.6% reflected differences between individuals within populations. When populations were examined in a hierarchical manner using this same structure, significant differences were found at all levels (Table 3). The only exception was between the populations from the Pelly River where no significant difference was found between the Ross River and Blind Creek collections.

Significant correlation was found between the geographic and genetic distances between pairs of populations within the baseline ($R = 0.40$, $P < 0.01$). A lowess trend line through a plot of the pairwise geographic and genetic distances (Figure 3) shows a general increase in genetic distance with increasing distance between populations up to approximately 1,000 km. There appears to be little correlation between geographic and genetic distances when populations are separated by greater distances.

Table 3. Hierarchical log-likelihood analysis of Chinook salmon populations from the Yukon River, Alaska. Test statistics were derived from simultaneous comparisons of allele frequencies at 22 allozyme loci.

	DF	Overall	P
Total	539	4355.6	0.000
Between Nations	32	1703.8	0.000
Within Nations	508	2651.8	0.000
United States	223	996.1	0.000
Among Regions	31	681.3	0.000
Within Regions	192	314.8	0.000
Lower Yukon	96	126.0	0.022
Middle Yukon	96	188.8	0.000
Canada	285	1655.7	0.000
Among Regions	93	1189.0	0.000
Within Regions[a]	192	466.7	0.000
Canada Border	32	152.6	0.000
Pelly River	32	36.7	0.262
Upper Yukon	128	277.4	0.000

[a]This comparison includes the Takhini River population.

Genetic Stock Identification

Chinook salmon populations were combined into groups for reporting estimates of stock composition of mixtures from the Yukon River. These reporting groups were defined based on the structure revealed in the previous analyses: 1) Lower Yukon—Andreafsky, Anvik, Nulato and Gisasa rivers, 2) Middle Yukon—Jim/Henshaw creeks, South Fork Koyukuk River, Chena and Salcha rivers, 3) Canada Border—Klondike and McQuesten rivers, 4) Pelly—Ross River and Blind Creek, 5) Upper Yukon—Tatchun, Big Salmon, Little

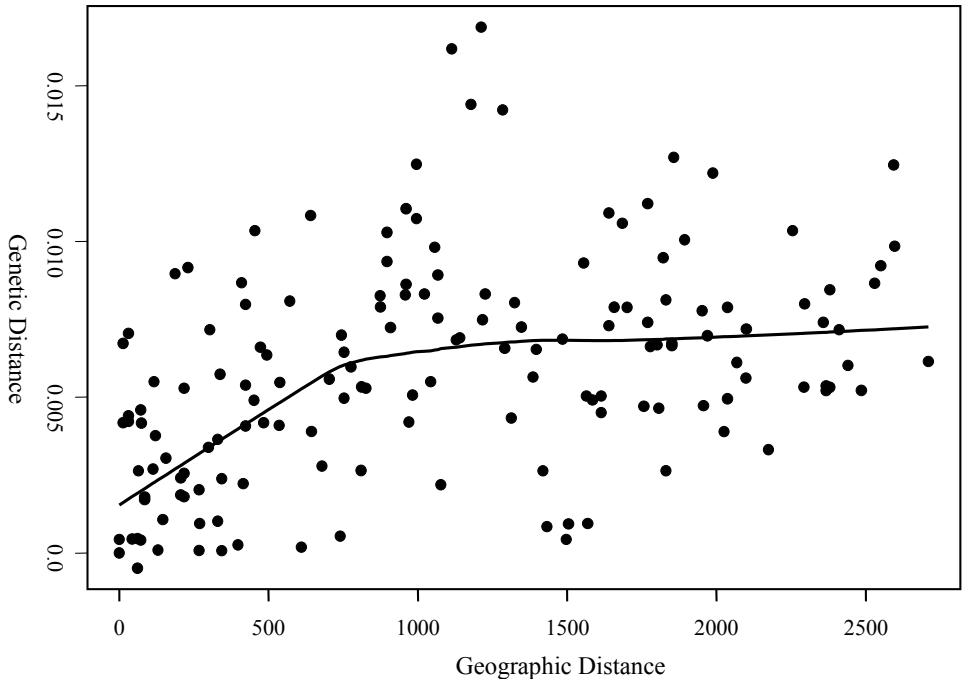

Figure 3. Plot of the geographic distances (river kilometer) and the genetic distances (Nei 1972) between pairs of Chinook salmon populations in the Yukon River, Alaska. The trend in genetic distance with geographic distance between populations is indicated by a lowess line through the data.

Salmon, Bear Feed, and Nisutlin rivers, and 6) Takhini River. Simulation studies based on this structure indicate that these reporting groups are highly identifiable in mixtures. When simulated mixtures composed entirely from a single reporting group were treated as mixtures of unknown origin on average more than 90% of the mixture was correctly identified to region-of-origin (Table 4). As expected, this high level of distinction was also seen when simulating mixtures from each nation. No significant reduction in the identifiability of these groups was found when the number of loci used in the analyses was reduced from the full set of 21 to the 11 loci available from axillary process tissues; all simulations continued to show greater than 90% mean correct allocation to group of origin.

Estimates of stock composition in the catches from the commercial and test fisheries near Emmonak between 1987 and 1990 indicate that Chinook salmon of Canadian origin contributed more than 50% of the harvest early in the summer (Table 5). Most of these salmon were estimated to be from the Pelly River and Upper Canada regions followed by contributions from the Canadian Border region. Early season salmon from the United States were generally from the Middle Yukon stocks.

As the season progresses, the Canadian contribution to the mixed fishery declines as Chinook salmon from the United States begin to dominate the fishery. The switch in relative contribution takes place sometime during the last week of June and corresponds to an increase in the presence of Chinook salmon from the Lower Yukon. By the middle of July, more than 50% of the harvest is estimated to be from these Lower Yukon populations. Usually the reduction in the Canadian portion of the harvest is accompanied by a corresponding reduction in the presence of salmon from the Canada Border and Pelly River reporting regions. The Upper Canada component of the harvest remains stable over the course of the season, only dropping below 10% in two of the 17 samples. The Takhini River region makes only a small contribution to the harvest during the month of June, but it does show a consistent pattern across the four years with its greatest contribution coming during the first part of July, after the decline of the Canada Border and Pelly River stocks. Similar patterns of stock composition were seen in the samples from the Pilot Station species apportionment fishery (Table 6) showing a consistent presence of upriver stocks early in the season followed by lower river stocks as the season progresses.

Estimates of the stock composition of the radio telemetry samples in 2002 and 2003 were calculated for comparison with the tagging results (Table 7). During both years, the portion of the mixture attributed to the United States was underestimated by genetic stock identification; the 90% confidence interval for the estimate did not contain the value from the tagging results. When the tagging results were segregated at the mouth of the Tanana River (the furthest upstream United States populations represented in the baseline) rather than at the United States/Canada border, the genetic stock identification estimates were closer to the tagging results and within the 90% confidence interval of the genetic stock identification estimates for both 2002 and 2003.

Table 4. Mean regional allocation of simulated mixtures of Yukon River Chinook salmon from the baseline of allozyme data. Each set of mixtures (N=400) was created from a single reporting region based on allelic frequencies for that region. The results reported are the mean of 1,000 bootstrap iterations where both the mixture and the baseline were parametrically resampled. Column totals equal 1.0, and correct allocations are in bold type.

		Regional Allocation					
	Region	1	2	3	4	5	6
1	Lower Yukon	**0.97**	0.01	0.01	0.00	0.00	0.00
2	Middle Yukon	0.01	**0.97**	0.00	0.00	0.00	0.00
3	Canada Border	0.01	0.01	**0.97**	0.00	0.01	0.00
4	Pelly	0.00	0.00	0.01	**0.94**	0.02	0.00
5	Upper Yukon	0.01	0.00	0.01	0.04	**0.95**	0.04
6	Takhini River	0.00	0.00	0.00	0.01	0.02	**0.95**

DISCUSSION

The management of mixed-stock salmon fisheries is made more effective when stock components of the harvest can be accurately identified. Such information becomes imperative when the fishery harvests salmon from multiple management jurisdictions. This stock-specific harvest information can be acquired using genetic stock identification provided that the level of quantifiable genetic differences among stocks or stock groups is sufficiently high.

The baseline of allozyme data presented in this study provides important insights into the Chinook salmon populations within the Yukon River drainage. Collections were obtained from populations in most of the major tributaries producing Chinook salmon. Target sample sizes were achieved in almost every population, with most populations represented by more than 100 individuals. No evidence was detected of a consistent lack of Hardy-Weinberg equilibrium in any population or at any locus. Allele frequencies were stable across years in nine of the 10 populations sampled in more than a single year indicating that the baseline should be stable across several generations.

Table 5. Proportional contributions (P) and number of fish harvested (No.) in samples from the commercial and test fisheries in District 1 of the Yukon River, 1987 to 1990. Estimates are given for each reporting region and summed for estimates of national origin. The unknown category contains the proportions of individual genotypes with a probability of less than 1.0×10^{-45} of belonging to any population in the baseline.

1987

	June 5 to 13 N=186			June 16 to 23 N=225			June 26 to July 3 N=224			July 6 to 15 N=132		
	P	90% CI	No.	P	90% CI	No.	P	90% CI	No.	P	90% CI	No.
Reporting Regions												
Lower Yukon	0.04	(0.00–0.13)	0	0.17	(0.10–0.26)	8,544	0.31	(0.23–0.41)	7,596	0.79	(0.64–0.86)	1,515
Middle Yukon	0.22	(0.13–0.29)	0	0.09	(0.05–0.16)	4,704	0.12	(0.07–0.19)	2,884	0.04	(0.00–0.09)	74
Canada Border	0.25	(0.14–0.33)	0	0.12	(0.04–0.21)	6,078	0.07	(0.00–0.14)	1,727	0.00	(0.00–0.06)	0
Pelly	0.27	(0.13–0.37)	0	0.21	(0.13–0.32)	10,721	0.07	(0.00–0.14)	1,756	0.06	(0.00–0.11)	116
Upper Yukon	0.16	(0.07–0.34)	0	0.39	(0.20–0.47)	19,578	0.37	(0.22–0.50)	9,057	0.00	(0.00–0.20)	6
Takhini River	0.04	(0.00–0.08)	0	0.00	(0.00–0.09)	0	0.05	(0.00–0.14)	1,171	0.10	(0.00–0.16)	199
Unknown	0.02		0	0.02		899	0.00		0	0.01		15
Nations												
United States	0.26	(0.18–0.35)	0	0.26	(0.19–0.36)	13,247	0.43	(0.35–0.54)	9,969	0.83	(0.69–0.90)	1,589
Canada	0.72	(0.62–0.80)	0	0.72	(0.62–0.79)	36,377	0.57	(0.46–0.65)	13,043	0.17	(0.09–0.31)	322
Total Harvest			0			50,524			23,012			1,925

1988

	June 5 to 10 N=215			June 14 to 17 N=140			June 21 to 29 N=232			June 30 to July 8 N=205			July 11 to 15 N=99		
	P	90% CI	No.	P	90% CI	No.	P	90% CI	No.	P	90% CI	No.	P	90% CI	No.
Reporting Regions															
Lower Yukon	0.12	(0.06–0.23)	393	0.19	(0.09–0.28)	4,436	0.39	(0.31–0.52)	9,071	0.45	(0.34–0.56)	3,087	0.60	(0.41–0.72)	277
Middle Yukon	0.24	(0.14–0.31)	783	0.16	(0.09–0.28)	3,645	0.10	(0.03–0.16)	2,274	0.07	(0.02–0.14)	452	0.09	(0.03–0.21)	44
Canada Border	0.13	(0.05–0.20)	417	0.08	(0.00–0.14)	1,792	0.03	(0.00–0.07)	782	0.08	(0.00–0.16)	547	0.08	(0.00–0.22)	38
Pelly	0.26	(0.15–0.34)	860	0.18	(0.08–0.27)	4,196	0.07	(0.03–0.15)	1,643	0.05	(0.00–0.12)	333	0.00	(0.00–0.03)	0
Upper Yukon	0.24	(0.12–0.35)	785	0.33	(0.21–0.44)	7,728	0.39	(0.25–0.47)	9,044	0.21	(0.06–0.35)	1,402	0.21	(0.04–0.34)	97
Takhini River	0.00	(0.00–0.04)	0	0.01	(0.00–0.06)	176	0.00	(0.00–0.06)	0	0.14	(0.04–0.25)	978	0.02	(0.00–0.14)	9
Unknown	0.03		93	0.06		1,510			198	0.00			0.00		0
Nations															
United States	0.35	(0.27–0.47)	1,175	0.34	(0.26–0.47)	8,081	0.49	(0.41–0.61)	11,345	0.52	(0.42–0.63)	3,540	0.69	(0.55–0.81)	322
Canada	0.62	(0.50–0.70)	2,062	0.59	(0.46–0.67)	13,893	0.50	(0.38–0.57)	11,469	0.48	(0.37–0.57)	3,259	0.31	(0.19–0.45)	143
Total Harvest			3,268			22,645			23,012			6,799			465

-continued-

Table 5. Page 2 of 2.

1989

	June 10 to 16 N=245			June 20 to 25 N=409			June 27 to 30 N=160			July 4 to 14 N=181		
	P	90% CI	No.	P	90% CI	No.	P	90% CI	No.	P	90% CI	No.
Reporting Regions												
Lower Yukon	0.10	(0.04–0.21)	718	0.26	(0.19–0.33)	8,447	0.65	(0.50–0.74)	6,829	0.60	(0.47–0.71)	1,129
Middle Yukon	0.25	(0.15–0.32)	1,732	0.19	(0.14–0.26)	6,220	0.15	(0.05–0.25)	1,552	0.08	(0.03–0.16)	147
Canada Border	0.08	(0.02–0.17)	557	0.02	(0.00–0.08)	589	0.00	(0.00–0.11)	34	0.08	(0.01–0.17)	154
Pelly	0.14	(0.07–0.23)	997	0.10	(0.04–0.17)	3,372	0.04	(0.00–0.09)	391	0.00	(0.00–0.00)	0
Upper Yukon	0.37	(0.23–0.48)	2,564	0.35	(0.22–0.44)	11,360	0.15	(0.08–0.24)	1,567	0.16	(0.07–0.28)	304
Takhini River	0.03	(0.00–0.07)	173	0.05	(0.00–0.11)	1,561	0.00	(0.00–0.05)	0	0.06	(0.00–0.13)	113
Unknown	0.02		141	0.02		631	0.01		65	0.01		21
Nations												
United States	0.36	(0.27–0.45)	2,450	0.46	(0.39–0.53)	14,671	0.80	(0.66–0.86)	8,381	0.68	(0.57–0.78)	1,277
Canada	0.62	(0.53–0.71)	4,291	0.52	(0.45–0.59)	16,878	0.19	(0.14–0.33)	1,992	0.31	(0.21–0.42)	571
Total Harvest			6,882			32,180			10,437			1,868

1990

	June 7 to 15 N=250			June 19 to 22 N=250			June 25 to 29 N=230			July 2 to 15 N=209		
	P	90% CI	No.	P	90% CI	No.	P	90% CI	No.	P	90% CI	No.
Reporting Regions												
Lower Yukon	0.07	(0.02–0.15)	1,313	0.37	(0.24–0.45)	8,843	0.56	(0.44–0.65)	3,641	0.54	(0.44–0.64)	899
Middle Yukon	0.27	(0.16–0.34)	5,048	0.13	(0.06–0.22)	3,110	0.05	(0.00–0.14)	321	0.10	(0.04–0.16)	161
Canada Border	0.16	(0.08–0.28)	2,989	0.04	(0.00–0.13)	866	0.04	(0.00–0.11)	276	0.08	(0.00–0.15)	137
Pelly	0.19	(0.12–0.28)	3,568	0.09	(0.03–0.19)	2,138	0.04	(0.00–0.09)	239	0.09	(0.00–0.15)	142
Upper Yukon	0.30	(0.14–0.38)	5,699	0.30	(0.15–0.41)	7,211	0.24	(0.13–0.36)	1,530	0.10	(0.03–0.26)	172
Takhini River	0.00	(0.00–0.06)	0	0.06	(0.00–0.14)	1,543	0.06	(0.00–0.14)	396	0.09	(0.00–0.15)	147
Unkown	0.02		303	0.01		286	0.01		84	0.00		8
Nations												
United States	0.34	(0.24–0.42)	6,361	0.50	(0.39–0.57)	11,952	0.61	(0.52–0.70)	3,962	0.64	(0.54–0.73)	1,060
Canada	0.65	(0.56–0.75)	12,256	0.49	(0.42–0.60)	11,756	0.38	(0.28–0.46)	2,440	0.36	(0.26–0.45)	597
Total Harvest			18,920			23,994			6,486			1,665

Table 6. Proportional contributions (P) in samples of Chinook salmon from the species apportionment fishery at the Pilot Station sonar site (river kilometer = 196) on the Yukon River, 2002 and 2003. Estimates are given for each reporting region and summed for estimates of national origin. The unknown category contains the proportions of individual genotypes with a probability of less than 1.0×10^{-45} of belonging to any population in the baseline.

2002

	June 12 to 22 N = 215		June 23 to July 19 N = 183	
	P	90% CI	P	90% CI
Reporting Regions				
Lower Yukon	0.25	(0.13–0.35)	0.50	(0.34–0.65)
Middle Yukon	0.28	(0.15–0.41)	0.15	(0.05–0.22)
Canada Border	0.10	(0.00–0.25)	0.13	(0.00–0.28)
Pelly	0.10	(0.00–0.29)	0.00	(0.00–0.09)
Upper Yukon	0.28	(0.06–0.42)	0.19	(0.03–0.33)
Takhini River	0.00	(0.00–0.08)	0.03	(0.00–0.10)
Unknown	0.00		0.01	
Nations				
United States	0.53	(0.36–0.63)	0.64	(0.49–0.76)
Canada	0.47	(0.36–0.63)	0.36	(0.23–0.51)

2003

	June 10–14 N = 213		June 15–20 N = 185		June 22 to July 17 N = 155	
	P	90% CI	P	90% CI	P	90% CI
Reporting Regions						
Lower Yukon	0.06	(0.00–0.15)	0.35	(0.15–0.44)	0.47	(0.34–0.63)
Middle Yukon	0.35	(0.24–0.44)	0.14	(0.03–0.29)	0.16	(0.05–0.25)
Canada Border	0.09	(0.00–0.21)	0.07	(0.00–0.22)	0.00	(0.00–0.07)
Pelly	0.03	(0.00–0.21)	0.01	(0.00–0.19)	0.14	(0.00–0.27)
Upper Yukon	0.43	(0.27–0.57)	0.42	(0.19–0.52)	0.08	(0.00–0.35)
Takhini River	0.03	(0.00–0.08)	0.01	(0.00–0.12)	0.14	(0.00–0.21)
Unknown	0.01		0.00		0.01	
Nations						
United States	0.41	(0.28–0.50)	0.49	(0.33–0.59)	0.63	(0.49–0.75)
Canada	0.59	(0.48–0.70)	0.51	(0.41–0.67)	0.37	(0.24–0.50)

Genetic distances calculated among the populations (Figure 2) reflect a geographic component to the population structure within the Yukon River drainage. Populations were genetically more similar to neighboring populations than they were to those which were more geographically distant. These tributary groups cluster together into regional and national groups in a way that lends itself to hierarchical analyses. Both gene diversity analysis and hierarchical log likelihood tests, based on the structure suggested by genetic distances, indicated that significant genetic variation was associated with geographic structure, potentially sufficient to provide acceptable precision for stock identification purposes.

This regional group-based structure is complemented by the relationship between geographic and genetic distances (Figure 3). While there is evidence of isolation by distance between populations (significant correlation between geographic and genetic distances), it only appears to explain differences between populations within small regions and not over the entire drainage. For populations that are not separated by more than 1,000 km genetic distance increases with geographic distance, but above 1,000 km there does not appear to be correlation between genetic and geographic distances. This suggests that group membership plays an important role in explaining the genetic diversity of these populations. Similar patterns are described by Hutchinson and Templeton (1999) as indicative of populations that have not reached migration/drift equilibrium.

Failure to reach migration/drift equilibrium may explain the regional grouping observed between the populations of the upper Koyukuk River and the Tanana River (Figure 2). The Gisasa River, located lower in the Koyukuk River drainage, was more similar to the Nulato River and the Lower Yukon populations, consistent with geographic structuring, as the conflu-

Table 7. Proportional contributions (P) to samples from the Chinook salmon radio telemetry project on the Yukon River, 2002 and 2003, estimated from (a) genetic stock identification (GSI), and (b) based on radio telemetry tag results (Eiler et al. In press; John Eiler, NMFS Auke Bay Laboratory, personal communication). GSI estimates are given for each reporting region and summed for estimates of national origin. Two methods of dividing the radio telemetry results are shown: 1) separating returns at the United States/Canada border, and 2) separating at the confluence of the Tanana and Yukon rivers. The unknown category contains the proportions of individual genotypes with a probability of less than 1.0×10^{-45} of belonging to any population in the baseline.

	2002 N=421		2003 N=399	
	P	90% CI	P	90% CI
(a) GSI				
Reporting Regions				
Lower Yukon	0.25	(0.15–0.37)	0.24	(0.16–0.37)
Middle Yukon	0.08	(0.00–0.17)	0.07	(0.00–0.15)
Canada Border	0.18	(0.09–0.30)	0.21	(0.06–0.33)
Pelly	0.00	(0.00–0.12)	0.07	(0.00–0.19)
Upper Yukon	0.45	(0.29–0.53)	0.40	(0.25–0.52)
Takhini River	0.03	(0.00–0.06)	0.00	(0.00–0.07)
Unknown	0.00		0.02	
Nations				
United States	0.33	(0.25–0.43)	0.30	(0.22–0.43)
Canada	0.66	(0.56–0.74)	0.68	(0.55–0.76)
(b) Radio Telemetry				
United States/Canada Border				
United States	0.53		0.44	
Canada	0.47		0.56	
Above Tanana				
United States	0.43		0.35	
Canada	0.57		0.65	

ence of the Koyukuk and Yukon rivers lies near the boundary between the Lower and Middle Yukon regions. Chinook salmon spawning in the Gisasa River travel a distance similar to many other Lower Yukon populations (<1,000 river km). However, Chinook salmon spawning in the upper reaches of the Koyukuk River drainage must migrate approximately 1,600 river km, a distance similar to the migrations of the Tanana River populations (approximately 1,500 river km). While there is significant genetic difference within the Middle Yukon group (Table 3), the relative genetic similarity between these populations is noteworthy because they are separated by more than 1,400 river km (past the threshold where isolation by distance seems to apply [Figure 3]) and occupy two separate major tributaries. The cause of this geographic pattern of genetic similarity is beyond the range of this study and insufficient information is available to extricate the potential effects of colonization, migration, and genetic drift. More genetic and historical information may eventually enable a better understanding of the metapopulation dynamics of the Chinook salmon in the Yukon River. For example, this pattern is corroborated for Yukon River Chinook salmon by data from single nucleotide polymorphisms (SNPs, Smith et al. In press).

Six reporting regions were defined based on genetic population structure for reporting the results of genetic stock identification: 1) Lower Yukon—Andreafsky, Anvik, Nulato and Gisasa rivers, 2) Middle Yukon—Jim/Henshaw creeks, South Fork Koyukuk, Chena and Salcha rivers, 3) Canada Border—Klondike and McQuesten rivers, 4) Pelly—Ross River and Blind Creek, 5) Upper Yukon—Tatchun, Big Salmon, Little Salmon, Bear Feed, and Nisutlin rivers, and 6) Takhini/Stony River. These reporting regions generally correspond to the geographic groups used for stock composition studies using SPA (lower, middle and upper river; Lingnau 2000). Grouping of the populations for use in genetic stock identification is supported by the 100% simulations studies where on average between 94% and 98% of mixtures composed entirely of genotypes from a single reporting region were correctly reassigned to the region of origin. These results are well above the 90% threshold commonly used to define population groups that are highly identifiable in mixtures. When similar simulations were run using mixtures composed of genotypes from each nation, the results (United States, 98%; Canada, 99%) were also sufficient to qualify as highly identifiable.

The applicability of genetic stock identification to Yukon River Chinook salmon fisheries is supported by the accuracy and precision displayed in the computer simulations as well as the consistency and concurrence of temporal patterns of composition demonstrated over the six years of commercial and species apportionment sampling. From 1987 to 1990, United States stocks comprised from 33% to 53% of the Chinook salmon harvested in District 1, annually. This corresponds to a mean harvest of 24,973 United States-origin Chinook salmon and 33,004 Canadian-origin Chinook salmon over the four-year period. Not every reporting region was identified as contributing to the fishery every year, but each region was a significant contributor at least once during the four years. These estimates are similar to results provided by a combination of scale pattern analysis, age composition and geography, where the United States component of the harvest for these four years ranged from 39% to 52% (Joint Technical Committee 2004).

Unrepresented populations in the baseline remain a concern, and evidence from the radio telemetry study indicates there is bias in the estimation of stock composition. When the baseline was initially constructed, tributaries between the Tanana River and the border were not considered to be major producers of Chinook salmon. Tag retrievals from the radio telemetry study (Eiler et al. In press; John Eiler, NMFS Auke Bay Laboratory, personal communication) have revealed that significant numbers do spawn within this region. In addition, the occasional presence of unexplainable genotypes in the fishery samples (as much as 6% of the entire mixture) indicates that the baseline may not completely represent the Chinook salmon populations in the area. Genetic estimates of the United States portion of the radio telemetry samples were significantly lower than estimates based on tag returns in both years; 90% confidence intervals of the genetic estimates did not include the tagging result. In 2003 the lower bound of the 90% confidence interval for the Canadian portion just included the proportion based on the radio telemetry data. When the geographic division of the tag results into sets from the United States and Canada was moved from the border to the mouth of the Tanana River (including all United States tag returns above the Tanana River with the Canadian tag returns) the proportion of United States salmon in the tag results was much closer to the estimate based on genetic markers. This indicates that populations that spawn within this missing region may be genetically more similar to Canadian populations, and that Canadian contributions to United States fisheries using this allozyme baseline are probably overestimated.

Currently, two other studies are analyzing DNA-based markers, SNPs (Smith et al. In press) and microsatellites (ADF&G, unpublished), in Chinook salmon populations from the Yukon River drainage. The results among the three marker groups should be generally concordant (e.g. Scribner et al. 1998; Allendorf and Seeb 2000), but the DNA-based markers are using a greatly expanded baseline, including some from the region between the Tanana River and the United States/Canada border. The sensitivity of the DNA-based markers combined with the more comprehensive geographic coverage of populations represented by these studies holds promise for the future application of genetic stock identification to Yukon River Chinook salmon fisheries.

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Appendix 1. Baseline allele frequencies at 22 polymorphic loci for Chinook salmon sampled from the Yukon River, 1987–1990. Variant alleles are labeled according to their mobility relative to the most common allele designated *100 (not shown).

	sAAT-3		*sAAT-4*			*ADA-1*		*sAH*				*ALAT*		*GPI-B1*	
Population	N	*90	N	*130	*63	N	*83	N	*86	*116	*69	N	*94	N	*24
United States															
Andreafsky River	92	0.168	90	0.000	0.039	98	0.133	100	0.050	0.000	0.000	100	0.110	100	0.000
Anvik River	85	0.194	80	0.031	0.037	99	0.136	96	0.036	0.000	0.000	100	0.095	95	0.000
Nulato River	95	0.200	90	0.011	0.039	98	0.138	100	0.040	0.000	0.000	100	0.085	100	0.000
Gisasa River	136	0.261	133	0.049	0.011	137	0.179	138	0.036	0.000	0.000	135	0.122	138	0.000
Jim/Henshaw creeks	166	0.301	157	0.006	0.010	157	0.019	164	0.006	0.000	0.000	164	0.073	164	0.000
SF Koyukuk River	84	0.351	82	0.000	0.006	81	0.031	88	0.006	0.000	0.000	83	0.102	87	0.000
Chena River	234	0.397	227	0.000	0.013	224	0.000	236	0.000	0.000	0.000	232	0.056	238	0.000
Salcha River	95	0.311	99	0.000	0.005	97	0.000	100	0.000	0.000	0.000	100	0.075	100	0.000
Canada															
North Klondike River	189	0.111	194	0.000	0.028	190	0.011	194	0.031	0.010	0.000	190	0.121	190	0.000
McQuesten River	237	0.173	238	0.000	0.124	238	0.109	238	0.057	0.000	0.002	237	0.055	237	0.008
Ross River	44	0.330	42	0.000	0.119	43	0.012	43	0.093	0.000	0.012	44	0.000	43	0.070
Blind Creek	138	0.348	149	0.000	0.087	150	0.013	150	0.047	0.000	0.037	150	0.003	150	0.020
Tatchun River	73	0.308	61	0.000	0.082	76	0.02	73	0.075	0.000	0.007	75	0.000	78	0.000
Little Salmon River	59	0.161	53	0.047	0.085	56	0.054	55	0.173	0.000	0.000	60	0.033	56	0.000
Bear Feed River	87	0.172	85	0.012	0.212	87	0.063	87	0.132	0.000	0.000	87	0.011	87	0.006
Big Salmon River	126	0.198	123	0.000	0.110	126	0.048	127	0.165	0.012	0.000	122	0.020	127	0.000
Takhini/Stony River	168	0.152	170	0.000	0.094	171	0.041	170	0.394	0.000	0.000	170	0.003	171	0.000
Nisutlin River	70	0.286	70	0.021	0.029	70	0.000	70	0.221	0.000	0.000	71	0.000	70	0.000

	IDDH-1		*sIDHP-1*			*sIDHP-2*			*LDH-B2*		*sMDH-B1,2*			*sMEP-1*		
Population	N	*0	N	*74	*142	N	*127	*50	N	*71	N	*121	*70	N	*92	*86
United States																
Andreafsky River	99	0.045	100	0.000	0.000	97	0.000	0.041	100	0.000	100	0.005	0.000	100	0.995	0.000
Anvik River	99	0.015	96	0.010	0.000	94	0.000	0.000	100	0.000	100	0.020	0.000	99	0.995	0.000
Nulato River	94	0.021	95	0.000	0.005	100	0.000	0.035	100	0.000	100	0.025	0.000	100	0.990	0.000
Gisasa River	135	0.022	138	0.000	0.000	138	0.000	0.007	138	0.000	138	0.000	0.000	134	0.985	0.004
Jim/Henshaw creeks	68	0.029	165	0.000	0.000	164	0.000	0.015	166	0.003	166	0.057	0.021	157	0.933	0.016
SF Koyukuk River	50	0.000	87	0.000	0.000	87	0.000	0.011	88	0.006	88	0.063	0.085	82	0.982	0.006
Chena River	215	0.044	243	0.000	0.000	243	0.002	0.000	249	0.012	247	0.047	0.053	248	0.992	0.008
Salcha River	95	0.058	100	0.000	0.000	100	0.000	0.000	100	0.025	100	0.020	0.040	100	0.995	0.005
Canada																
North Klondike River	194	0.044	190	0.000	0.000	190	0.000	0.000	194	0.000	190	0.000	0.000	194	0.982	0.018
McQuesten River	238	0.042	238	0.000	0.000	238	0.000	0.000	238	0.000	238	0.002	0.000	238	0.975	0.025
Ross River	43	0.105	44	0.000	0.000	44	0.000	0.000	44	0.000	44	0.000	0.000	44	1.000	0.000
Blind Creek	150	0.030	150	0.000	0.000	150	0.003	0.000	150	0.000	150	0.000	0.000	150	0.997	0.000
Tatchun River	67	0.015	59	0.000	0.000	59	0.000	0.000	78	0.000	78	0.000	0.000	77	1.000	0.000
Little Salmon River	61	0.041	59	0.000	0.000	59	0.000	0.000	59	0.000	62	0.000	0.000	62	1.000	0.000
Bear Feed River	87	0.040	87	0.000	0.000	87	0.000	0.000	87	0.000	87	0.000	0.000	87	0.994	0.000
Big Salmon River	126	0.028	124	0.000	0.000	124	0.000	0.000	127	0.000	124	0.000	0.000	126	0.988	0.008
Takhini/Stony River	171	0.018	171	0.000	0.000	171	0.003	0.003	171	0.000	171	0.000	0.000	171	1.000	0.000
Nisutlin River	71	0.000	71	0.000	0.000	64	0.000	0.000	71	0.000	71	0.000	0.000	68	0.963	0.022

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Appendix 1. Page 2 of 2.

Population	*sMEP-2*		*MPI*		*PEPA*		*PEP-B1*				*PGM-1*			*mSOD-1*	
	N	*78	N	*109	N	*90	N	*130	*-350	*60	N	*210	*50	N	*90
United States															
Andreafsky River	100	0.120	100	0.075	100	0.050	98	0.138	0.000	0.000	100	0.000	0.000	100	0.115
Anvik River	100	0.110	100	0.085	99	0.030	98	0.128	0.000	0.000	100	0.000	0.000	97	0.036
Nulato River	100	0.050	100	0.130	100	0.045	100	0.185	0.000	0.000	100	0.000	0.000	100	0.070
Gisasa River	138	0.094	137	0.128	138	0.033	136	0.173	0.000	0.004	138	0.000	0.000	136	0.088
Jim/Henshaw creeks	139	0.151	163	0.012	165	0.058	160	0.209	0.000	0.006	164	0.000	0.000	62	0.065
SF Koyukuk River	80	0.362	87	0.023	88	0.045	85	0.253	0.000	0.000	88	0.000	0.000	67	0.127
Chena River	247	0.227	247	0.012	253	0.063	237	0.251	0.000	0.000	248	0.000	0.000	240	0.113
Salcha River	100	0.290	100	0.010	100	0.055	100	0.215	0.005	0.000	99	0.000	0.000	100	0.085
Canada															
North Klondike River	194	0.335	194	0.052	190	0.124	190	0.076	0.000	0.000	190	0.000	0.003	44	0.000
McQuesten River	238	0.282	238	0.067	238	0.105	237	0.046	0.000	0.000	238	0.000	0.061	38	0.000
Ross River	44	0.159	44	0.273	44	0.000	44	0.011	0.000	0.000	44	0.000	0.000	44	0.034
Blind Creek	150	0.133	150	0.160	150	0.003	150	0.030	0.000	0.000	150	0.000	0.000	100	0.000
Tatchun River	77	0.416	77	0.091	78	0.000	78	0.000	0.006	0.013	77	0.000	0.000	76	0.086
Little Salmon River	62	0.323	62	0.129	61	0.008	62	0.000	0.000	0.008	62	0.008	0.000	61	0.025
Bear Feed River	85	0.400	87	0.075	87	0.006	87	0.000	0.000	0.000	87	0.000	0.000	74	0.014
Big Salmon River	126	0.349	127	0.122	126	0.016	122	0.012	0.004	0.004	127	0.000	0.000	127	0.024
Takhini/Stony River	171	0.263	171	0.099	171	0.000	171	0.000	0.000	0.000	171	0.000	0.000	158	0.092
Nisutlin River	71	0.254	71	0.113	70	0.000	68	0.000	0.000	0.044	71	0.000	0.000	68	0.015

Population	*sSOD-1*		*TPI-2*			*TPI-4*	
	N	*-260	N	*63	*-400	N	*104
United States							
Andreafsky River	94	0.059	100	0.000	0.000	99	0.081
Anvik River	100	0.025	100	0.000	0.000	100	0.105
Nulato River	99	0.045	99	0.000	0.000	100	0.085
Gisasa River	138	0.040	138	0.000	0.014	138	0.087
Jim/Henshaw creeks	159	0.019	165	0.000	0.000	165	0.130
SF Koyukuk River	88	0.011	88	0.000	0.000	88	0.097
Chena River	245	0.033	239	0.000	0.000	237	0.112
Salcha River	100	0.010	100	0.000	0.000	100	0.140
Canada							
North Klondike River	190	0.003	190	0.003	0.000	190	0.161
McQuesten River	238	0.000	238	0.002	0.000	238	0.090
Ross River	44	0.000	44	0.102	0.000	44	0.023
Blind Creek	150	0.000	150	0.060	0.000	150	0.003
Tatchun River	78	0.000	78	0.000	0.000	78	0.000
Little Salmon River	62	0.000	62	0.008	0.000	62	0.000
Bear Feed River	87	0.000	87	0.000	0.000	87	0.006
Big Salmon River	127	0.000	127	0.012	0.000	127	0.012
Takhini/Stony River	171	0.000	171	0.000	0.000	171	0.000
Nisutlin River	71	0.000	71	0.000	0.000	71	0.014