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GENETIC Stock IDENTIFICATION

of Yukon
RIVER

CHUM AND CHINOOK SALMON

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**GENETIC STOCK IDENTIFICATION
OF YUKON RIVER CHUM AND CHINOOK SALMON
1987 to 1990**

Progress Report

by

Richard L. Wilmot¹

Rebecca Everett²

William J. Spearman¹

Ramone Baccus²

¹Alaska Fish and Wildlife Research Center

²Fisheries Management Services

U.S. Fish and Wildlife Service

1011 East Tudor Road

Anchorage, AK 99503

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ABSTRACT

The chum and chinook salmon of the Yukon River are a shared resource between the United States and Canada. Negotiations began in 1985 to arrive at an equitable treaty between the two countries regarding the allocations of commercial and subsistence fisheries. One issue that needed to be addressed was the proportion of the U.S. catch that is of Canada origin. Protein electrophoresis was used to analyze the composition of commercial and test fish taken in District 1 (the lower Yukon River management area) throughout the fishing seasons of 1987 - 1990. Populations of Yukon River chum and chinook salmon of Alaska and the Yukon Territory were sampled from the tributaries to provide baseline data describing the genetic characteristics of individual stocks. Allelic data indicated that the genetic relationships among stocks generally followed a geographic pattern. Significant genetic differentiation was observed between the summer-run and fall-run chum salmon stocks. The level of differentiation within fall-run chum salmon stocks of Canada and U.S. was less than that observed between summer and fall-run stocks. Thus, genetic stock identification (GSI) estimates of stock composition estimates were more precise for separating summer and fall stocks than for U.S. and Canada stocks. The origin of chum salmon in the District 1 commercial fishery over the first four years of the study ranged from 82.0 to 91.0% U.S. summer-run ($\bar{x} = 85.7 \pm 5.8\%$), from 5.7 to 10.6% U.S. fall-run ($\bar{x} = 8.6 \pm 5.8\%$), and from 3.4 to 8.2% Canada fall-run chum salmon ($\bar{x} = 5.7 \pm 4.7\%$). Of the fall-run fish, the proportion of chum salmon that were of U.S. origin ranged from 54.3 to 68.5% ($\bar{x} = 60.6 \pm 44.7\%$). In numbers of fish, this equates to a four-year average harvest of 374,057 \pm 25,102 U.S. summer-run, 33,200 \pm 24,748 U.S. fall-run, and 22,208 \pm 20,198 Canada fall-run chum salmon. The genetic relationships among chinook salmon stocks included a clear genetic separation between those of the upper and lower Yukon River, which also corresponded geographically to the boundary between the U.S. and Canada. Because of the correspondence of geographic and genetic stock groupings, the estimates of the proportion of U.S. and Canada stocks in the fishery, using this method, were both accurate and precise. The origin of chinook salmon harvested in the District 1 commercial fishery from 1987 - 1990 averaged 46.8 \pm 5.1% United States-origin, and ranged from 38.7 to 58.1%. In numbers of fish, this equates to an average District 1 harvest of 27,623 \pm 3,012 U.S. origin and 31,419 \pm 3,012 Canada-origin chinook salmon. Based on the first four years of data, genetic stock identification is a feasible method for determining the relative magnitude of contribution to the fishery of chum and chinook salmon of the Yukon River drainage by country of origin and by major stock groups. Additional sampling and development of more genetic characters will be necessary to obtain accurate estimates of contributions by individual stocks were desired.

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INTRODUCTION

The United States and Canada began negotiations in 1985 concerning the allocation of Yukon River chum and chinook salmon. The Yukon River originates in the coastal mountains of British Columbia and flows for 3,250 km through the Yukon Territory and Alaska to the Bering Sea. The two most important commercial and subsistence fisheries in the Yukon River drainage are on chum salmon (*Oncorhynchus keta*) and chinook salmon (*O. tshawytscha*) (McBride et al. 1983). Fisheries in the Alaska portion of the drainage include salmon of Alaska and Canada origin, and Alaska fisheries have traditionally accounted for approximately 90% of the in-river harvest of both species in the Yukon River system (1961 - 1989 average; JTC 1990). An unknown proportion of the return of both species originates in the Canadian portion of the Yukon Drainage. To arrive at an equitable treaty between the two countries, the proportion of the U.S. catch of Canadian origin must be determined.

Chum salmon populations are found throughout the Yukon River drainage, and enter the river as two relatively distinct runs named for the seasons in which they spawn (Gilbert 1922). Summer-run chum salmon stocks are characterized by rapid maturation in fresh water, average 6-7 pounds in weight, and have a larger population size than the fall-run stocks (Bergstrom et al. 1991). Fall-run chum salmon stocks are characterized by robust body shape and bright silvery appearance, average 7-8 pounds, and have a smaller total population size (Bergstrom et al. 1991). Fall chum salmon are in great demand due to their appearance, size, and high oil content (Wilcock 1987).

The summer run enters the river beginning in early June and continuing until approximately mid-July (Buklis 1981). Summer-run chum salmon populations spawn throughout the summer months in runoff streams of the lower Yukon River up to the vicinity of Fairbanks, Alaska, 1,600 km from the river mouth.

In the lower Yukon River, the fall chum salmon run overlaps with the summer run in mid July, and continues usually until early September (Buklis 1981). Fall-run chum salmon spawn in September and October in spring-fed areas of tributaries of the middle and upper Yukon River (Bergstrom et al. 1991). Some major Yukon River tributaries support both summer- and fall-spawning chum salmon stocks, e.g., the Tanana River has predominantly fall-run chum salmon, but the Salcha River population spawns in the summer. The Koyukuk River system has both summer- and fall-run stocks occupying slightly different times and places (e.g., South Fork; Ken Troyer, USFWS, unpublished data).

Chinook salmon populations are widely distributed in the Yukon River drainage, with over 100 stocks identified (Barton 1984). Major chinook salmon-producing tributaries can be grouped geographically as lower (Andreafsky River and rivers draining the Kaltag Mountains), middle (Tanana River), and upper (Pelly River and rivers draining Big Salmon Mountains) Yukon River (McBride and Marshall 1983). Chinook salmon enter the Yukon River continuously from late May or early June through mid-July (summarized in Bergstrom et al. 1991), and they migrate to spawning grounds as much as 3,000 km from the river mouth (Milligan et al. 1986).

Two methods of estimating the composition of mixed-stock collections have been used to discriminate among U.S. and Canada stocks of chum and chinook salmon in Yukon River. Scale pattern analysis has demonstrated usefulness in Yukon River chinook salmon, and has been used for more than 10 years. Success using scale pattern analysis for discriminating among Yukon River chum salmon has been limited; the classification accuracies of discriminant models to apportion catch were low, not greatly different than expected by chance (Wilcock 1987). Because of low classification accuracies, the chum salmon mixed-stock fishery in District 1 has not been sampled for scale pattern analyses. The short interval during which chum salmon are affected by the freshwater environment may be responsible for lack of the discernible patterns of growth history that make scale pattern analyses a viable management tool for species like chinook salmon, which spend a year or more in fresh water environments. Preliminary genetic studies have shown detectable genetic differences among Yukon River chinook stocks (Beacham et al. 1989), and among chum salmon stocks (Beacham et al. 1988).

The results of the GSI study by the Canadian Department of Fisheries and Oceans (DFO) were based on seven genetically controlled proteins and used only fall-run chum salmon stocks in its baseline. The level of genetic separation between chum salmon stocks spawning near the border between Alaska and the Canadian Yukon Territory (Chandalar, Sheenjek, Fishing Branch, and Canadian mainstem stocks) was very low and attempts to apportion the catch by country of origin was unacceptable to the U.S. delegation. However, better precision (narrower confidence intervals) around stock composition estimates, and data gathered over the entire fishing season would better fulfill the needs of fisheries managers and negotiators.

Genetic stock identification (GSI) is a method that has been used on the west coast of North America to provide direct estimates of stock contributions to mixed stock salmon fisheries (e.g., Grant et al. 1980, Okazaki 1981, Wishard 1981, Miller et al. 1983, Beacham et al. 1985, Shaklee et al. 1990a). The method relies on identifying differences in relative frequencies of occurrences of genetically-controlled proteins of fish stocks (the baseline) using a technique called protein electrophoresis. Samples are then taken from a mixed stock fishery (the mixture sample) and the genetic characteristics of each fish are determined using protein electrophoresis. By comparing the genetic structure in the baseline to the genetic structure of the mixture sample, estimates can be determined for the contribution of each stock to the mixture. The model used to estimate the stock composition is based on pioneering work done by Grant et al. (1980), Milner et al. (1981), Miller et al. (1983), Fournier et al. (1984), Pella (1986), and Pella and Milner (1987).

In 1987, U.S. Fish and Wildlife Service (USFWS) research and management biologists in cooperation with the Alaska Department of Fish and Game (ADF&G) and DFO began to collect samples of Yukon River chum and chinook salmon from spawning stocks in tributaries, and from the mixed-stock fishery in District 1 near the Yukon River mouth. The goal of this preliminary study was to determine how accurately the GSI methodology could allocate the catch of chum and chinook salmon in District 1 by stock, by run timing, by major stock groups, and by country of origin. To build on the preliminary work of DFO, our objective was to add larger sample sizes to baseline and mixed-stock collections, add more genetic characters to the analyses, and to sample summer as well as fall chum salmon stocks. Chinook salmon were included in the study, as genetic studies showed detectable differences

among U.S. and Canada stocks, and scale pattern analysis results could be compared with the results of genetic studies.

METHODS

To establish baseline genetic data for mixed-stock analysis, populations of chum and chinook salmon were sampled from Yukon River tributaries by USFWS, ADF&G, and DFO (Tables 1 and 2; Figure 1). Collections were made at more than one site and/or more than one year to assess the stability of allele frequencies. Sample sites were chosen based on 1) the magnitude of the runs, so that major contributors to the total run would be sampled preferentially, and 2) opportunities to reach remote locations. Collections were made on the spawning grounds preferentially, and from mainstem sites of major Yukon River tributaries (e.g., at sonar or weir sites) when logistically necessary. Adults were sampled whenever possible, but juvenile chinook salmon were collected from some drainages where adults were not sufficiently concentrated, or if spawners were not present.

In baseline (tributary) collections, target sample sizes for adult salmon were 75 individuals from a population, or at least 50 individuals if collections were from more than one site within a drainage. When juveniles were sampled, we attempted to collect at least 100 per tributary, spread over several locations within a drainage to reduce sampling of family groups.

Mixed-stock samples of adult chum and chinook salmon were collected, by personnel of USFWS and ADF&G, from fish processors near Emmonak, Alaska during commercial fishing periods, and from test net sites when the fishery was both open and closed (Appendices I, II, III and IV). When available between fishing periods, all test net salmon were sampled for genetic studies. From the commercial catch, the target sample size was 150 of each species

Table 1. Chum salmon baseline sample collection summary. Populations are listed in order of their geographical occurrences from the mouth of the Yukon River.

Population	N	River System	Sample Period		
			Year	Start	End
UNITED STATES					
Andreafsky	150	Andreafsky	1987	04-Jul	14-Jul
Chulinak (Atchuelinguk)	100	Chulinak (Atchuelinguk)	1989	10-Jul	11-Jul
Anvik	150	Anvik	1987	07-Jul	12-Jul
Anvik	100	Anvik	1988	15-Jul	15-Jul
Rodo	78	Rodo	1989	18-Jul	18-Jul
Nulato, Main	61	Nulato	1987	30-Jul	30-Jul
Nulato, South Fork	71	Nulato	1987	28-Jul	29-Jul
Nulato, North Fork	50	Nulato	1988	28-Jul	28-Jul
Gisasa	97	Koyukuk	1989	23-Jul	23-Jul
Koyukuk, South Fork, early	75	Koyukuk	1990	07-Aug	13-Aug
Koyukuk, South Fork, late	75	Koyukuk	1990	11-Sep	16-Sep
Henshaw	43	Koyukuk	1987	11-Aug	11-Aug
Jim	101	Koyukuk	1987	13-Aug	13-Aug
Tozitna	85	Tozitna	1989	26-Jul	26-Jul
Toklat	135	Tanana	1987	14-Oct	14-Oct
Toklat	75	Tanana	1990	30-Oct	30-Oct
Salcha	50	Tanana	1988	03-Aug	03-Aug
Salcha	50	Tanana	1989	30-Jul	30-Jul
Delta	135	Tanana	1987	28-Oct	28-Oct
Delta	75	Tanana	1990	31-Oct	31-Oct
Bluff Cabin	135	Tanana	1987	16-Oct	16-Oct
Chandalar	150	Chandalar	1987	03-Sep	05-Sep
Chandalar	73	Chandalar	1988	04-Sep	06-Sep
Chandalar	75	Chandalar	1989	27-Sep	28-Sep
Sheenjek	135	Porcupine	1987	21-Sep	21-Sep
Sheenjek	80	Porcupine	1988	21-Sep	21-Sep
Sheenjek	80	Porcupine	1989	13-Sep	13-Sep
CANADA					
Fishing Branch	129	Porcupine	1987	13-Sep	04-Oct
Fishing Branch	50	Porcupine	1989	07-Oct	08-Oct
Kluane	135	White	1987	04-Nov	04-Nov
Big Creek	70	Yukon	1987	28-Oct	28-Oct
Minto	100	Minto	1989	27-Oct	28-Oct
Tatchun	75	Tatchun	1987	01-Nov	01-Nov
Teslin	95	Teslin	1989	06-Sep	06-Sep

Table 2. Chinook salmon baseline sample collection summary. Populations are listed in order of their geographical occurrences from the mouth of the Yukon River.

Population	N	River System	Sample Period		
			Year	Start	End
UNITED STATES					
Andreafsky	100	Andreafsky	1988	02-Aug	10-Aug
Anvik	40	Anvik	1987	18-Aug	18-Aug
Anvik	60	Anvik	1988	04-Aug	15-Aug
Nulato, South Fork	50	Nulato	1988	26-Jul	28-Jul
Nulato, North Fork	50	Nulato	1988	26-Jul	26-Jul
Gisasa	47	Koyukuk	1987	08-Aug	08-Aug
Gisasa	91	Koyukuk	1988	02-Aug	04-Aug
Henshaw	87	Koyukuk	1987	12-Aug	12-Aug
Koyukuk, South Fork	112	Koyukuk	1987	25-Aug	25-Aug
Jim	79	Koyukuk	1987	13-Aug	25-Aug
Chena	151	Tanana	1987	05-Aug	07-Aug
Chena	98	Tanana	1988	29-Jul	29-Jul
Salcha	100	Tanana	1988	30-Jul	30-Jul
CANADA					
Klondike, North Fork	50	Klondike	1990	23-Aug	26-Aug
Klondike, North Fork	44	Klondike	1989	01-Sep	01-Sep
McQuesten	38	Stewart	1989	31-Aug	31-Aug
McQuesten	200	Stewart	1990	23-Aug	26-Aug
Ross	14	Pelly	1988	?	?
Ross	30	Pelly	1989	25-Aug	26-Aug
Blind	150	Pelly	1989	27-Aug	27-Aug
Tatchun	49	Tatchun	1988	30-Aug	30-Aug
Tatchun	29	Tatchun	1989	26-Aug	28-Aug
Big Salmon	49	Big Salmon	1988	26-Aug	28-Aug
Big Salmon	77	Big Salmon	1989	24-Aug	25-Aug
Little Salmon	35	Big Salmon	1988	22-Aug	22-Aug
Little Salmon	27	Big Salmon	1989	23-Aug	29-Aug
Bear Feed	87	Big Salmon	1989	28-Aug	28-Aug
Takhini	26	Teslin	1988	30-Aug	31-Aug
Takhini	26	Teslin	1990	28-Aug	30-Aug
Stony	121	Teslin	1990	30-Aug	30-Aug
Nisutlin	71	Teslin	1989	20-Aug	25-Aug

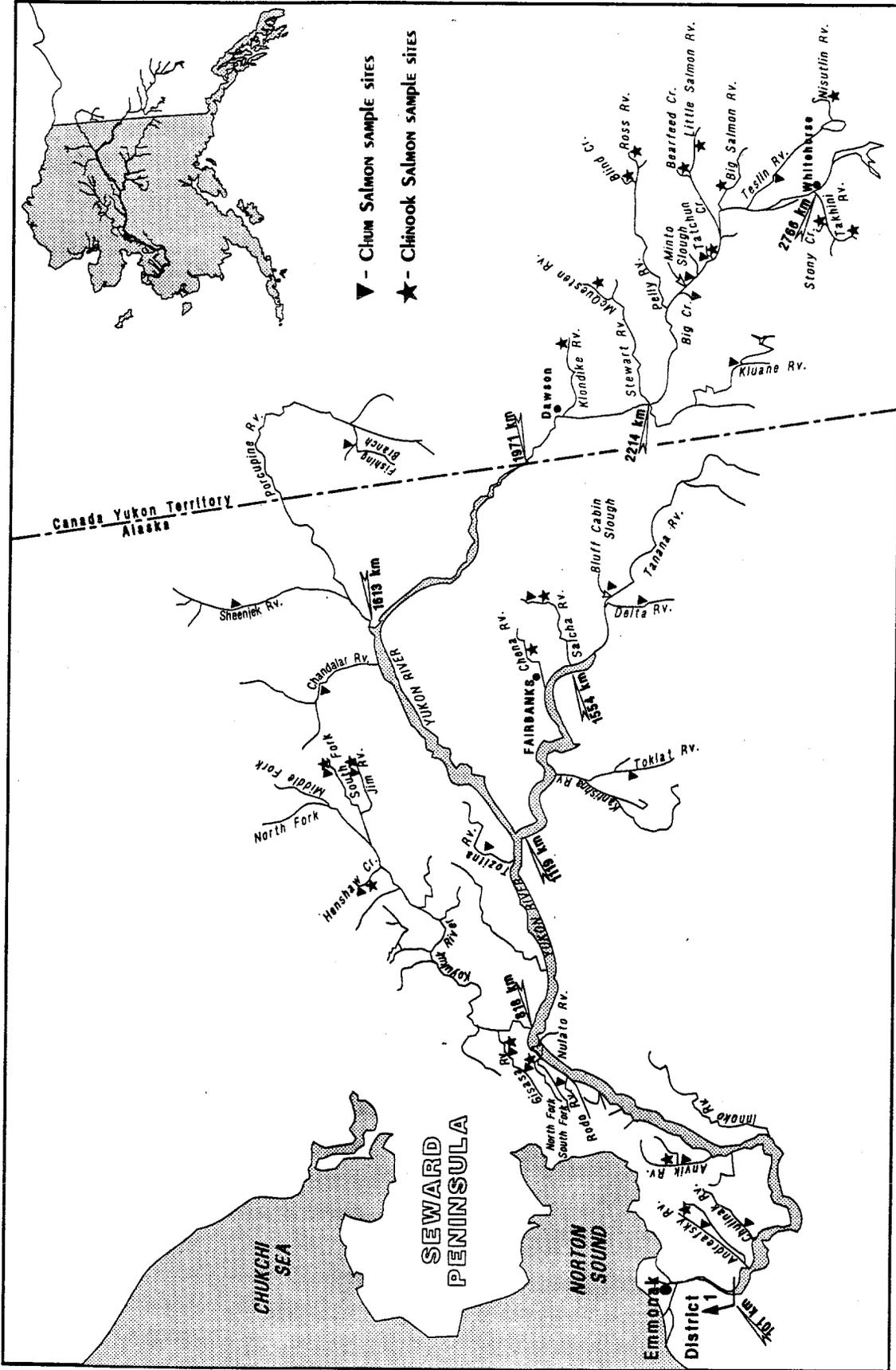


Figure 1. Map of the Yukon River system showing sample sites, species collected at those sites, Alaska Department of Fish and Game fishing District 1, and distances (in kilometers) from the river mouth to designated locations.

per fishing period, which were usually opened twice a week throughout the summer. The chum salmon fishery was closed for some periods in 1987, 1988, and 1990, and all genetic samples were from test nets during these periods.

Four tissues (muscle, liver, eye, and heart) were taken from each fish for protein electrophoresis; in the latter years of the study, cheek muscle was sampled instead of skeletal muscle for both chum and chinook salmon. Tissue samples were put in matching sets of individually labelled tubes, cross-referenced to an ADF&G sample number, frozen, and shipped to the USFWS laboratory in Anchorage, and stored at -70°C prior to analysis.

Protein electrophoresis followed standard techniques described by Aebersold et al. (1987) and Gall et al. (1989). Gene nomenclature follows recommendations of Shaklee et al. (1990b). A total of 48 proteins coded by 70 genetic loci were screened in chum salmon, and 50 proteins coded by 67 loci were screened in chinook salmon (Appendices V and VI).

Nineteen loci for chum salmon and 22 loci for chinook salmon were used for mixed-stock analyses (Appendices V and VI). The loci were selected based on four criteria: 1) they must have been analyzed and scored for all baseline and mixed-stock fishery collections; 2) the allelic variability must have been observed in at least one collection; 3) the observed banding patterns must have conformed to known models of inheritance among salmonid species; and 4) the patterns must have been repeatable among tissues.

For paired loci with protein products of indistinguishable mobility (isoloci; Allendorf and

Thorgaard 1984; e.g., *sAAT-1,2* in chum salmon), the observed genetic variation was assigned to a single locus of the pair. Only a low level of variation was observed at isoloci studied in Yukon River chum and chinook salmon (frequency of the alternate genotype less than 1% in any population). The observed genotype frequencies were not statistically different than expected using a single-locus model (using Pearson's chi-square to test goodness-of-fit).

Rare alleles (variants with an observed frequency less than 0.01), which offer little discriminatory power among stocks, were pooled with variants that were not rare prior to statistical analyses (Appendices VII and VIII).

In chinook salmon, the heterozygote at the *sMEP-2* locus could not be distinguished from the common homozygote. For the genetic stock identification analyses, this locus was treated as if it was a non-genetic trait with only two character states.

For each collection, the observed genotype distribution for each locus was tested against the proportions expected in a random mating, randomly sampled population (Hardy-Weinberg equilibrium) with a χ^2 goodness-of-fit test. 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 expected 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. The data sets for each of 34 stocks of chum salmon include up

to 19 variable loci, and 31 collections of chinook salmon include up to 22 variable loci; 1 in 20 tests are expected to give "false positive" (Type I errors) in each population by chance alone, assuming that the loci studied are segregating independently.

Baseline data sets from multiple collections from different times or different sites within river systems were compared using heterogeneity log-likelihood ratio statistics both pairwise and simultaneously among groups (G-test: Sokal and Rohlf 1981). Collections from the same site made at different times were not pooled prior to analyses if significantly different ($P < 0.01$). The more liberal significance level ($P < 0.01$ versus the standard 0.05) reflects the "decision" of the West Coast salmon genetics working group that pooled collections from multiple years provide a better estimation of actual allele frequencies of given population with overlapping generations than does a single collection (Robin Waples, NMFS, personal communication).

In this study, data sets from populations sampled at different sites within river systems generally were not pooled prior to GSI analyses, although pooling statistically indistinguishable stocks ($P > 0.05$), when many stocks are included in the baseline data set for a given project, is recommended by the aforementioned working group. For the Yukon River salmon study, relatively few stocks make up the baseline data set, and simulations with and without pooling of baseline data sets from stocks of different tributaries indicated that stock allocations were more accurate and precise when individual stocks were used in the baseline data set rather than pooled data. Only the Jim River and Henshaw Creek (Koyukuk River system) chinook salmon data were pooled prior to mixed-stock analyses since we were

missing data for the *mSOD-1* locus for the Henshaw Creek sample, and the data for the other loci examined were not significantly different ($P > 0.05$).

Geographic and temporal patterns of genetic relatedness between baseline populations were examined using a measure of genetic distance (Nei 1972) using only variable loci in the analyses. Cluster analysis of the genetic distance data was done using the unweighted pair-group method (UPGMA; Sneath and Sokal 1973), and the results are presented as dendrograms. The pattern of relationships among stocks indicated by the results of the cluster analysis was used in conjunction with geographical location to assign stocks to the genetic/management groups used for reporting results of the mixed-stock analyses. A computer program designed for analyzing genetic data (BIOSYS-1; Swofford and Selander 1989), was used for the analyses described previously.

Stock contribution estimates of the mixed-fishery collections from the commercial and test net catch of District 1, Yukon River were calculated using a conditional maximum likelihood computer program (GIRLSEM), originally developed for fisheries applications by Milner et al. (1981), and refined by the National Marine Fisheries Service (NMFS; Pella and Milner 1987, Masuda et al. 1991) to use both the Estimation Maximization (EM) algorithm (Dempster et al. 1977) applied to stock identification by Millar (1987), and an Iteratively Reweighted Least Squares (IRLS) algorithm (described in Pella 1986). The GIRLSEM program calculates the most likely combination of baseline stocks that would be required to form the observed mixed-stock data, based on the assumption that the frequencies in the baseline populations are known exactly; the infinitesimal jackknife procedure (Efron 1982),

applied to mixed-stock analysis by Millar (1987), was used as a measure of the precision of the estimates.

Since samples can only provide estimates of the actual genotype frequencies in the source populations and in the mixed-stock fisheries, bootstrap resampling (Efron 1982) of both the baseline and mixed-fishery data was used to provide a mean and standard deviation of 100 estimates of stock contribution for each collection. The bootstrap procedure estimates sampling error by drawing, with replacement, new random samples of the specified sample size from the data set being analyzed.

The sample size used for stock composition estimates depends on the level of precision required and the amount of variability among the stocks studied. For this study, data were combined so that each mixture included at least 180 individuals. The time periods used for the mixed-stock analyses for each year were chosen, where possible, to coincide with ADF&G commercial openings or test net periods. However, in several instances, data from samples collected during different ADF&G periods were combined in order to obtain an adequate sample size for analysis.

Simulated mixed-stock data sets, assembled from known proportions of baseline data, were analyzed for stock composition in order to test the accuracy and precision of stock allocations of Yukon River chum and chinook salmon to management groups. Three series of artificial mixtures were performed to determine how well the program could discriminate 1) between summer-run and fall-run chum salmon stocks, 2) between U.S. fall-run and Canada fall-run

chum salmon stocks, and 3) between U.S. and Canada chinook salmon stocks. A series of six artificial mixed-stock data sets were constructed for each pair of comparisons so that the proportion of each group being tested increased in frequency in the mixture incrementally by 20% from 0 to 100%. Equal proportions of all stocks belonging to each group, drawn from the baseline data set, were used to make up the mixtures.

A second set of simulations was done using all stocks from the baseline data set contributing to the appropriate group in proportions reflecting their relative abundance from ADF&G escapement counts for the years 1987-1990 (JTC 1990). These simulations were done using the program GIRLSYM (Pella, Masuda, and Nelson, NMFS, in preparation), which uses the maximum likelihood algorithms described above as well as "drawing" the data from the baselines to form the artificial mixed-stock data sets. Individual stock contribution estimates were summed across stock groups. The precision of the estimates is reported as one standard deviation of the mean stock proportions, derived from 100 iterations of bootstrap resampling. The data are presented as accuracy graphs, which illustrate the expected and observed allocations to baseline stocks.

A second simulation program (SIMOBS: Michele Masuda, NMFS, personal communication) was used to test for the ability of the maximum likelihood procedure to detect the addition of data from a stock or stock group, specified by the investigator, to actual mixed-fishery data. Data from the stock being investigated was generated from baseline data, and added incrementally to constitute from 0 to 45% of the mixed-stock data. Two mixed-stock collections were tested in this manner. First, the chum salmon collected during the time

period from June 22 to June 29, 1990, estimated using mixed-stock analysis to include less than 1% fall-run fish, were tested with incremental additions of data from six different fall-run stocks or combinations of stocks (Tanana, Chandalar/Sheenjek, Fishing Branch, Mainstem Canada, Kluane/Teslin, and Canada fall run). Second, the August 3 to August 8, 1990 chum salmon collection, with no summer-run stocks detected using mixed-stock analysis, was tested for detection of additions of Koyukuk River data, then Anvik River data (both summer-run stocks). As in the previous procedures, estimates of the stock proportions of these combination artificial and actual mixture files were estimated using maximum likelihood statistics, with 100 iterations of bootstrap resampling to determine the magnitude of the error associated with the estimates.

RESULTS

Chum Salmon

Relationships among stocks

Of the 70 loci screened in Yukon River chum salmon, variation was observed at 39, and 19 met the criteria for genetic stock identification (Appendix VII). When tested for conformance to random mating (Hardy-Weinberg) proportions, only 7 of 587 variable loci studied in Yukon River chum salmon were significantly different, less than the number expected by chance (29): *ALAT* in the 1987 Toklat collection ($\chi^2 = 5.297/1$ df); *SIDHP-2* in the 1987 Toklat collection ($\chi^2 = 10.228/3$ df), the Bluff Cabin collection ($\chi^2 = 9.229/3$ df), the 1987 Fishing Branch collection ($\chi^2 = 13.956/3$ df), and the Big Creek collection ($\chi^2 = 9.922/3$ df) collections; and *LDH-A1* in the Bluff Cabin ($\chi^2 = 7.085/1$ df), and 1988 Sheenjek ($\chi^2 = 4.625/1$ df) collections.

Statistical comparisons (multiple simultaneous G-tests) among fall-run chum salmon collections, using the loci and stocks in common between this study and that of Canada (Beacham et al. 1988), indicated no significant differences in allele frequencies among the collections from Minto (three years), Kluane (three years), Fishing Branch (four years), Teslin (two years), Toklat (four years), Delta (four years), Sheenjek (five years), and Chandalar (four years) collections. Only at a single locus (*mMEP-2*, Sheenjek River stock: $G = 12.335/4$ df;

$P < 0.05$) was a significant difference observed among data from stocks sampled in different years.

Data from 34 chum salmon collections, from both multiple sites of the same drainage and the same site in different years (Table 1), were pooled to form a 26-stock baseline data set. No significant differences ($p > 0.01$) were detected among chum salmon collections from different years from Salcha, Toklat, Delta, Chandalar, Sheenjek, and Fishing Branch Rivers. The two collections from the same site on the Anvik River (1987 and 1988) were significantly different genetically ($G = 55.820/15$ df; $P < 0.001$), and were not pooled prior to the analysis.

Two major groups were apparent in the dendrogram of genetic distances among the 26 Yukon River chum stocks analyzed: a summer-run group and a fall-run group (Figure 2). The Teslin and Kluane River stocks (fall-run fish) did not group closely with either temporal group or with each other. Within the summer-run group, two major subdivisions were apparent, those of the lower river (below river kilometer [rkm] 800) and those of the mid river (rkm 800 to 1150). The collections from the Gisasa River, which is a tributary of the Koyukuk River, might have been expected to group with other mid-river stocks of that drainage; however, that collection was genetically more similar to the geographically more proximate lower river stocks. Within the fall-run group, the Toklat, Delta, and Bluff Cabin stocks form a separate group. The other major group evident from the dendrogram includes two U.S. stocks (of the Chandalar and Sheenjek Rivers) joined with the remaining four Canada stocks, though a significant difference ($P < 0.05$) was observed between U.S. stocks

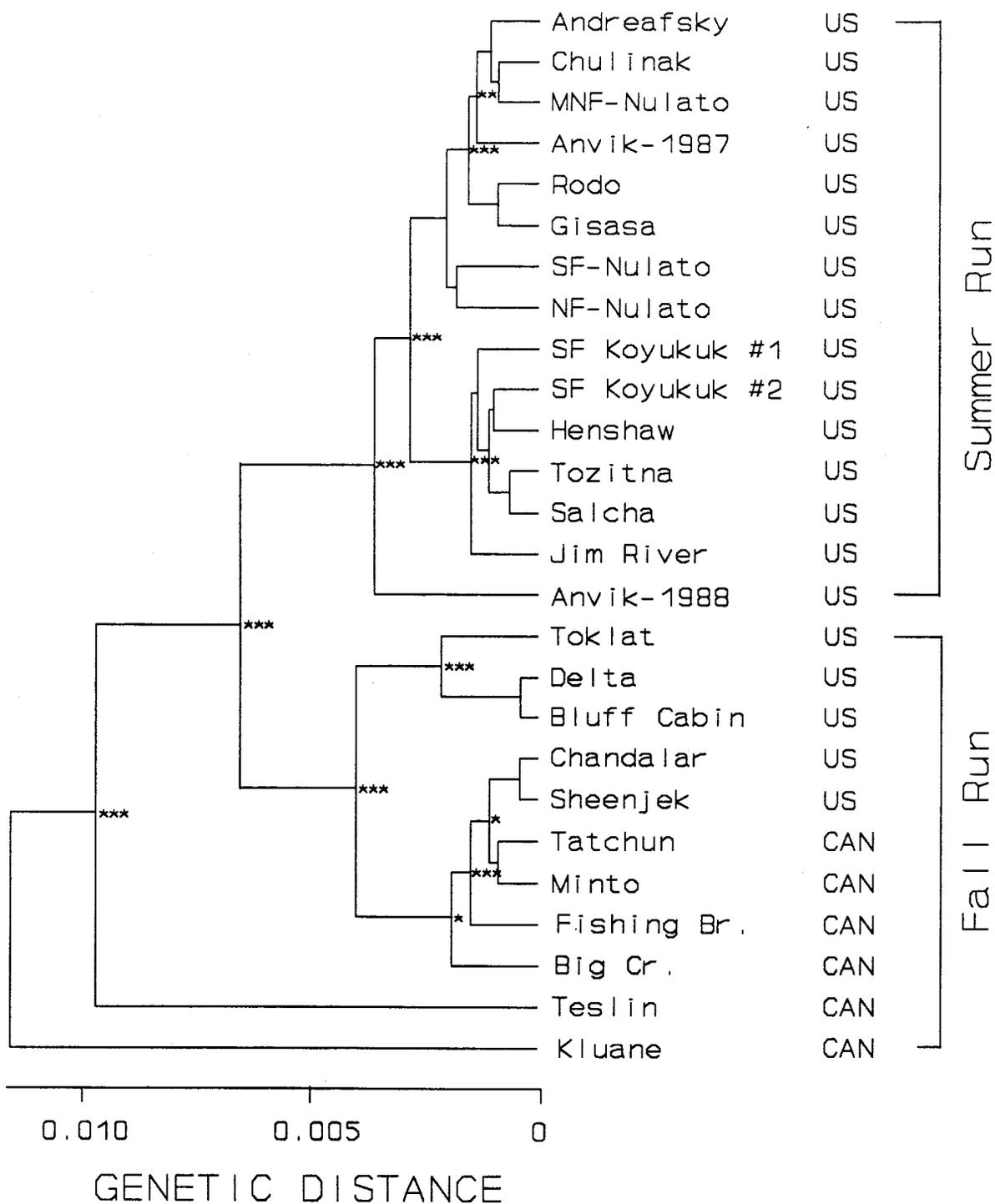


Figure 2. Dendrogram based on Nei's (1972) genetic distance showing the genetic relationship between stocks of Yukon River chum salmon. (US = United States, CAN = Canada). Asterisks designate significant branch points (* P < 0.05, ** P < 0.01, and *** P < 0.001).

and the Tatchun/Minto group. The Fishing Branch collection was significantly different ($P < 0.001$) from both the Chandalar/Sheenjek stocks and the Tatchun/Minto stocks, with the Big Creek collection significantly different ($P < 0.05$) than the others in the upper fall-run group.

Sequentially removing data for each stock prior to reanalyzing the relationships among chum salmon stocks resulted in one change in the order of grouping among summer-run stocks and one change among the fall stocks. With all 26 stocks in the analysis, the Anvik-88 stock was a separate branch grouped with the lower- and middle-river groups. Removing any one of Chulinak, Anvik-87, North Fork Nulato, Henshaw, Gisasa, Tozitna, or Salcha data sets from the analysis caused Anvik-88 to group with the lower river stocks, though still on a separate branch. For the fall-run stocks, when all 26 stocks were included, Kluane and Teslin grouped with neither the fall- nor summer-run stocks; these stocks were genetically divergent from all other stocks and from each other. When the Toklat River data set was removed from the analysis, the Kluane stock then grouped with the fall-run stocks, as a unique branch, while the Teslin stock remained separate from all other stocks.

Simulations

Simulations demonstrated that the maximum likelihood procedures accurately discriminated between summer-run and fall-run chum salmon stocks, but that the estimated proportion of U.S. and Canada fall chum salmon stocks were less precisely allocated. In the series of simulations testing the identification of summer- versus fall-run stocks, the estimated contribution of each run to the artificial mixture was included within one standard deviation

of the actual value at all proportions tested except at the extremes, 0.0 and 100.0% (Figure 3). For the simulations testing the ability of the program to discriminate between U.S. and Canada fall chum stocks, the true proportion of each group in the artificial mixture was also within one standard deviation of the estimated value at all proportions tested except the extremes; however, the associated error terms were greater at each increment tested in the U.S. versus Canada simulations than the summer- versus fall-run simulations. The misallocation between summer-run and fall-run stocks was predominantly an overestimate, by 4.5 to 7.3%, of the proportion of summer-run stocks in the mixtures (Figure 4). A higher percentage of misallocation to summer-run stocks occurred when U.S. fall stocks were present at higher proportions because U.S. fall-run chum salmon stocks were more genetically similar to (U.S.) summer stocks than Canada fall-run stocks were to summer-run stocks.

Adjusting the relative stock contributions composing the artificial mixture for the simulations to reflect escapement size did not change the results substantially. Both sets of estimates were within one standard deviation of each other throughout the range of increments tested (R. L. Wilmot, unpublished data).

In the simulations (SIMOBS) where data from each of six fall-run test stocks were added incrementally to actual mixed-stock data (identified above as being composed of more than 99% summer stocks), the observed decrease in the proportion of summer-run fish identified was within 2 - 5% of the expected values as the contributions of Tanana River, Canada main-stem Yukon River, Kluane/Teslin Rivers, and a Canada fall-run stock mixture to artificial mixed-stock data sets were increased; in these four tests, little misallocation by the computer

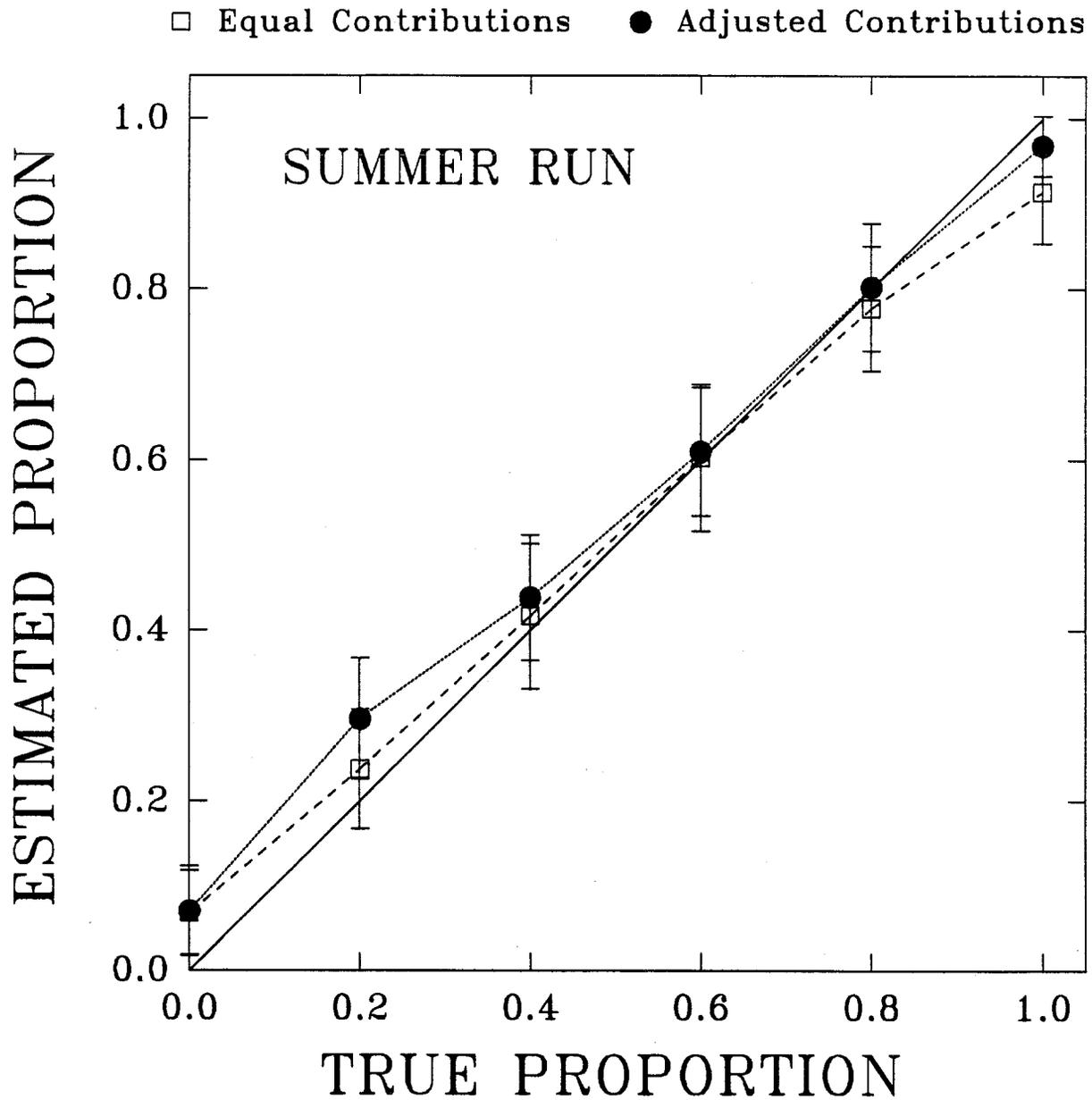


Figure 3. Estimated versus true proportion of fall-run versus summer-run chum salmon in the Yukon River. Estimates are the mean of 100 bootstrap resamplings, and error bars are one standard deviation around the mean. The clear squares represent the results when stocks are added in equal proportion and solid circles represent results when the stocks are added in proportion to their 1987-1990 escapement averages.

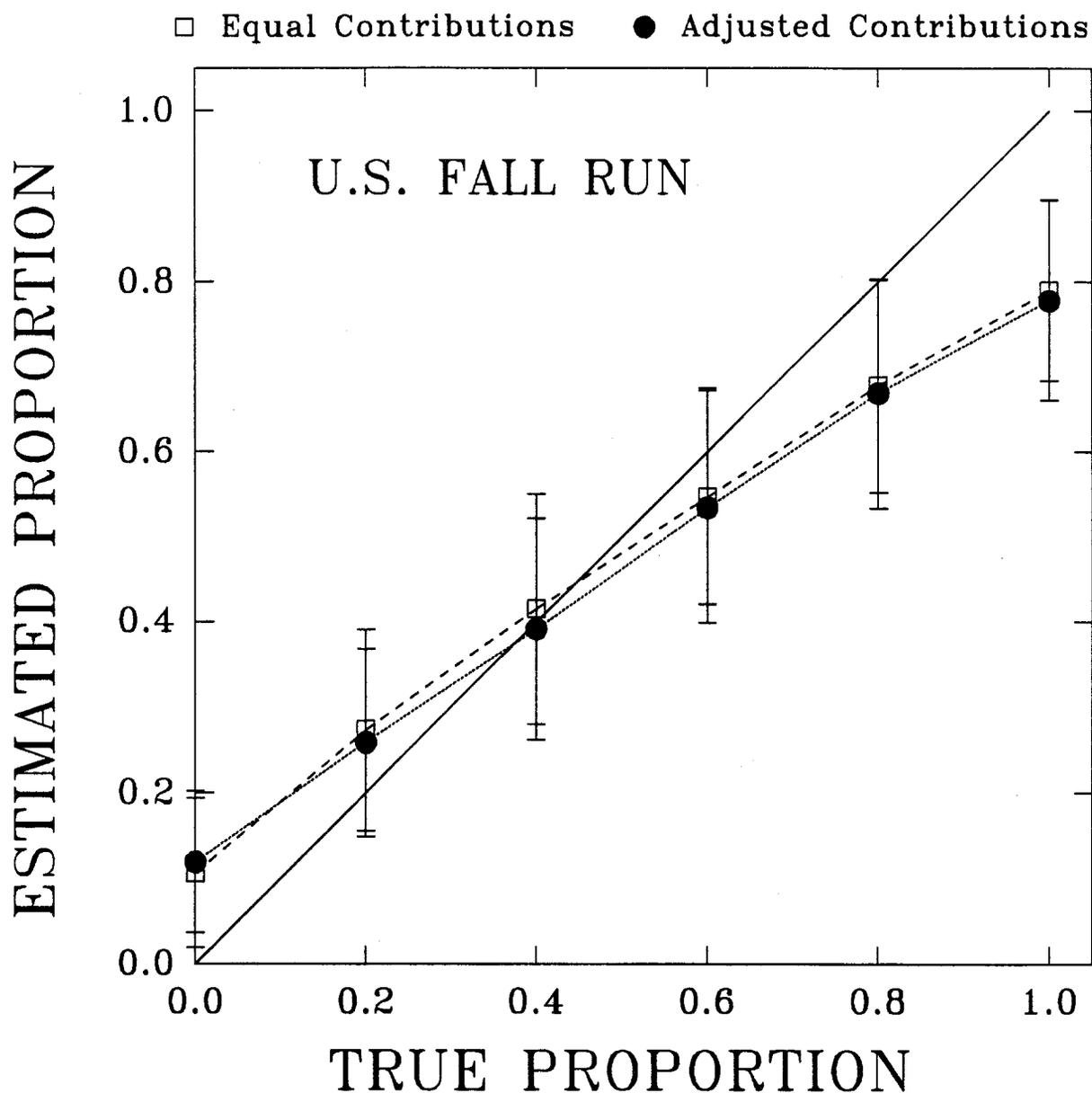


Figure 4. Estimated versus true proportion of United States and Canadian fall runs of chum salmon in the Yukon River. Estimates are the mean of 100 bootstrap resamplings, and error bars are one standard deviation around the mean. The clear squares represent the results when stocks are added in equal proportion and solid circles represent results when the stocks are added in proportion to their 1987-1990 escapement averages.

program of fall-run fish to summer-run stocks was observed (Figure 5). In the same series of simulations applied first to the Chandalar/Sheenjek stocks, then the Fishing Branch River stocks, the actual proportion of these fall-run stocks in the artificial mixtures was underestimated by as much as 25% over the range of increments tested; however, the misallocation from these fall run stocks was to other fall-run stocks, predominately to the Canadian mainstem stocks.

In the simulations where data from the Anvik and Koyukuk River (summer-run) stocks were added incrementally to actual mixed-stock data (identified above as being composed of more than 99% fall-run stocks), the proportion of fall-run fish detected in the mixtures decreased only slightly as the proportion of Anvik and Koyukuk River data was increased (Figure 6). The contributions to the artificial mixture of both of these summer-run stocks were consistently underestimated in the series of incremental simulations, but only up to 25% of the misallocated fish were assigned to fall-run stocks rather than to other summer-run stocks.

Stock composition estimates of commercial and test catch

Estimates of the stock composition of collections from District 1 commercial and test net fisheries indicated that, in all four years, the Yukon River lower river summer-run chum salmon stocks (of U.S. origin) contributed 75 - 100% of the catch until mid-July (Figures 7, 8; Appendices IX through XVI), and up to 42% of the catch for the rest of the fishing season. Less than 17% of the chum salmon sampled in June were allocated to fall-spawning stocks of the U.S. or Canada.

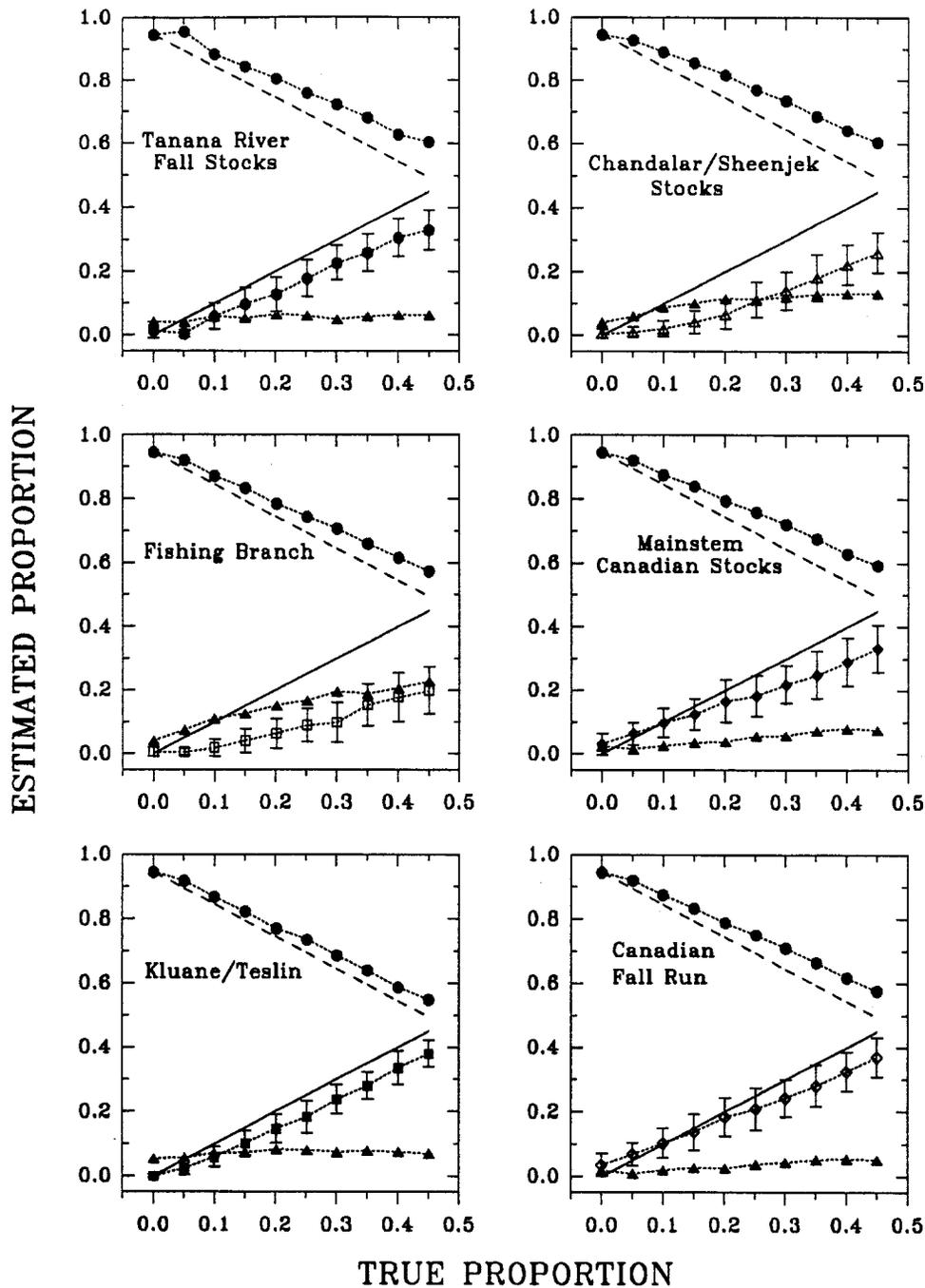


Figure 5. Results of the SIMOBS tests to determine the accuracy of estimates of fall run chum stocks in a mixture. Proportions of a known stock or stocks are added at 5% increments from 0 to 45%. The solid line represents 100% accuracy, and the error bars are derived from 100 bootstrap resamplings (∇ = Tanana, \triangle = Chandalar/Sheenjek, \square = Fishing Branch, \blacklozenge = Canadian Mainstem, \blacksquare = Kluane/Teslin, \diamond = total Canadian fall run, \circ = Summer-run stocks, and \blacktriangle = remainder of fall run).

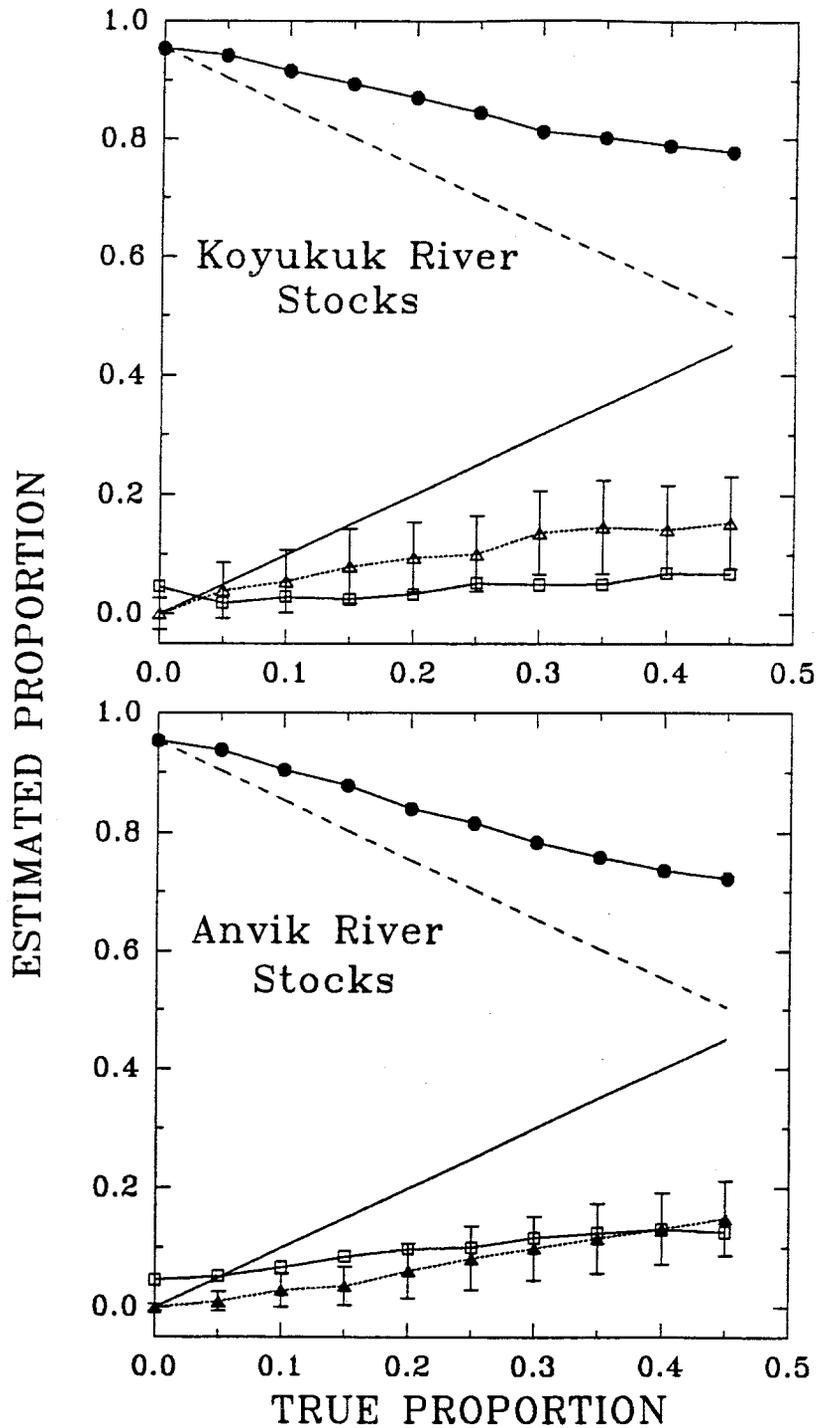


Figure 6. Results of the SIMOBS tests to determine the accuracy of estimates of two summer-run stocks in a mixture sample. Proportions of a known stock were added in 5% increments from 0 to 45%. The solid line represents 100% accuracy, and error bars are derived from 100 bootstrap resamplings (● = fall run stocks, □ = remainder of summer run, △ = Koyukuk stocks, and ▲ = Anvik stocks).

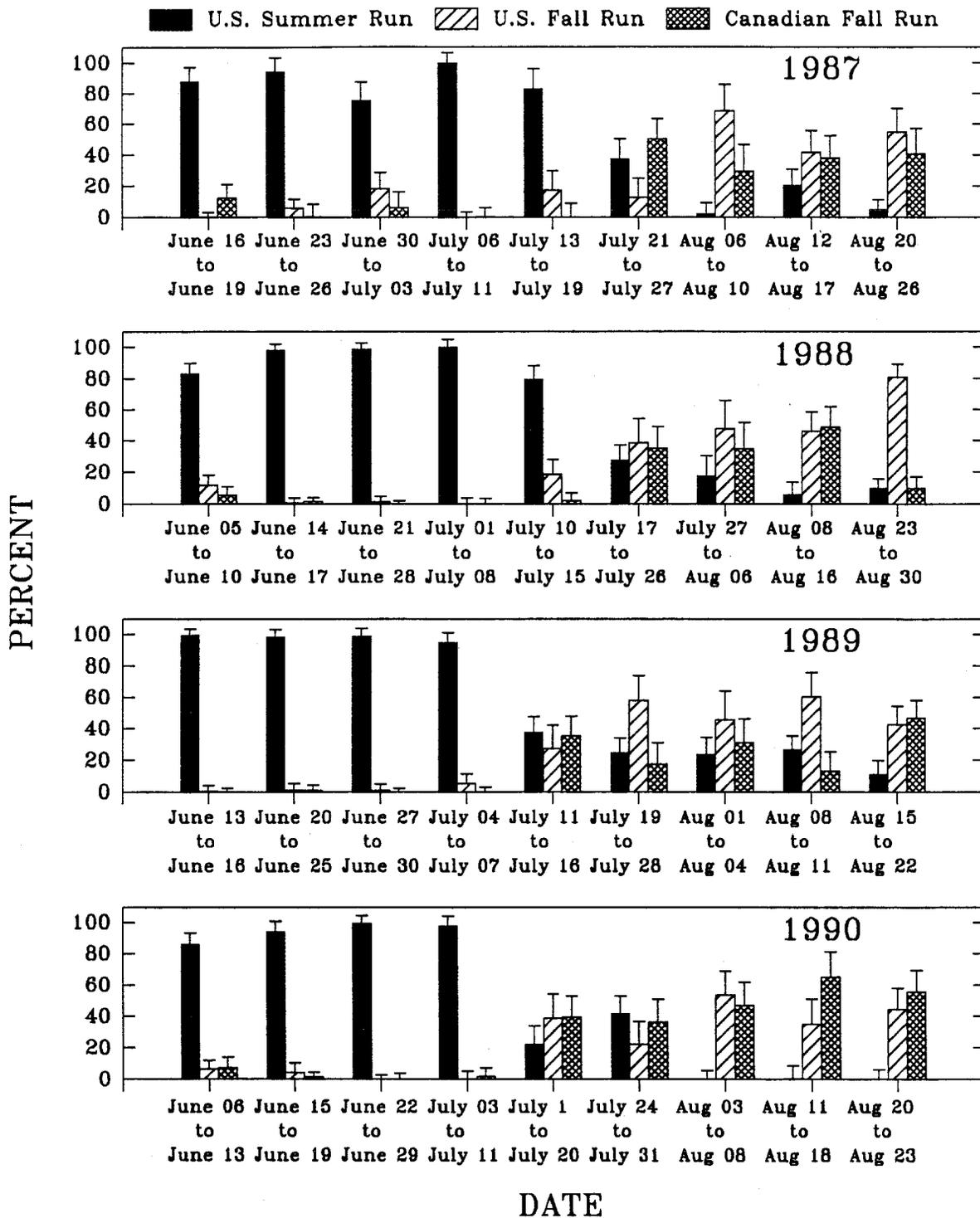


Figure 7. Percent of United States summer- and fall-run fish and Canadian fall-run fish caught in the Lower Yukon River chum salmon fishery (1987, 1988, 1989, and 1990). Error bars represent one standard deviation derived from 100 bootstrap resamplings of the baseline and mixture samples.

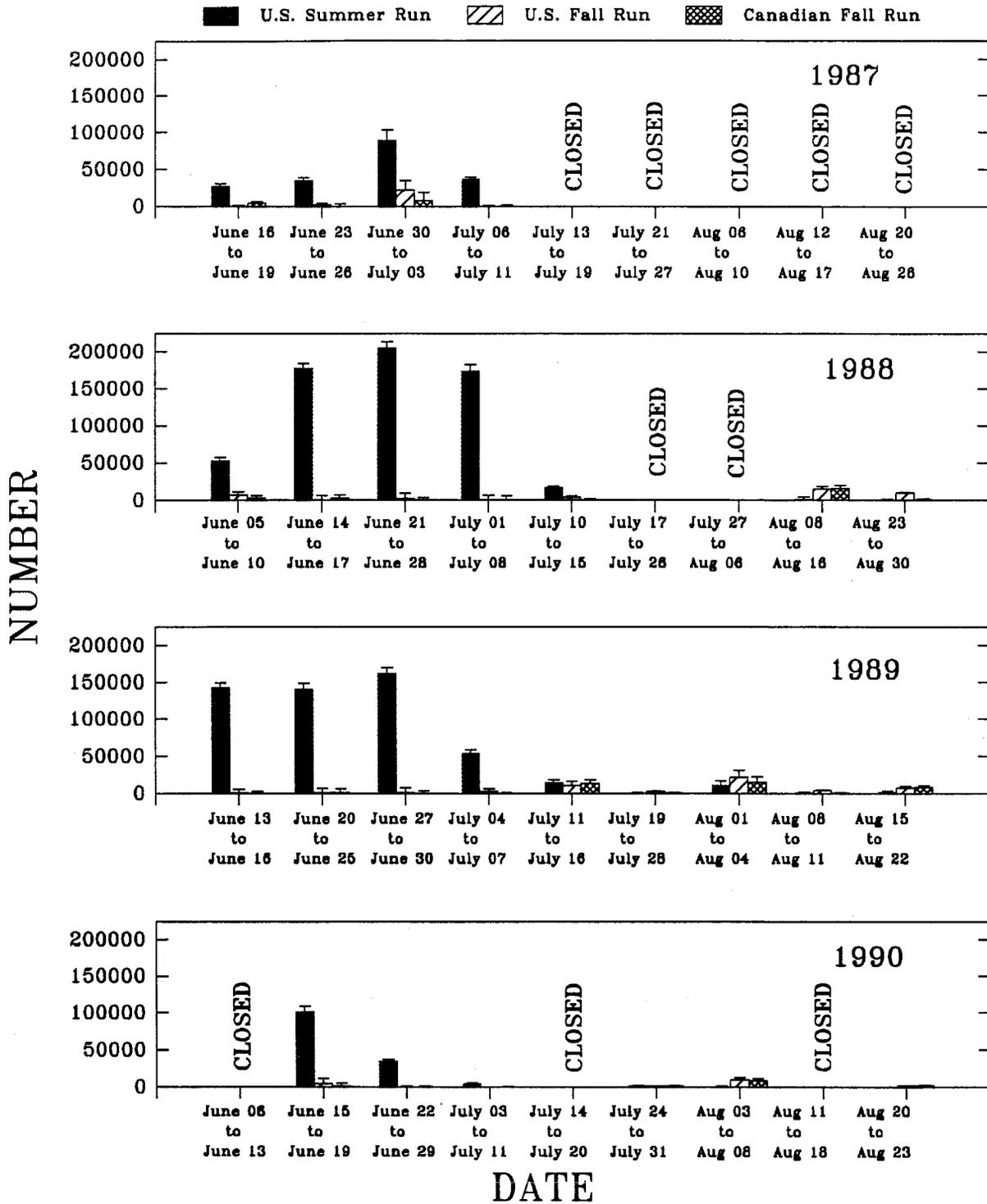


Figure 8. Number of United States summer- and fall-run fish and Canadian fall-run fish caught in the Lower Yukon River chum salmon fishery (1987, 1988, 1989, and 1990). Error bars represent one standard deviation derived from 100 bootstrap resamplings of the baseline and mixture samples.

While up to 11.9% Canada fall-run chum salmon stocks were identified in collections from District 1 as early as GSI Period 1 in 1987, no statistically significant contributions from Canada stocks were identified before an interval which ranged from July 11 - 14 over the course of the study. The proportions of Fishing Branch and main-stem Canada Yukon River chum salmon in the catch were highest during mid-July to mid-August. The timing of the maximum proportion of the catch sampled in District 1 that was attributed to Kluane and Teslin River stocks varied from year to year, occurring from mid-July in 1988 and 1990, to early August in 1989, and late August in 1987; the time period in 1990 that had the highest estimated proportion of Kluane/Teslin stocks, 20.4%, was not open to commercial fishing.

Excluding two early-season, statistically non-significant allocations, the Tanana fall-run stocks were responsible for 13.8 to 70% of the total catch from mid-July to the end of the fishing season. Whereas 17.7% of the catch in GSI Period 1 in mid-June, 1987 was identified as the Chandalar/Sheenjek stock, most statistically significant contributions by this stock group were made between mid-July and mid-August each year.

From 1987 to 1990, the composition of the total District 1 chum salmon catch ranged from 82.0 to 91.0% ($\bar{x} = 85.7 \pm 5.8\%$) summer-run fish, from 5.7 to 10.6% ($\bar{x} = 8.6 \pm 5.8\%$) U.S. fall-run fish, and from 3.3 to 8.2% ($\bar{x} = 5.7 \pm 4.7\%$) Canada fall-run fish (Table 3). Of the proportion of chum salmon identified as fall-run stocks, 60.6% were of U.S. origin (range: 54.3 to 68.5%), and an average of 39.4% were of Canada fall-run origin. When these percentages were applied to the total number of chum salmon caught in District 1 during the four-year period of the study, the estimated number of summer-run fish ranged from 144,606

Table 3. Summary of the estimated contributions by origin to the fishery in District 1 for chum salmon - 1987 to 1990. Errors are one standard deviation. Percentages in parentheses are based on the fall-run totals only.

Run	1987		1988		1989		1990		Average	
	%	Number	%	Number	%	Number	%	Number	%	Number
Summer	84.5±10.0	188,335±22,382	91.0±4.7	630,581±32,207	85.2±5.6	532,705±35,299	82.0±6.0	144,606±10,516	85.7±5.8	374,055±25,102
Fall	10.6±7.5 (68.5±48.2)	23,689±16,670	5.7±4.4 (62.5±48.7)	39,155±30,497	8.4±6.4 (56.9±43.0)	52,760±39,867	9.8±6.8 (54.3±37.8)	17,195±11,953	8.6±5.8 (59.9±44.7)	33,200±24,748
Fall	4.8±9.0 (31.5±57.8)	10,874±19,986	3.3±3.4 (37.5±37.4)	23,466±23,440	6.4±4.6 (43.1±31.0)	40,043±28,739	8.2±4.9 (45.7±27.2)	14,447±8,621	5.7±4.7 (40.1±36.5)	22,208±20,198

U.S.

Canadian

to 630,581 ($\bar{x} = 374,055$); the number of fall-run chum salmon of U.S. origin ranged from 17,195 to 52,760 ($\bar{x} = 33,200$), and the number of Canadian-origin (fall-run) chum salmon ranged from 14,447 to 40,043 ($\bar{x} = 22,208$) (Table 3). Error terms are the 4-year average of the one standard deviation errors on the yearly estimates. The standard deviations associated with the stock composition estimates in the early portion of the season, when the majority of fish are of the summer run and only a few fall-run stocks were present, ranged from 2.0 to 5.0%. Later in the season, when the genetically close fall-run stocks from near the border made greater contributions to the catch, the error terms associated with the estimated stock contribution estimates ranged between 10.0 and 15.0%. The estimated percentage of U.S. chum salmon stocks in the total catch from 1987 to 1990 ranged from 91.8 to 96.6% of the annual harvest.

Chinook Salmon

Relationships among stocks

Of 67 loci screened in Yukon River chinook salmon collections, 35 were variable and 21 met the criteria for GSI analysis; 22 loci were actually used in the analyses because variation at *TPI-1* was observed in the mixed-stock collections, though not in the collections from the tributaries used as baseline data. Of twenty-one loci (excluding *sMEP-2*, which was treated as a non-segregating character) tested for conformance to random mating (Hardy-Weinberg) proportions in 31 collections, only genotype proportions for 4 loci were significantly different than expected: *PEP-A* in the Andreafsky collection ($\chi^2 = 15.268/1$ df), *sMEP-1* in the Jim

River ($\chi^2 = 55.643/3$ df) and Henshaw Creek ($\chi^2 = 9.915/3$ df), and *MPI* in the North Fork Nulato River ($\chi^2 = 10.349/1$ df). In 377 tests of loci variable in 31 stocks, 19 loci are expected to be identified as significantly different by chance.

Statistical comparisons of allele frequency data from this study and that of Beacham et al. (1989) showed significant differences in allele frequencies among Canada Yukon River chinook salmon collections from different years and between collections representing different life history stages (adults versus juveniles). The data from Tatchun (1987, 1988, and 1989 adults), Nisutlin (1987 and 1989 adults), Blind Creek (1986, 1987, and 1989 juveniles), McQuesten River (1986, 1987, 1989, and 1990 juveniles), Takhini River (1986 and 1987 juveniles, 1988 adults), and Ross River (1987 juveniles, 1988 and 1989 adults) were significantly different ($P < 0.001$). The North Klondike collections (1986, 1987, 1989, and 1990 juveniles) were also significantly different ($P < 0.01$).

Data from the 31 collections in this study (Table 2, Appendix IV), including those from sites of the same drainage sampled in different years, were pooled to represent 20 stocks for estimating the genetic distance among stocks. Only between the collections from the Takhini River system were significant differences ($P < 0.01$) detected among data from the same stock sampled at the same site in different years. Data from the 1988 collections from the Takhini River adult chinook salmon differed statistically from the 1990 juvenile collections ($G = 17.428/6$ df, $P < 0.01$), due predominately to a single locus, *MPI-1*; the data were pooled in spite of the allelic differences at the *MPI* locus because the sample size in both collections was very small ($N=26$ in both 1988 and 1990). After pooling allele frequency data from

chinook salmon stocks sampled in more than one year and pooling the Jim River data with that of the Henshaw Creek stock (because of data missing for one locus), a 20-stock baseline was used for calculating genetic distances among stocks and for mixed-stock analyses.

From the dendrogram showing the relationships among the 20 Yukon River chinook salmon stocks, two major groups were evident, corresponding to U.S. and Canada stocks (Figure 9). Among the U.S. stocks, a lower river group (below river km 800) and a mid-river group (between river km 800 and 1150) joined. As with chum salmon, the chinook salmon collection of the Koyukuk River tributary, Gisasa River, were genetically more similar to lower river stocks than to other Koyukuk River stocks. The Canada stocks were grouped as: McQuesten and North Klondike River collections (from near the U.S./Canada border); the Pelly River collections (from Ross River and Blind Creek); the Takhini River collections (from Stony Creek and main-stem Takhini River); and a group consisting of the remaining upriver stocks (except Takhini, and including the collections from Tatchun Creek, Little Salmon River, Bear Feed Creek, Big Salmon River, and Nisutlin River).

Sequentially removing data for each stock prior to reanalyzing the relationships among chinook salmon stocks resulted in four changes in the order of grouping on the dendrogram of genetic relationships: 1) removing McQuesten data from the analysis caused Klondike to group with U.S. stocks, but as a separate branch; 2) removing Ross River data from the analysis caused Blind Creek to group with U.S. lower Yukon stocks as a separate branch; 3) removing Takhini data from the analysis caused the Stony Creek stock to group with the Canada mid-river group; and 4) removing Stony Creek data from the analysis caused Takhini

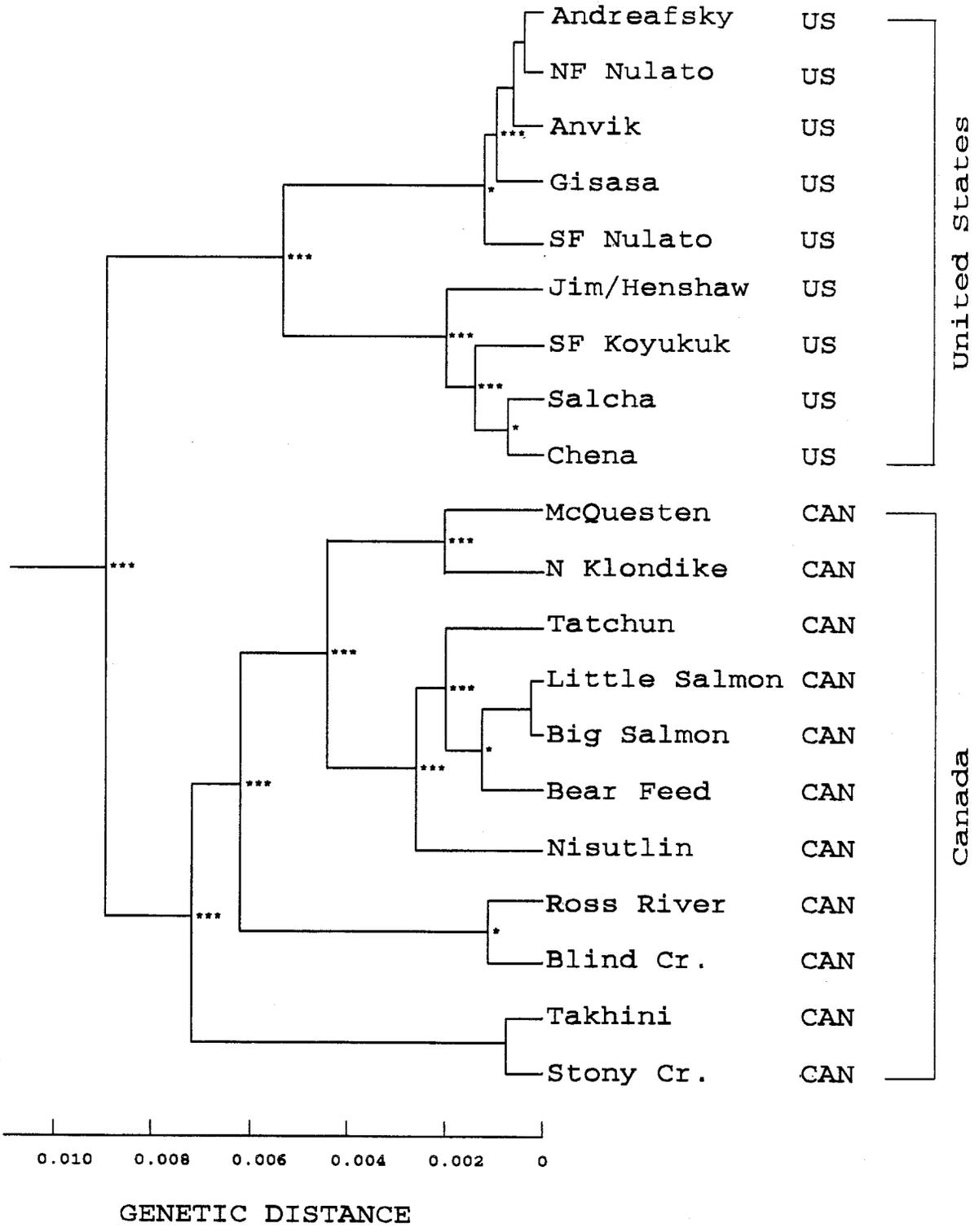


Figure 9. Dendrogram based on Nei's (1972) genetic distance showing the genetic relationship among stocks of Yukon River chinook salmon. Asterisks designate significant branch points (* P < 0.05, ** P < 0.01, and *** P < 0.001).

to become a branch, separate from both the U.S. and Canada groups.

Simulations

In simulations to determine the degree of accuracy in distinguishing between U.S. and Canada chinook salmon in mixed-stock collections, the expected and estimated proportions of U.S. and Canada stocks were within one standard deviation of each other at all increments from 0 to 100% whether the simulations were done using equal proportions of each baseline to create the mixture, or using stock sizes proportional to escapement estimates (Figure 10). The proportion of either group (U.S. or Canada) was overestimated at low contributions, and underestimated at high proportions. The standard deviations of the estimates ranged from 1 to 6%.

Stock composition estimates of commercial and test catch

Estimates based on mixed-stock analyses indicated that, in all four years, the Yukon River chinook salmon stocks of Canada origin contributed more than 50% of the catch until mid-June (Figures 11, 12; Appendices XVII through XXIV). During the early part of the season, the Pelly River stock was the largest contributor to the catch, followed by the Big Salmon River, and the Tatchun Creek stock. After mid-June, the U.S. stocks were responsible for more than 50% of the catch. The Nulato River stocks contributed the most U.S. fish to the District 1 catch, followed by the stocks of the Koyukuk River system. Besides the stocks listed above, the contributions of any one stock of either Alaska or Canada averaged less than

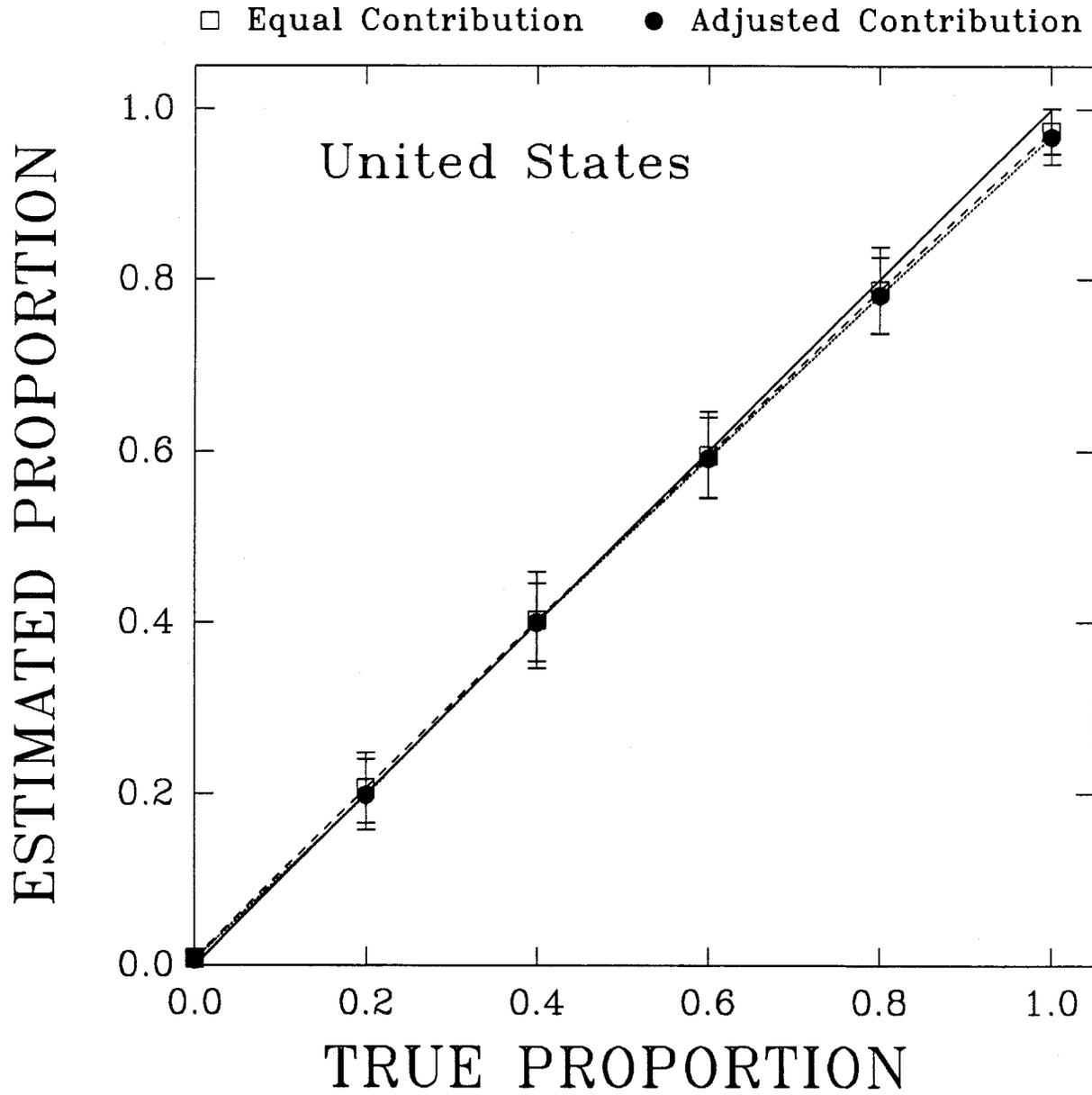


Figure 10. Estimated versus true proportions of United States and Canadian stocks of Yukon River chinook salmon. Estimates are the mean of 100 bootstrap resampling, and error bars are one standard deviation around the mean.

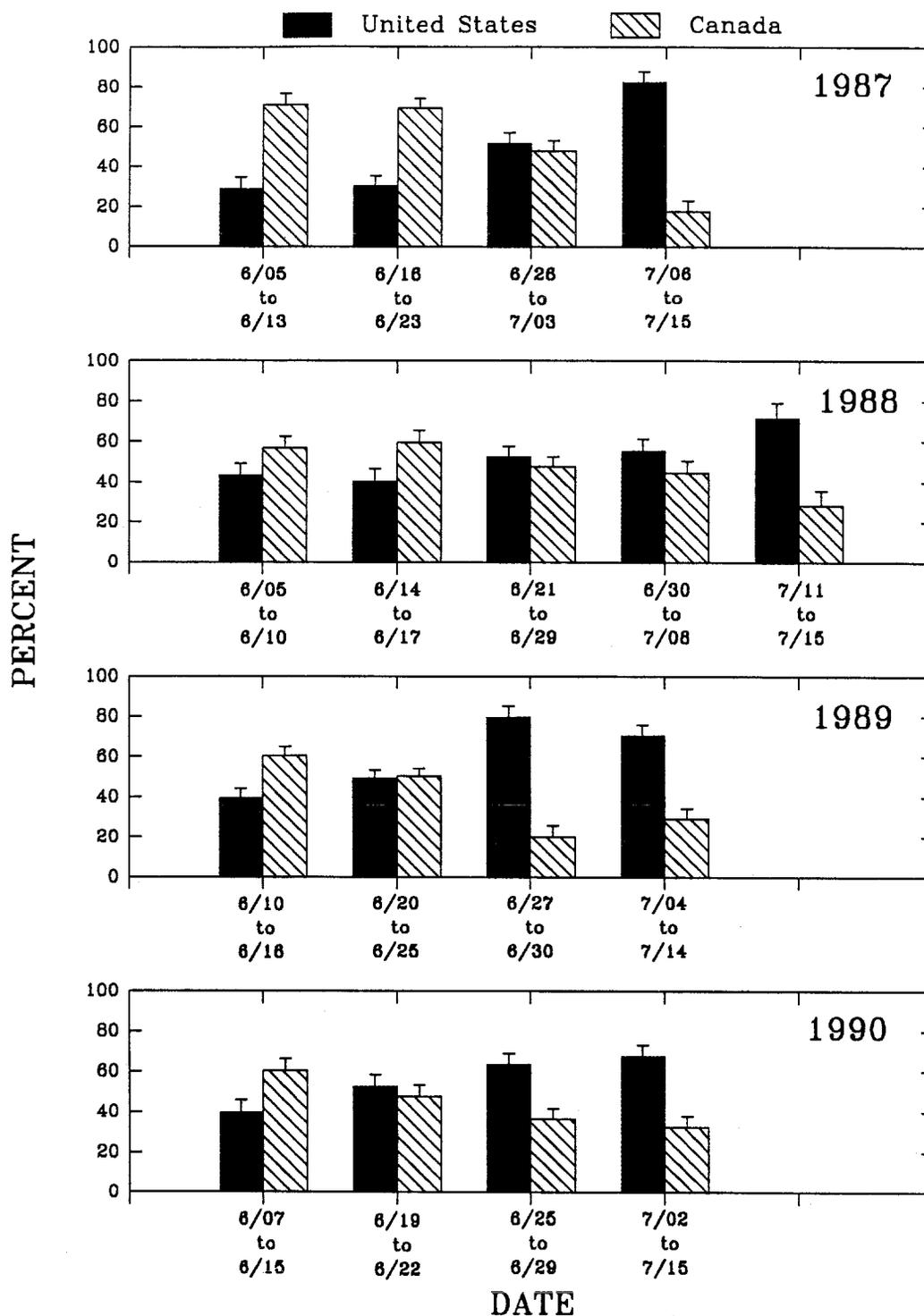


Figure 11. Percent of United States- and Canadian-origin chinook salmon caught in the Lower Yukon River fishery (1987, 1988, 1989, and 1990). Error bars represent one standard deviation derived from 100 bootstrap resamplings of the baseline and mixture samples.

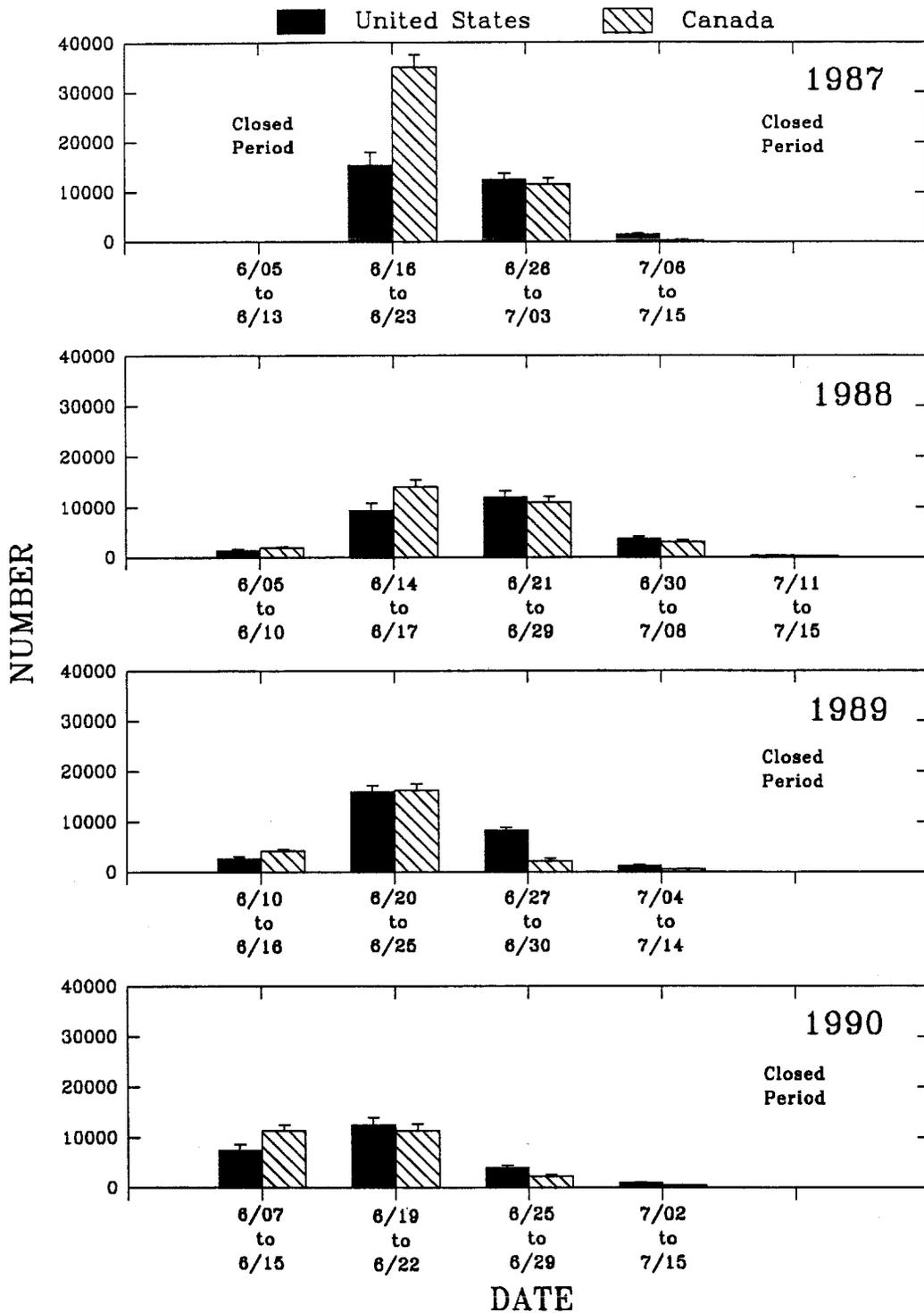


Figure 12. Number of United States- and Canadian-origin chinook salmon caught in the Lower Yukon River fishery (1987, 1988, 1989, and 1990). Error bars represent one standard deviation derived from 100 bootstrap resamplings of the baseline and mixture samples.

5.0% of the total catch in all years and during all sampling periods.

From 1987 to 1990, U.S. chinook salmon stocks comprised from 38.7 to 55.1% ($\bar{x} = 46.8 \pm 5.1\%$) and from 44.9 to 61.3% ($\bar{x} = 53.2 \pm 5.1\%$) Canadian origin stocks of the fish harvested in District 1 (Table 4). In numbers, the U.S. chinook salmon harvested ranged from 25,374 to 29,648 ($\bar{x} = 27,623 \pm 3,012$) and Canada chinook salmon from 23,046 to 46,993 ($\bar{x} = 31,419 \pm 3,012$).

Table 4. Summary of the estimated contributions by origin to the fishery in District 1 for chinook salmon - 1987 to 1990. Errors are one standard deviation.

Run	1987		1988		1989		1990		Average	
	%	Number								
U.S.	38.7±5.0	29,648±3,805	47.6±5.5	27,148±3,115	55.1±4.3	28,322±2,194	49.7±5.7	25,374±2,932	46.8±5.1	27,623±3,012
Canadian	61.3±5.0	46,993±3,805	52.4±5.5	29,941±3,115	44.9±4.3	23,046±2,194	50.3±5.7	25,694±2,932	53.2±5.1	31,419±3,012

DISCUSSION

Management of mixed-stock fisheries, especially of a multi-national origin, requires a method of accurately identifying the components of the catch. For stock composition estimates to be accurate and precise enough to meet management needs, the level of quantifiable genetic differences among stocks or stock groups must be sufficiently high. Four years of genetic data from Yukon chum and chinook salmon baseline and mixed-stock samples allowed us to determine the genetic relationships among stocks, the estimated composition of the District 1 harvest by country-of-origin, the run-timing of stocks or stock groups through District 1, the levels of precision and accuracy of the estimates, and the strengths and limitations of the data sets using computer simulations. We also compared our results to previous studies and made conclusions about the overall utility of the genetic stock identification method in the management of Yukon River salmon stocks.

Chum Salmon

To build on the previous chum salmon genetic study by the Canadian Department of Fisheries and Oceans, the scope of Yukon River chum salmon was expanded to include larger sample sizes for the genetic baseline data set and for mixed-stock collections from the fishery; add more genetic characters to the analyses; sample summer-run as well as fall-run chum salmon stocks and fisheries; and add more consecutive years of data.

Relationships among stocks

No evidence was found that any of the 34 chum salmon collections from Yukon River tributaries was composed of a non-random group of individuals. Individual loci not in random mating (Hardy-Weinberg) proportions were observed in a few stocks, but no significant differences from those expected were observed when all loci for each stock were considered. Collections not in random mating (Hardy-Weinberg) proportions can indicate 1) non-random sampling; 2) inclusion of more than one population in a collection; 3) disproportionate survival of certain genotypes (selection); or 4) chance inclusion of genotypes disproportionate to their presence in the population studied. Though the statistics used to test for these problems are not highly sensitive to small differences among stocks in relatively small sample sizes (Waples and Smouse 1990), lack of deviations from random mating proportions provides some confidence in use of these collections for baseline data for mixed-stock analyses.

The observed stability of allele frequencies from year to year in Yukon River chum salmon collections demonstrated that baseline data can be used for mixed-stock analysis for more than one year without resampling. Of the Yukon River chum salmon populations sampled (this study; Beacham et al. 1988), statistically significant divergence in gene frequencies between collections from the same site made in different years was rare. Only two summer-run collections, taken from the Anvik River in July of 1987 and 1988, were significantly different. The Anvik River is a large, productive river system that likely supports numerous spawning stocks in headwater tributaries, plus an unknown quantity of mainstem spawners.

For logistical reasons, the collections were made at a mainstem sonar site, which is undoubtedly a migratory corridor for upstream spawners of several populations. Since most studies of salmonid population genetics support temporal stability in allele frequencies between multiple collections from the same location (e.g., Grant et al. 1980, Beacham et al. 1987), different combinations of upriver, genetically distinct stocks most likely were included in the Anvik River mainstem collections made in 1987 and 1988.

Analyses of the genetic relationships among chum salmon stocks demonstrated that Yukon River summer-run stocks and the fall-run stocks have diverged genetically (Figure 4). These two runs correspond roughly to geographic lower-river (summer-run) and upper-river (fall-run) stocks, and middle-river stocks with both summer- and fall-run fish. However, not all the fall-run chum salmon stocks of the U.S. and Canada were sufficiently genetically distinct from each other for accurate stock identification. The Tanana River stocks (excluding summer-run Salcha) were genetically distinct from the upriver fall-run stocks. The Kluane and Teslin River stocks were distinct from all other stocks and from each other. However, problems in stock discrimination among the other fall-run group, which includes the Chandalar and Sheenjek stocks of the U.S., and the Fishing Branch and upper Yukon mainstem collections of Canada, can be anticipated due to their close genetic relationship.

Simulations

Simulations of stock composition analyses demonstrated the strengths and limitations of the chum salmon genetic baseline data set and the stock identification method for certain cases.

Using these baseline data, the maximum likelihood program was able to discriminate accurately between Yukon River summer-run and fall-run chum salmon stocks with little bias. However, the estimates of the relative contributions of U.S and Canada fall-run chum stocks were not as accurate, and were biased at extreme values, e.g., when the actual contribution were near 0 or 100%. This type of bias is typical (Jerome Pella, NMFS, unpublished manuscript), and the known direction of the bias can aid in interpretation of actual mixed-stock contribution estimates. At high or low proportions the estimates of the proportion of U.S. or Canada fall-run stocks may be under or overestimated if the contributing stocks are not genetically distinct.

The bias at extreme values observed in the simulations means that the small estimated proportions of fall-run fish observed during the early summer fishing periods may be either 1) statistical artifacts, or 2) real, as some the stocks identified (e.g., Kluane and Teslin River) were genetically distinct from the other stocks sampled. In the mixed-stock collections from late July through August, the observed stock group contributions for U.S. and Canada fall-run stocks were usually not near 0 or 100%, so this type of bias was not an issue during this period.

The levels of accuracy and precision observed in the simulations of stock identification of fall-run chum salmon stocks suggest that individual stock contribution estimates were not accurate or precise with the exceptions of genetically distinct stocks like those of the Kluane or Teslin Rivers. The estimates from the GIRLSEM and the bootstrap resampling methods were not close until individual stock allocations were summed into the six major stock

groupings (Appendices IX to XVI). The standard deviations observed using either of these two methods of analysis were equal or nearly equal to the associated estimates unless the estimates were summed by stock groups. This approach has been recommended by several authors (Milner et al. 1981, Millar 1987, Pella and Milner 1987, Wood et al. 1987).

The estimated proportions of four of the fall-run stock groups (Tanana River stocks, excluding the summer-run Salcha River stock; Kluane and Teslin River stocks; Canada mainstem stocks; and a composite of all Canadian fall-run stocks) were underestimated by less than 10% in the simulations that added fall-stock data to a predominately summer-run mixed-stock data set (Figure 5), indicating that these stocks were genetically distinct from each other. The Chandalar/Sheenjek (U.S.) and Fishing Branch (Canada) stocks were not as distinct genetically, and both of these stock groups misallocated to Canada mainstem stocks.

This misallocation may be related to how the mainstem baseline samples were collected. The Minto and Tatchun collections were taken from Canada mainstem and slough habitats, and Big Creek is a short mainstem tributary. Because these sites were sampled so close to the main river, conglomerations of upstream migrants may have inadvertently been included in the collections. Use of composites of multiple stocks can result in an indistinct average mixed-stock baseline data set rather than a discrete stock (Shaklee 1991), possibly explaining some of the observed misallocation to mainstem stocks from other fall-run stocks, including Fishing Branch and Chandalar/Sheenjek.

In a series of simulations with data from summer-run stocks added in known proportions to a

predominantly fall-run mixed-stock collection, the contributions of the two summer-run stocks (Anvik and Koyukuk) most often observed during the mid-July through late August time period were consistently underestimated, with misallocation to fall-run stocks (except Kluane and Teslin stocks). These results suggest that some of the contribution of fall-run stocks to the late July and August catch may be overestimated at the expense of summer-run stocks. The simulations to test the overall ability of the program to discriminate between summer-run and fall-run stocks that showed an overestimation of summer stocks at proportions 0 to 50% may be true in general, but may be contradicted when certain individual stocks are in the catch. Future studies may show that misallocation between certain summer-run and fall-run stocks reflect actual genetic similarities between fall-run stocks and certain late summer-run stocks, e.g., the upper Koyukuk River system. Overall, the simulations indicate that 1) summer-run and fall-run chum salmon stocks can be accurately identified, 2) the proportion of U.S. fall-run stocks was underestimated due to misallocation of Chandalar/Sheenjek stocks to mainstem Canadian stocks, and 3) the proportion of summer-run stocks in the District 1 catch during mid-July through August was probably underestimated due to misallocation of certain summer-run stocks to fall-run stocks.

Stock composition estimates of commercial and test catch

Four years of stock composition estimates generally corresponded with what was known about run-timing of the Yukon River chum salmon stocks in the lower river. Both historical data and genetic analyses of collections of chum salmon from District 1 have demonstrated the predominance of the numerically greater lower river stocks in the early season, followed

by predominantly upriver stocks. The date when fall-run fish become proportionally dominant varied from July 7 to July 21 over the four years. Part of the observed variability in timing of the summer- and fall-run components was likely due to the way commercial and test fishing periods were set (when the samples were taken), and how data for genetic stock identification periods were pooled to accumulate an adequate sample size. The remainder reflects the natural variability in timing of seasonal and stock components of the Yukon River chum salmon run. Our data indicated that a small proportion of the catch (less than 12%) in the lower river during June were fall-run stocks, and that the summer-run component remains significant through all of August. In three of the four years (1987 to 1989), a significant portion of the run entering the lower river throughout August was identified as summer-run fish, mainly from the Koyukuk River. A late season chum salmon run has been documented in the upper Koyukuk (Ken Troyer, USFWS, personal communication), supporting the stock composition estimates observed. A tagging study conducted from 1976 to 1978 showed that upper Yukon River fall chum salmon entered the river before the fall-run Tanana stocks (Buklis 1981). Our data show the Tanana River fall stocks entering the river in late July, the Chandalar/Sheenjek and Fishing Branch/Canadian mainstem stocks in mid July, and the Kluane/Teslin stocks arriving from mid to late July.

Based on estimates from this study of four years of mixed-stock analysis of the District 1 Yukon River fishery sampled during June to August each year, the total catch averaged 374,055 (85.7%) U.S.-origin summer-run chum salmon; 33,200 (8.6%) U.S.-origin fall-run chum salmon, and 22,208 (5.7%) Canadian-origin fall-run chum salmon. Of the total catch allocated to fall-run chum salmon, 59.9% were U.S.-origin fish and 40.1% were Canada-

origin fish.

In the previous genetic stock identification study, limited to the fall fishing season from mid-July to late August each year, the estimates of the proportions of the 1985 and 1986 District 1 commercial harvest of Canada origin ranged from 18 - 90% of the chum salmon sampled weekly or bi-weekly (JTC 1988). The average proportion of Canada fall-run stocks in the nine collections made during those two seasons were 37.5% in 1985, and 60.6% in 1986.

In our study, the average estimates of the contribution of Canada chum salmon stocks to the District 1 harvest during the fall season for four years were weighted by catch, and included only the periods that were open to fishing. Thus, the four-year average of Canada-origin chum salmon in the fall season catch was 38.7%. This value was not directly comparable to the DFO study results for 1985 and 1986, which were not weighted by catch figures.

Also, the presence of summer-run fish in the fall season was not accounted for in the DFO study, which used only fall-run stocks in their genetic baseline data set. Our stock composition simulations showed that the actual number of U.S. chum salmon in the lower river harvest during the fall season was probably underestimated because some summer-run stocks were misallocated to fall-run stocks. In addition, some of the periods with high proportions of summer-run stocks during the four years of this study were closed to fishing, and were not represented in the four-year fall season stock composition estimate. Therefore, proportions of the catch allocated to Canada stocks using numbers of fish for 1987 - 1990 did not reflect the true proportion of the total fall season run that was of summer-run origin, but

instead represented the proportions of the commercial catch (during open periods) of Canada origin during those years. Computer simulations also showed that (U.S.) Chandalar/Sheenjek stocks misallocated to Canada mainstem stocks, causing another source of underestimation of the U.S. component of the fall-run fishery.

Differences in the results between this study and those of DFO were probably also related to the number of genetic characters used in the analyses and the sample size of the mixed-stock collections. Seven protein loci were used in the DFO analyses compared to 19 in this study. Simulations comparing the same 7-locus data set used by DFO to a 22-locus chum salmon data set for stock identification in Washington and British Columbia showed lower discriminatory power with fewer genetic characters in the analysis (Shaklee 1991). Also, the sample sizes used for the 1985 and 1986 chum salmon mixed-stock fisheries collections were less than 114 fish for each period. Possibly due to the small sample sizes, a 95% confidence interval around the DFO estimates of the proportion of Canada chum salmon in the catch included zero in four of the nine sampling periods studied over two years.

The limitations of our study of the Yukon River chum salmon stock composition estimates for 1987 - 1990 were: under-representation of subpopulations (e.g., Anvik River stocks, and late-run lower and middle Yukon River stocks) in the genetic baseline data set; only 12 loci in 1987 analyses; combining data from commercial and test catch in GSI periods; combining data from different fishing periods; combining data from samples caught with different types of fishing gear; and possible non-random sampling of the District 1 catch.

In general, the concurrence between what is known about Yukon River chum salmon run timing and the genetic stock identification results indicated that the estimates of stock composition in the lower river are credible. Simulations demonstrated accurate and precise discrimination between summer-run and fall-run chum salmon stocks, but less power in separating U.S. and Canada fall-run stocks. Chandalar/Sheenjek and some summer-run stocks misallocate to other fall-run stocks, suggesting that both these U.S. stock groups may be underestimated during in the fall fishing season. Simulations demonstrated that discrimination among stock groups were accurate, but allocations to individual stocks were imprecise with this data set. More genetic characters to describe each stock and larger sample sizes in mixed-stock collections would improve the estimates. An assumption of the GSI model is that all stocks contributing to the fishery are represented in the baseline data set. Therefore, unsampled stocks, such as the Anvik River tributary stocks and late-run stocks in lower and middle Yukon River area, should be sampled for analysis.

Chinook Salmon

Relationships among stocks

The number of loci used in the chinook salmon analyses that did not conform to random mating (Hardy-Weinberg) proportions was less than the number expected by chance alone. Stability in allele frequencies between collections made in different years was observed in this study, except the two Takhini River collections (1988 and 1990). However, the size of the collections made in both years was small and the differences between data sets were due to a

single locus. We therefore pooled the data for these two collections.

Statistical comparisons between data from this study and those of Beacham et al. (1989) of stocks common to both studies demonstrated genetic differences among several collections.

Most of the collections where differences were detected were comprised of juveniles.

Juveniles are difficult to sample due to the ease of including family groups rather than a random sample of a population, and because chinook juveniles in particular are known to migrate extensively among freshwater tributaries and to mainstem locations (e.g., Murray and Rosenau 1989). Allelic frequencies derived from juveniles may not be representative of the returning adult population (Allendorf and Phelps 1981), but multiple juvenile collections are probably a better representation of the entire run than a single collection would be (Robin Waples, NMFS, personal communication). The Takhini River drainage, like several of the other upper Yukon River drainages, is a large system with several lakes which could support several populations in the type of lake-outlet habitat often inhabited by chinook salmon. The differences among Takhini River chinook collections observed may relate to having sampled from different populations from mainstem and tributary sites. However, the observed level of differentiation among collections from within each major river system was less than the magnitude of the differences among stocks of different major river systems.

Data from all the collections that came from different sites of the same major Yukon River tributary typically could be pooled, as collections from the same tributary were not statistically different. One exception was the collection from the large and complex Koyukuk River drainage. The Gisasa River collection was genetically similar to the lower Yukon River

stocks, whereas the collections from the Jim River, Henshaw Creek, and South Fork Koyukuk River were more closely allied genetically to mid-river stocks. Chinook salmon samples from Jim and South Fork Koyukuk Rivers were used as a standard in stock composition studies using scale pattern characteristics because in analysis of variance tests using run of origin data for age-1.4 fish, scale variable in samples from the Jim and South Fork Rivers taken in 1986 suggested distinction from other Alaskan escapement samples (Merritt et al. 1988). Though misclassification to lower and upper river groups and the lack of precision in the estimates made Jim and Koyukuk stocks too indistinct to be useful for scale pattern analysis, the differences correspond roughly to the pattern also observed in the genetic relationships measured. The confluence of the Koyukuk and Yukon Rivers is geographically between the lower and middle river regions, but spawning chinook salmon populations in the upper Koyukuk are nearly as far from the Yukon River mouth as is the U.S./Canada border. The genetic divergence between the upper Koyukuk River stocks and the lower river stocks may be related to the geographic distance, e.g., due to reproductive isolation, founding events, or different selection pressure.

Genetic distance relationships observed among the Yukon River chinook salmon stock groups studied (Figure 5) corresponded generally to the geographic groups (lower, middle, and upper river) used for stock composition studies using analysis of scale patterns. Again, the exception was that, using genetic methods, the upper Koyukuk stocks grouped with the middle river stocks rather than the lower river stocks. As the lower and middle river runs correspond to the stocks of the United States, and the upper river run includes only Canada stocks, allocations of the lower river harvest of chinook salmon to the U.S. and Canada

should be both accurate and precise.

Simulations

The simulations to test the ability of the maximum likelihood method to separate U.S. and Canada stocks indicated that the estimates of the contribution of Yukon River chinook salmon stocks to mixed-fishery collections were both accurately and precise by country-of-origin. Some individual stocks were genetically too similar to place a high degree of confidence on contribution estimates to the fishery. Six major stock groups, apparent from the dendrogram (Figure 9), were genetically distinct enough to provide acceptable precision in stock allocations.

Stock composition estimates of commercial and test catch

From 1987 to 1990, U.S. chinook salmon stocks comprised from 38.7 to 55.1% ($\bar{x} = 46.8 \pm 5.1\%$) of the fish harvested in District 1. In numbers this corresponds to a four-year average of $27,623 \pm 3,012$ U.S.-origin chinook salmon, and $31,419 \pm 3,012$ Canada-origin chinook salmon. As with chum salmon, not all chinook salmon stocks were identified as contributing to the fishery every year. However, every stock was identified as a significant contributor to the fishery in at least one of the four years studied.

Analyses of scale patterns to make stock composition estimates has been more successful with chinook salmon than with chum salmon of the Yukon River drainage. Stock composition

estimates for the District 1 chinook salmon catch have been made since 1980 by region of origin (McBride and Marshall 1983, Wilcock and McBride 1983, Wilcock 1984, 1985, 1986, Merritt et al. 1988, Merritt 1988, Wilcock 1990). Scale pattern classification accuracies for lower, middle, and upper Yukon River chinook salmon have been high (e.g., 0.965, 0.758, and 0.779 for the age-1.4 1986; Merritt et al. 1988). The upper Yukon River stock group identified using this method corresponds to Canada stocks.

Estimates of the stock composition of chinook salmon samples from the District 1 catch from 1987 to 1990 made using analysis of scale patterns were within a 95% confidence interval of the estimates made using genetic methods. Using scale pattern analysis, the estimated proportion of the catch of Canada origin were: 51.0% in 1987 (age-1.4 only: Merritt 1988); 53.8% in 1988 (Wilcock 1990); 47.0% in 1989 (Schneiderhan and Wilcock 1992); and 51.0% in 1990 (Schneiderhan, personal communication). The corresponding estimates, using genetic stock identification methods (this study), of the proportion of Canada-origin stocks in the catch were: 61.3% for 1987, 52.4% for 1988, 48.9% for 1989, and 50.3% for 1990.

The applicability of genetic methods to Yukon River chinook salmon stock identification in the lower river was supported by the accuracy and precision of U.S. and Canada allocations demonstrated by computer simulations, and by the correspondence of these genetic data with the estimates from analysis of scale patterns. Additional collections to represent unsampled populations should be analyzed, particularly from the Canada Yukon River tributaries, for which mainstem collections were frequently used. Larger sample sizes from the District 1 catch would increase the precision of the estimates and therefore the utility of the data.

CONCLUSIONS

The GSI methodology has been extensively used and evaluated for the Lower Columbia River chinook salmon fishery, the coastal Washington chinook salmon fishery, and the Puget Sound chum salmon fishery (Shaklee et al. 1990b). A large proportion of hatchery fish contribute to the harvest in all of the above fisheries, and because they are marked with coded wire tags, allow an alternative estimate of stock contribution to these fisheries. Acceptable levels of accuracy and precision for management of mixed-stock fisheries have been established for GSI estimates by blind tests (Milner et al. 1981), and computer simulations (e.g., Pella and Milner 1987, Wood et al. 1987, Shaklee 1991).

Based on the results of this study, the usefulness of the GSI methodology for management of Yukon River chum and chinook salmon stocks was evaluated. The utility of the method is based to a large degree on the level of discrimination required for management purposes. If the question is "what is the relative magnitude of summer- and fall-run stocks, or U.S. and Canada stocks in the mixed-stock fishery?" simulations demonstrate that the stock composition estimates are within $\pm 15\%$ (one standard deviation) for chum salmon and $\pm 8\%$ for chinook salmon. Stock composition estimates through the District 1 fishing season (June-August) show the proportional change from predominately summer-run to fall-run stocks. A small proportion of chum salmon caught in June were identified as fall-run stocks, and a statistically significant proportion of the chum salmon sampled in August were from summer-run stocks. Some problems exist in estimating the contribution of U.S. fall-run fish and Canadian fall-run fish to the District 1 fishery were due to the relatively close genetic affinity

between the Chandalar/Sheenjek, the Fishing Branch, and the Canadian mainstem stocks. On the other hand, the close agreement between the two independent estimates of stock contribution to the chinook salmon fishery by scale pattern analysis and by GSI helps establish considerable validity to these estimates.

Estimates of mixed-stock composition below these levels of discrimination must be viewed with caution. The error on estimates of contribution of the six major stock groups in chum salmon can run as high as $\pm 20\%$ and up to $\pm 10\%$ in chinook salmon. At this time, the error terms on estimates of individual stocks for both species are too large and should not be used until the baseline data set is expanded.

The current baseline for both chum and chinook salmon is adequate for estimates of contributions of U.S. and Canadian stocks in the fishery. Additional genetic characters in the baseline data set would improve the accuracy and precision of the estimates and could eventually lead to the capability to make estimates of contributions by individual stocks. Other improvements would include larger sample sizes, making sure that samples are taken over the entire course of the run, and insuring that all major contributing stocks are included in the baseline data set. Estimates could also be improved by insuring the mixed-stock fishery sample is as large as feasible (300 fish per time period), and that the collection represents a random sample of the fishery. Future analyses will address questions regarding pooling data from fish caught by different gear types, and pooling data from fish caught in test and commercial catch. In the future, GSI methods should be applied to the fisheries that occur in the other fishing districts.

Adding more genetic characters to the baseline data mixture sample can potentially increase the resolution to acceptable levels for estimates for individual stocks. For example, using the current 19 loci baseline for chum salmon, we cannot discriminate between the early and late run South Fork Koyukuk River samples. Recently, we have been able to resolve a total of 33 variable loci for these two collections, and the genetic differences between these stocks were significant. Preliminary results with mtDNA analysis for both Yukon River chum and chinook salmon stocks also show promise, as an additional discriminating character (Cronin et al. In preparation). Analysis of nuclear DNA may also provide additional characters, and already appears useful in Fraser River chinook salmon stock discrimination (Terry Beacham personal communication).

While there are limitations in the precision of the stock composition estimates, the strengths are the general agreement of the results with the known run-timing of Yukon River chum and chinook salmon stocks, and the close agreement between chinook salmon stock composition estimates derived from scale pattern analysis and the estimates using GSI. In addition, the stability of the genetic characters over time means the baseline does not need to be resampled every year, and timely estimates of stock contributions to the fishery are possible.

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Appendix I. Distributions of the sample catch (N) for chum salmon from Emmonak, Alaska, by year, month, GSI period, and commercial opening. GSI period reflects the pattern of sample pooling that was used in data analyses.

Year	N	Month	N	GSI Period	N	Commercial Opening	N
1987	1295	JUN	375	1	160	1	160
				2	140	2	140
				3	150	3	150
		JUL	475	4	153	4	153
				5	87	5	87
				6	160	6	160
		AUG	445	7	126	8	126
				8	170	9	170
				9	149	10	149
		TOTALS			1295		1295
1988	2016	JUN	664	1	224	1	92
				2	217	2	67
						3	75
		JUL	614	4	224	4	75
						5	73
						6	75
		AUG	738	7	140	7	75
				8	239	8	75
				9	420	9	74
						10	74
				11	61		
				12	74		
				13	179		
				14	128		
				15	171		
				16	121		
		TOTALS			2016		2016

Year	N	Month	N	GSI Period	N	Commercial Opening	N
1989	1683	JUN	620	1	225	1	176
				2	235	2	235
				3	160	3	160
		JUL	566	4	158	4	158
				5	238	5	238
				6	170	6	170
		AUG	497	7	115	7	115
				8	155	8	155
				9	227	9	227
TOTALS			1683		1683		1634
1990	1595	JUN	606	1	150		
				2	230	1	150
						2	80
		JUL	529	3	226	3	70
						4	77
				4	185	5	38
		AUG	460	5	205		
				6	139	6	30
						7	40
						8	55
				7	192	9	80
				10	40		
		8	130				
		9	138	11	80		
TOTALS			1595		1595		740