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Yukon River Chum Salmon: Report for Genetic Identification Studies, 1992-1997

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Penelope A. Crane[2]
William J. Spearman[3]
Lisa W. Seeb[3]

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P.O. Box 25526, Juneau, Alaska 99802-5526 **Commissioner**

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[2]Division of Fishery Resources, U.S. Fish and Wildlife Service, 1011 East Tudor Road, Anchorage, Alaska 99503

[3]Alaska Department of Fish and Game, Division of Commercial Fisheries, 333 Raspberry Road, Anchorage, AK 99518

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ABSTRACT

In 1987 a joint research effort between Alaska Department of Fish and Game, Canadian Department of Fisheries and Oceans, and U.S. Fish and Wildlife Service was initiated to determine the efficacy of the genetic stock identification (GSI) method for Yukon River chum salmon *Oncorhynchus keta* to aid in U.S./Canada treaty negotiations. Wilmot et al. (1992) constructed a genetic baseline of allozyme data collected from populations of chum salmon sampled between 1987 to 1991 and used it to estimate stock contributions of fishery samples collected in the Lower Yukon River (Wilmot et al. 1992). Since 1991, 48 additional collections of chum salmon have been made in the Yukon drainage. In this report, we assembled a new baseline using all available genetic data. Potential reporting regions identifiable in mixtures were tested using simulations where 100% of the artificial mixture was sampled from a single reporting region. Correct mean allocations from 100 simulations exceeded 90% for five reporting regions: Lower Summer, Fall Tanana, Chandalar/Sheenjek/Fishing Branch/Canadian Mainstem, Teslin River, and Kluane River. Results of simulated mixtures composed of multiple stock groups indicated that the presence of a reporting region could accurately be detected if that reporting region formed greater than 20% of the mixture.

INTRODUCTION

In 1985 the United States and Canada began negotiations addressing allocation of chum salmon *Oncorhynchus keta* and chinook salmon *O. tshawytscha* in Yukon River fisheries. An initial research objective was to identify chum salmon stocks and to determine if the proportion of U.S.- versus Canadian-origin stocks could be estimated for in-river fisheries. Several techniques, including genetic stock identification (GSI), were suggested as methods to delineate stocks and identify stocks in mixtures.

Chum salmon enter the Yukon River as two runs, summer and fall. Together, summer and fall run chum salmon are a mainstay of the Yukon River ecosystem and are an important resource for communities along the Yukon River where subsistence and commercial fishing plays a vital role in their economies and culture. Summer run chum salmon begin to enter the river in late May, and by mid July fall run chum salmon are thought to be predominant (Buklis and Barton 1984). Summer run chum salmon tend to be smaller than fall run chum salmon, are not as "ocean bright" on river entry, and spawn in the lower portion of the drainage. However, there is considerable overlap in the runtiming and physical appearance of summer and fall run chum salmon; and they cannot be distinguished by runtiming and visual inspection alone.

The first study of genetic population structure of chum salmon in the Yukon drainage looked at fall run populations only. Beacham et al. (1988), using allele frequency data for seven allozyme loci from 10 populations, detected genetic differences among chum salmon from the Tanana drainage and the Porcupine River and the Canadian portion of the Yukon drainage. Wilmot et al. (1992) expanded on the initial work of Beacham et al. (1988) by sampling chum salmon from both runs. Substantial genetic divergence was detected between and within 34 summer and fall run populations (italicized populations, Table 1) using data from 19 allozyme loci (Wilmot et al. 1992).

Wilmot et al. (1992) also used these data to estimate the contribution to mixed-fishery samples. Simulation studies showed that the genetic data could be used to distinguish between summer and fall run stocks. However, though fall run Tanana (Alaska) stocks and Kluane/Teslin (Canada) stocks could be accurately identified, estimates for Sheenjek River (Alaska), Fishing Branch (Canada), and Canadian mainstem populations were neither accurate nor precise limiting the use of the data for estimating country of origin of fishery samples.

In this report we summarize additions made to the Yukon River chum salmon baseline since the Wilmot et al. (1992) study, describe relationships among populations based on the new data, and the use of these data for mixture analysis. The allozyme data indicate that chum salmon populations in the Yukon River do not segregate along political lines; however, these data have sufficient power to identify major stock groups in mixtures and could be used to investigate the runtiming and migration patterns of these aggregates.

METHODS

From 1991 to 1995, 24 collections of summer run chum salmon and 24 collections of fall run chum salmon were taken (non-italicized populations, Table 1) and assayed for genetic variation by ADF&G and USFWS. These data were standardized for 22 loci with the Wilmot et al. (1992) baseline (italicized populations, Table 1). Loci standardized were *sAAT-1,2**, *mAAT-1**, *mAH-3**, *ALAT**, *ESTD**, *G3PDH-2**, *GPI-B1,2**, *mIDHP-1**, *sIDHP-2**, *LDH-A1**, *LDH-B2**, *sMDH-A1**, *sMDH-B1,2**, *mMEP-2**, *MPI**, *PEPA**, *PEPB-1**, *PEP-LT**, *PGDH**, and *TPI-1**. All available data for chum salmon in the Yukon River were used in the following analyses, except two collections of chum salmon sampled in the Anvik River mainstem. Allele frequency heterogeneity was detected between these collections, possibly indicating multiple stocks within the Anvik River (Wilmot et al. 1992). Instead we used data from actual spawning aggregates sampled throughout the Anvik River system.

Genetic Relationships Among Yukon River Chum Salmon

We tested for allele frequency heterogeneity among populations sampled over multiple years at the same location using a G-Statistic (Sokal and Rolf 1981). Multiple-year collections were pooled if no allele frequency differences were detected (α=0.05, adjusted for multiple tests using a sequential Bonferroni adjustment [Rice 1989]). Allele frequency estimates for highly polymorphic loci (common allele frequency $\leq$ 0.95) were plotted against rivermile of the collection location and a LOWESS curve fitted to determine if there was a relationship between allele frequency and rivermile. Genetic relationships among populations were assessed using a metric multidimensional scaling analysis (MDS, Krznowski and Marriott 1994) of Cavalli-Sforza and Edwards chord distances (Cavalli-Sforza and Edwards 1967). This analysis plots the distances in multidimensional space such that the observed distances match as closely as possible the plotted distances.

The results of the MDS, geographic proximity, and runtiming were used to assign the populations in a hierarchy. We used G-statistics to compare allele frequencies within- and among hierarchical levels (Smouse and Ward 1978). In this analysis, if an allele is observed in a population, we assumed it could be seen in any population, potentially at an infinitely small frequency. The degrees of freedom and the likelihood statistics are then summable, and hierarchical comparisons can be made simultaneously. However, this assumption makes this a conservative analysis. Finally, a gene diversity analysis (Nei 1973) was used to partition genetic variation into hierarchical levels. G_{st}, a measure of population subdivision, was calculated.

Application to Genetic Stock Identification

A genetic baseline for application of GSI of mixed fisheries was constructed from the allele frequency data using the general guidelines of Shaklee and Phelps (1990) and White (1996). First, multiple-year collections were tested for allele frequency heterogeneity using G-statistics, and pooled if no significant differences were detected. Second, allele frequencies among adjacent populations within a drainage were compared using G-statistics and also pooled if no

significant differences were detected. For both these series of tests, we used α=0.05 and corrected for multiple tests (Rice 1989). The goal of these tests is improve model performance by pooling populations with statistically indistinguishable allele frequencies, but not to create pooled population groups that do not represent any "true" baseline population (Shaklee and Phelps 1990).

Reporting regions for the new baseline were delineated using the results of the MDS analysis and management interests. A simulation study was used to determine if reporting groups could be accurately identified in mixtures. In each simulation, new baseline and mixture genotypes were randomly generated from the baseline using Hardy-Weinberg expectations. Average mixture estimates were derived from 100 simulations for each region, where each region comprised 100% of the mixture (N=400). When more than one stock was included in the reporting region, each stock contributed equally to the total mixture. We also performed a simulation study on the Wilmot et al. (1992) baseline using the reporting regions defined in that study to compare to the expanded baseline.

Finally, five simulations were performed using realistic stock compositions that fishery managers could expect to see passing through District 1 during July and August (see Table 5). The simulated mixture sample sizes were 400. The coefficient of variation (c.v.) of the estimate for each reporting region was used to evaluate the accuracy and precision of the estimates. A reporting region estimate with a c.v. of less than 50% can be shown to have contributed to the mixture with 95% confidence, i.e. the mixture estimate is significantly different from zero (Marlowe and Busack 1995).

RESULTS

Description of Baseline

Allele frequency estimates for all baseline collections are in Appendix 1. G-tests were used to compare allele frequencies among multiple-year collections from the same location. No allele frequency heterogeneity was observed at any site when alpha levels were adjusted for multiple tests (Table 2), indicating temporal stability of allele frequencies. Allele frequencies for multiple-year collections were pooled for all further analyses.

Clinal relationships were observed at eight of the 14 highly polymorphic loci plotted against rivermile. Generally increasing trends were found for the *100 allele for *mAH-3**, *ALAT**, *mMEP-2**, and *MPI**, and decreasing trends were observed for the *100 allele for *ESTD**, *LDH-A1**, *sMDH-A1**, and *PEPB-1** (Figure 2).

Allele frequencies were summarized into pairwise genetic distances (Cavalli-Sforza and Edwards 1967), and used in a metric multidimensional scaling analysis (Figure 3). Summer run populations in the Lower Yukon River (population numbers 1-12), early run populations in the Koyukuk River (population numbers 13-16), and the Melozitna River (21) formed a tight cluster separate from all other populations. Later run Koyukuk populations (population numbers 17-20) and the Tozitna (22), Chena (24), and Salcha (25) Rivers were plotted more closely with fall run populations than with summer run populations. The Toklat River (23) was distinct from other fall run Tanana River populations (population numbers 26-28). The Chandalar (29) and Sheenjek (30) Rivers were plotted very close together, as were the Canadian Mainstem populations (population numbers 33-35). Fishing Branch (31) appeared intermediate to these two clusters. The Teslin River (38) and populations of the White River (36,37) formed the two most divergent fall run groups.

A hierarchical analysis using G-tests was used to test for allele frequency heterogeneity within and among tributaries and runtimes (Table 3). Significant allele frequency differences were found among (G-statistic=4082.1, df=576, $P<0.001$) and within (G-statistic=1270.1, df=756, $P<0.001$) Yukon River tributaries. No significant differences were detected among collections in the Andreafsky River ($P=0.80$), Anvik River ($P=0.82$), Porcupine River ($P=0.34$), the Canadian Mainstem ($P=1.00$), or the White River ($P=1.00$). Allele frequency heterogeneity existed among early and late run populations in the Koyukuk River ($P<0.001$) and the Tanana River ($P<0.001$). Within the Koyukuk River, no allele frequency differences were detected among the early run populations ($P=1.00$) or the late run populations ($P=0.47$). Within the Tanana River, no allele frequency heterogeneity was detected among the summer run populations ($P=0.16$), but significant allele frequencies did occur between the Toklat River and fall run populations in the Upper Tanana River ($P<0.001$).

A gene diversity analysis was performed to partition genetic variation hierarchically into within population, among population within runtime, between runtime within tributary, and among tributary components (Table 4). Overall, most of the genetic variation was within population (96.9%), followed by among tributary (2.4%), between runtime within tributary (0.5%), and

among populations of a tributary within runtime (0.1%). The loci contributing the most to the among tributary component were *mAH-3** (7.9%) and *ESTD** (3.1%). G_{st}, the degree of differentiation among subpopulations, was 0.031.

Application to Genetic Stock Identification

In creating a baseline for use in mixture analyses, data from the 79 collections were condensed into a baseline of 23 pooled-population groupings using the general guidelines of Shaklee and Phelps (1990) and White (1996). First, all multiple-year collections from the same location were pooled because no allele frequency differences were detected (Table 2, see above). Secondly, adjacent populations within drainages were tested for allele frequency heterogeneity. The following populations were pooled: W. Fork Andreafsky and E. Fork Andreafsky Rivers (G-statistic=29.90, df=19, *P*=0.05); Beaver Creek, Yellow River, Swift River, Otter Creek, and Canyon Creek (G-statistic=128.19, df=100, *P*=0.03); Gisasa River, Huslia River, Dakli River, and Clear Creek (G-statistic=73.23, df=72, *P*=0.44); Henshaw Creek, South Fork Koyukuk River-late, and Jim River (G-statistic=57.34, df=42, *P*=0.06); Bluff Cabin Slough, Delta River, and Tanana Mainstem (G-statistic=43.19, df=38, *P*=0.26); Big River, Minto, and Tatchun River (G-statistic=22.18, df=32, *P*=0.90); and Kluane River and Donjek River (G-statistic=17.34, df=16, *P*=0.37). Allele frequencies for the pooled population groupings are in Appendix 2.

From the MDS analysis (Figure 4), we selected eight reporting regions for simulation analyses: 1) Lower Summer, 2) Middle Summer, 3) Toklat River, 4) Upper Fall Tanana, 5) Chandalar/Sheenjek, 6)Fishing Branch/Canadian Mainstem, 7)White River, and 8)Teslin River (Figure 4).

Simulations where each reporting region formed 100% of the mixture were used to evaluate the reporting regions and compared to the Wilmot et al. (1992) baseline. For the updated baseline, we used a multilevel hierarchy for summing regional estimates. Individual stock estimates were summed into estimates for all eight reporting regions; we also combined Toklat River and Upper Fall Tanana into a Fall Tanana reporting region and Chandalar/Sheenjek and Fishing Branch/Canadian Mainstem into a Border reporting region.

The following reporting regions had correct allocations greater than 90%: Lower Summer, Upper Fall Tanana, White River, and Teslin River. Middle Summer and Toklat River had correct allocations of 85% and 88%, respectively (Table 5a). For mixtures composed of 100% Middle Summer, most of the misallocation was to Lower summer; for the Toklat River mixture, most of the misallocation was to Middle Summer and Upper Fall Tanana. The two reporting groups surrounding the US/Canada border had the lowest mean allocations. Chandalar/Sheenjek had a correct mean allocation of 81% and Fishing Branch/Mainstem had a correct allocation of 83%; with the majority of the misallocation occurring between these two reporting groups. The enlarged reporting regions of Fall Tanana and Border had correct allocations exceeding 90%.

For the Wilmot et al. (1992) baseline, we used the reporting regions delineated for the mixed stock analysis in the Wilmot et al. (1992). One reporting group, Teslin/Kluane Rivers had a

mean estimate of greater than 90% (Table 5b). Middle Summer and Sheenjek/Chandalar had the lowest mean allocations, with regional estimates of approximately 75%.

We also performed five simulations using realistic stock compositions. For these, we used the multilevel hierarchy for reporting regions used in the 100% simulation study, with a third level: summer run and fall run. In general, if a reporting region contributed greater than 10% to the mixture, the c.v. was less than 50% (Table 6). Not surprisingly, expanding the reporting regions resulted in smaller c.v.s. This was most noticeable when combining Chandalar/Sheenjek and Fishing Branch/Canadian Mainstem into a "Border" reporting region.

DISCUSSION

Genetic Diversity

The baseline for chum salmon in the Yukon drainage is one of the most comprehensive baselines assembled to date. Over 8,000 individuals have been assayed for genetic variation. Twenty-one of the populations analyzed have been sampled over multiple years and temporal stability of allele frequencies has been demonstrated.

Interestingly, clinal relationships between allele frequency and river mile of the population location were observed for over half of the highly polymorphic loci analyzed in all populations. This type of allele frequency pattern could possibly have developed through at least two scenarios. One possibility is that populations at the extreme ends of the range of chum salmon in the Yukon drainage are sufficiently isolated to allow drift to have altered allele frequencies. Alternatively, the Yukon drainage may have been inhabited by chum salmon from two separate gene pools, with gene flow occurring between the two gene pools in the center of the Yukon drainage. The glacial history of the Yukon River makes the second scenario possible.

The Yukon River was only very slightly impacted by glaciation during the Pleistocene. Glacial activity only occurred in the headwaters of the Teslin and White Rivers. The entire drainage probably formed a large portion of the spawning habitat for chum salmon during the Pleistocene, and was part of the Beringian refugium. Chum salmon populations in the upper reaches of the Yukon drainage are among the oldest in North America; the upper River was not heavily glaciated, river channels were relatively stable, and therefore recolonization events have probably not occurred.

This is not the case for populations in the lower portion of the river. The original outlet to the Yukon River was by Nunivak Island, very close to the outlet of the Kuskokwim and Nushagak drainages which shared a common outlet. Genetic exchange may have occurred between chum salmon populations in the lower portion of the Yukon drainage and the Kuskokwim and Nushagak Rivers, and this is supported by the similar allele frequencies shared by populations in these areas (Seeb and Crane 1999).

Overall genetic diversity, as measured by G_{st}, was 0.031 for chum salmon in the Yukon River drainage and is equivalent to that observed for chum salmon in the Pacific Northwest (G_{st}=.028, Phelps et al. [1994]) and Southeast Alaska (Gst=0.027; Kondzela et al. [1994]).Both runtiming and geography contribute to genetic differences among populations in the Yukon River. Significant allele frequency differences were observed between early and late run populations from the Koyukuk River and from the Tanana River. Significant allele frequency differences were also observed among tributaries to the Yukon River. The loci contributing the most to among tributary differences were *mAH-3** and *ESTD** as can be seen from both the heterogeneity and gene diversity analyses.

We used a multidimensional scaling analysis to depict genetic relationships. Similar to the findings of Wilmot et al. (1992), the most unique populations were the Teslin and White Rivers.

This is not surprising; these are the only populations analyzed that were likely affected by Pleistocene glaciation (Lindsey and McPhail 1986) and founder affects following recolonization of these areas may be responsible for unusual allele frequencies. Interestingly, summer run populations from the Koyukuk and Tanana Rivers appeared more similar to fall run populations than to other summer run populations in this analysis. This contrasted with the data of Wilmot et al. (1992), where there was a clear distinction between summer and fall run populations.

Summer run populations from the lower Yukon River grouped more tightly together than any other group, indicating small genetic distances among these populations. This may be because during the last 11,000 to 16,000 years, the mouth of the Yukon River has slowly been moving north (Knebel and Creager 1973). The lower river channels were not stabilized during this time, undoubtedly forcing fish to recolonize when previous spawning habitat was no longer available. Therefore, there may not have been enough time since spawning habitat stabilized (if indeed it has yet) for drift to allow genetic differences to emerge among populations.

Baseline Evaluation

The addition of new populations and genetic markers and re-evaluation of reporting regions improved the identifiability of stocks in mixtures. Accuracy and precision of maximum likelihood estimates are affected by 1) representation of all major contributing populations in the baseline, 2) stability of baseline frequencies, and 3) level of genetic divergence among stocks (Pella and Milner 1987).

From 1992 to 1995, data from 48 new collections were added to the baseline. While coverage may still not be complete, the addition of these new populations has changed our understanding of genetic relationships of chum salmon in the drainage, and has improved the ability of the baseline to identify stocks in mixtures. In addition, 15 populations have been resampled. Sample sizes for each population group in the baseline range from 88 to over 1000 individuals. Allele frequency estimates for population groups are therefore highly accurate (Gregorius 1980).

The new baseline incorporates four new loci, *mAH-3**, *GPI-B1,2**, *LDH-B2**, *PEPA**, and deleted three loci from the old baseline, *bGLUA**, *sMDH-A2**, and *PEPB-2**. These loci were deleted because of insufficient resolution by ADF&G or because of the difficulty of standardization among laboratories. The locus accounting for most of the variation among regions is *mAH-3**, not included in the Wilmot et al. (1992) baseline because it was missing in two populations sampled in 1987. Approximately 8% of the variation observed at this locus is attributed to the among tributary component, more than twice as much as any other locus.

Waples and Smouse (1994) show that loci with two alleles, where the common allele varies between 0.2 and 0.8, provides the greatest resolution in mixture models. Several loci in the model fall near this range, *mAH-3**, *ESTD**, *sIDHP-2**, *LDH-A1**, *mMEP-2**, and *PEPB-1**.

Reporting regions used in the simulation studies for the updated baseline differed from those used in Wilmot et al. (1992) in one major area. Though Wilmot et al. (1992) also observed a

close genetic relationship between Gisasa River and lower river summer run stocks, they incorporated this population with their Midriver Summer region. We separated the Toklat River from the Wilmot et al. (1992) Fall Tanana region; allele frequencies for the Toklat River do not show a strong genetic similarity to Upper Tanana populations. Finally, Kluane/Donjek Rivers and Teslin River were made into individual reporting regions because they are so divergent instead of pooling them into a single reporting region as in Wilmot et al. (1992).

These factors (expanded geographic and temporal coverage of populations, addition of new markers, and changes in reporting regions) has led to great improvement in the mixture model. Each of the reporting groups in the updated baseline performed at or near the 90% level; while the mean correct allocations for reporting regions in the Wilmot et al. (1992) baseline was generally below 90%.

We used two simulation studies to evaluate the baseline. The first created simulated mixtures composed of 100% of the reporting region under evaluation. Mean allocation from simulated mixtures should be close to 100%; our threshold for a reporting region is a mean contribution of 90% (the expected is 100%). This analysis also shows where misallocation occurs.

Based on the simulation study, the following stock groups can be identified in mixtures using the 90% criteria: Lower summer, Upper Fall Tanana, White River, and Teslin River. If Toklat River and Upper Fall Tanana are combined into a Fall Tanana reporting group and Sheenjek/Chandalar and Fishing Branch/Mainstem are combined a single reporting group, these also become identifiable in mixtures. Middle summer had a correct allocation of 85%; however it is difficult to determine how to expand this reporting region. Misallocation was almost equivalent to summer and fall run reporting groups.

The second simulation study evaluated realistic mixtures that could be observed in District 1 fisheries. For these simulations, if a reporting region had a c.v. of less than 50%, we interpreted that this reporting region could be detected in mixtures using a 95% confidence interval (Marlowe and Busack 1995). Using this criterion, these simulations showed that a reporting region needed to comprise approximately 20% of a mixture to be detected.

In summary, significant heterogeneity exists among populations of Yukon River chum salmon. These differences can be used to identify the following stock groups in mixtures: 1) Lower Summer; 2) Fall Tanana; 3) Chandalar/Sheenjek/Fishing Branch/Canadian Mainstem; 4) White River; and 5) Teslin River. The Middle Summer stock grouping did not perform at quite the same level of accuracy and precision due to intermediate allele frequencies between the Lower Summer and fall stock groups. The presence of particular stock groupings can generally be detected in a mixture if that stock group forms greater than 20% of the mixture.

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Table 1. Sampling location, year collected, sample size, and source of data of populations used in genetic stock identification studies on the Yukon River. Non-italicized populations have been added to the baseline presented in Wilmot et al. (1992, italicized populations).

Location	Year	N	Source of Data
Summer Run			
Andreafsky	*1987*	*150*	*Wilmot et al. 1994*
(1) Andreafsky, East Fork	1993	100	Seeb and Crane 1999
(2) Andreafsky, West Fork	1993	100	Seeb and Crane 1999
Chulinak	*1989*	*100*	*Wilmot et al. 1994*
(3) Innoko	1993	88	ADF&G, this report
Anvik			
Anvik Mainstem	*1987*	*150*	*Wilmot et al. 1994*
Anvik Mainstem	*1988*	*100*	*Wilmot et al. 1994*
(4) Beaver	1992	100	Seeb and Crane 1999
Beaver	1993	100	Seeb and Crane 1999
(5) Yellow	1992	100	Seeb and Crane 1999
(6) Swift	1992	100	Seeb and Crane 1999
Swift	1993	100	Seeb and Crane 1999
(7) Otter	1993	100	Seeb and Crane 1999
(8) Canyon	1993	50	Seeb and Crane 1999
Rodo	*1989*	*78*	*Wilmot et al. 1994*
(9) Kaltag	1992	100	USFWS, this report
Nulato, Main	*1987*	*61*	*Wilmot et al. 1994*
Nulato, South Fork	*1987*	*71*	*Wilmot et al. 1994*
Nulato, North Fork	*1988*	*50*	*Wilmot et al. 1994*
(10) Nulato	1994	100	ADF&G, this report
Koyukuk			
Gisasa	*1989*	*97*	*Wilmot et al. 1994*
(11) Gisasa	1994	100	ADF&G, this report
(12) Dakli	1992	100	USFWS, this report
(13) Huslia	1993	100	Seeb and Crane 1999
(14) Clear	1995	100	ADF&G, this report
Henshaw	*1987*	*43*	*Wilmot et al. 1994*
(15) Henshaw	1995	62	ADF&G, this report
South Fork Early	*1990*	*75*	*Wilmot et al. 1994*
South Fork Late	*1990*	*75*	*Wilmot et al. 1994*
(16) South Fork Late	1995	100	ADF&G, this report
Jim River	*1987*	*101*	*Wilmot et al. 1994*
(17) Melozitna	1994	100	ADF&G, this report
Tozitna	*1990*	*85*	*Wilmot et al. 1994*
(18) Tozitna	1992	71	USFWS, this report
Tanana			
(19) Chena	1992	87	Seeb and Crane 1999
Chena	1994	100	ADF&G, this report
Salcha	*1988*	*50*	*Wilmot et al. 1994*
Salcha	*1989*	*50*	*Wilmot et al. 1994*

Table 1. Continued.

Location	Year	N	Source of Data
Fall Run			
Tanana			
Toklat	*1987*	*135*	*Wilmot et al. 1994*
Toklat	*1990*	*75*	*Wilmot et al. 1994*
(21) Toklat	1991	60	Seeb and Crane 1999
Toklat	1992	155	Seeb and Crane 1999
Toklat, Sushana	1993	200	ADF&G, this report
Toklat, Sushana	1994	100	Sarafin 1995
Toklat, Geiger Creek	1994	100	Sarafin 1995
Toklat, Mainstream	1994	100	Sarafin 1995
Toklat, Downstream Geiger Geek	1994	100	Sarafin 1995
Delta	*1987*	*135*	*Wilmot et al. 1994*
Delta	*1990*	*75*	*Wilmot et al. 1994*
(22) Delta	1991	100	Seeb and Crane 1999
Delta	1992	100	Seeb and Crane 1999
Delta	1994	100	ADF&G, this report
Bluff	*1987*	*135*	*Wilmot et al. 1994*
(23) Bluff	1992	100	Seeb and Crane 1999
(24) Tanana Mainstem	1992	97	ADF&G, this report
Tanana Mainstem	1993	100	ADF&G, this report
Chandalar	*1987*	*150*	*Wilmot et al. 1994*
Chandalar	*1988*	*73*	*Wilmot et al. 1994*
Chandalar	*1989*	*75*	*Wilmot et al. 1994*
Porcupine			
Sheenjek	*1987*	*135*	*Wilmot et al. 1994*
Sheenjek	*1988*	*80*	*Wilmot et al. 1994*
Sheenjek	*1989*	*80*	*Wilmot et al. 1994*
(25) Sheenjek	1992	100	Seeb and Crane 1999
Sheenjek	1993	63	Seeb and Crane 1999
Fishing Branch	*1987*	*129*	*Wilmot et al. 1994*
Fishing Branch	*1989*	*50*	*Wilmot et al. 1994*
(26) Fishing Branch	1992	100	USFWS, this report
Fishing Branch	1994	100	ADF&G, this report
(27) Pelly	1993	84	ADF&G, this report
Big	*1987*	*70*	*Wilmot et al. 1994*
(28) Big	1992	100	USFWS, this report
Big	1994	100	ADF&G, this report
Minto	*1989*	*100*	*Wilmot et al. 1994*
Tatchun	*1987*	*75*	*Wilmot et al. 1994*
(29) Tatchun	1992	98	USFWS, this report
White			
Kluane	*1987*	*135*	*Wilmot et al. 1994*
(30) Kluane	1992	100	USFWS, this report
(31) Donjek	1994	70	ADF&G, this report
Teslin	*1989*	*95*	*Wilmot et al. 1994*
(32) Teslin	1992	99	USFWS, this report

Table 2. G-statistic analysis testing allele frequency heterogeneity among multiple-year collections sampled at the same location adjusted for multiple tests (Rice 1989).

Population	G-Statistic	df	*P*	Critical Value
Salcha River	91.18	60	0.006	0.002
Teslin River	31.39	16	0.012	0.003
Kluane River	30.73	16	0.015	0.003
Gisasa River	39.37	23	0.018	0.003
Henshaw Creek	30.94	18	0.029	0.003
E. Fork Andreafsky River	29.9	19	0.053	0.003
Tatchun River	25.69	16	0.059	0.003
Tozitna River	29.82	20	0.073	0.004
Bluff Cabin Slough	26	17	0.075	0.004
Fishing Branch	67.34	54	0.105	0.004
Beaver Creek	28.52	21	0.126	0.005
Sheenjek River	84.49	72	0.149	0.005
Toklat River	177.77	160	0.160	0.006
Chandalar River	43.17	36	0.192	0.006
Swift River	27.62	23	0.230	0.007
Tanana River Mainstem	20.32	18	0.315	0.008
S.Fork Koyukuk River (Late)	22.02	20	0.339	0.010
Big Creek	30.92	32	0.521	0.013
Chena River	17.04	19	0.587	0.017
Delta River	66.88	72	0.649	0.025
Nulato River	62.13	69	0.708	0.050

Table 3. G-statistic analysis testing allele frequency heterogeneity at different hierarchical levels for chum salmon populations sampled in the Yukon River.

Populations	DF	*sAAT-1,2**	DF	*mAAT-1**	DF	*mAH-3**	DF	*ALAT**	DF	*ESTD**	DF	*G3PDH-2**
Among	32	40.90	32	62.68	16	924.28	32	188.46	16	545.29	16	105.90
Within	42	50.91	42	81.75	21	223.41	42	50.52	21	173.81	21	35.84
Andreafsky River	2	0.09	2	1.72	1	0.16	2	4.23	1	0.13	1	2.49
Anvik River	8	4.85	8	7.40	4	5.47	8	4.36	4	1.10	4	6.21
Koyukuk River	14	10.81	14	41.44	7	143.90	14	21.23	7	6.16	7	11.97
Among	2	6.97	2	10.74	1	137.90	2	7.09	1	3.95	1	6.44
Within	12	3.84	12	30.70	6	5.98	12	14.13	6	2.21	6	5.52
Early Run	6	2.18	6	2.91	3	2.24	6	8.45	3	1.11	3	2.71
Late Run	6	1.66	6	27.79	3	3.74	6	5.68	3	1.10	3	2.81
Tanana River	10	25.97	10	27.75	5	71.82	10	16.86	5	162.80	5	13.74
Among	2	21.04	2	11.49	1	2.41	2	7.69	1	145.30	1	0.03
Within	8	4.92	8	16.25	4	69.41	8	9.16	4	17.52	4	13.69
Summer Run	2	0.15	2	3.03	1	1.43	2	0.00	1	1.87	1	4.81
Fall Run	6	4.77	6	13.22	3	67.98	6	9.16	3	15.65	3	8.88
Among	2	2.41	2	11.95	1	59.84	2	0.00	1	15.38	1	6.97
Within	4	2.36	4	1.27	2	8.13	4	9.16	2	0.27	2	1.90
Upper Tanana	4	2.36	4	1.27	2	8.13	4	9.16	2	0.27	2	1.90
Porcupine River	2	6.04	2	1.68	1	0.00	2	0.86	1	1.34	1	0.94
Canadian Mainstem	4	2.17	4	1.32	2	0.63	4	1.59	2	0.98	2	0.25
White River	2	0.98	2	0.44	1	1.43	2	1.39	1	1.30	1	0.24
Total	74	91.83	74	144.47	37	1147.70	74	239.00	37	719.17	37	141.75

Populations	DF	*GPI-B*1,2*	DF	*mIDHP-1**	DF	*sIDHP-2**	DF	*LDH-A1**	DF	*LDH-B2**	DF	*sMDH-A1**
Among	16	11.06	32	136.32	48	362.11	32	254.67	32	11.31	32	143.94
Within	21	11.51	42	90.97	63	90.15	42	45.72	42	5.04	42	49.79
Andreafsky River	1	0.00	2	2.58	3	0.12	2	0.43	2	0.00	2	5.08
Anvik River	4	2.35	8	3.59	12	19.48	8	6.08	8	3.32	8	10.36
Koyukuk River	7	4.48	14	16.06	21	27.76	14	9.82	14	0.00	14	18.81
Among	1	0.26	2	0.56	3	5.42	2	2.49	2	0.00	2	3.86
Within	6	4.21	12	15.49	18	22.33	12	7.32	12	0.00	12	14.94
Early Run	3	2.30	6	9.49	9	8.48	6	2.39	6	0.00	6	11.23
Late Run	3	1.91	6	6.00	9	13.85	6	4.93	6	0.00	6	3.71
Tanana River	5	4.68	10	67.45	15	37.32	10	26.80	10	1.72	10	5.33
Among	1	3.22	2	7.73	3	4.65	2	3.22	2	0.44	2	0.24
Within	4	1.45	8	59.72	12	32.66	8	23.58	8	1.28	8	5.07
Summer Run	1	1.45	2	10.83	3	1.85	2	0.57	2	0.00	2	1.66
Fall Run	3	0.00	6	48.89	9	30.81	6	23.01	6	1.28	6	3.41
Among	1	0.00	2	47.32	3	27.42	2	18.08	2	1.28	2	2.30
Within	2	0.00	4	1.57	6	3.38	4	4.93	4	0.00	4	1.11
Upper Tanana	2	0.00	4	1.57	6	3.38	4	4.93	4	0.00	4	1.11
Porcupine River	1	0.00	2	1.29	3	2.80	2	2.53	2	0.00	2	7.85
Canadian Mainstem	2	0.00	4	0.00	6	2.59	4	0.05	4	0.00	4	2.07
White River	1	0.00	2	0.00	3	0.08	2	0.01	2	0.00	2	0.29
Total	37	22.58	74	227.30	111	452.28	74	300.42	74	16.36	74	193.75

Table 3. Continued.

Populations	DF	*sMDH-B1,2**	DF	*mMEP-2**	DF	*MPI**	DF	*PEPA**	DF	*PEPB-1**	DF	*PEPLT**
Among	80	119.48	16	390.70	16	124.94	16	64.00	48	371.61	32	133.36
Within	105	108.90	21	59.50	21	25.65	21	14.35	63	81.13	42	44.57
Andreafsky River	5	0.69	1	0.07	1	1.91	1	4.72	3	2.24	2	0.18
Anvik River	20	9.66	4	10.30	4	4.64	4	2.66	12	11.48	8	12.19
Koyukuk River	35	36.05	7	33.90	7	4.45	7	6.97	21	28.27	14	18.19
Among	5	14.57	1	31.88	1	0.09	1	5.18	3	17.49	2	6.05
Within	30	21.48	6	2.01	6	4.35	6	1.79	18	10.77	12	12.13
Early Run	15	7.54	3	0.27	3	1.52	3	1.79	9	5.50	6	2.80
Late Run	15	13.94	3	1.74	3	2.83	3	0.00	9	5.27	6	9.33
Tanana River	25	60.82	5	3.99	5	8.77	5	0.00	15	28.48	10	11.11
Among	5	46.60	1	1.73	1	1.74	1	0.00	3	6.89	2	0.30
Within	20	14.21	4	2.25	4	7.03	4	0.00	12	21.58	8	10.80
Summer Run	5	0.99	1	0.16	1	0.30	1	0.00	3	14.46	2	0.54
Fall Run	15	13.22	3	2.09	3	6.73	3	0.00	9	7.12	6	10.26
Among	5	10.09	1	0.23	1	5.20	1	0.00	3	6.33	2	8.70
Within	10	3.13	2	1.86	2	1.53	2	0.00	6	0.78	4	1.55
Upper Tanana	10	3.13	2	1.86	2	1.53	2	0.00	6	0.78	4	1.55
Porcupine River	5	1.20	1	0.59	1	2.97	1	0.00	3	5.63	2	1.05
Canadian Mainstem	10	0.00	2	4.94	2	2.09	2	0.00	6	3.08	4	0.24
White River	5	0.48	1	5.71	1	0.82	1	0.00	3	1.95	2	1.61
Total	185	228.40	37	450.23	37	150.63	37	78.37	111	452.77	74	177.94

Populations	DF	*PGDH**	DF	*TPI-1**	DF	Overall	*P*
Among	16	84.61	16	6.44	576	4082.10	0.000
Within	21	26.18	21	0.00	756	1270.11	0.000
Andreafsky River	1	1.89	1	0.00	36	28.81	0.797
Anvik River	4	2.62	4	0.00	144	128.20	0.823
Koyukuk River	7	2.32	7	0.00	252	442.60	0.000
Among	1	0.07	1	0.00	36	261.10	0.000
Within	6	2.24	6	0.00	216	181.53	0.958
Early Run	3	0.26	3	0.00	108	73.23	0.996
Late Run	3	1.98	3	0.00	108	108.30	0.473
Tanana River	5	16.55	5	0.00	180	592.00	0.000
Among	1	0.15	1	0.00	36	264.90	0.000
Within	4	16.39	4	0.00	144	327.05	0.000
Summer Run	1	0.08	1	0.00	36	44.25	0.163
Fall Run	3	16.31	3	0.00	108	282.80	0.000
Among	1	16.12	1	0.00	36	239.60	0.000
Within	2	0.19	2	0.00	72	43.19	0.997
Upper Tanana	2	0.19	2	0.00	72	43.19	0.997
Porcupine River	1	2.12	1	0.00	36	38.98	0.337
Canadian Mainstem	2	0.14	2	0.00	72	22.18	1.000
White River	1	0.54	1	0.00	36	17.34	0.996
Total	37	110.82	37	6.44	1332	5352.20	0.000

Table 4. Gene diversity analysis (Nei 1973) of Yukon River chum salmon partitioning genetic variation into within-population, among population within runtime, between runtimes within tributary, and among tributary levels.

Locus	Within Population	Among population within runtime	Between runtimes within tributary	Among tributary
*sAAT-1,2**	0.9973	0.0003	0.0014	0.0010
*mAAT-1**	0.9938	0.0014	0.0019	0.0030
*mAH-3**	0.9013	0.0019	0.0182	0.0787
*ALAT**	0.9829	0.0020	0.0026	0.0125
*ESTD**	0.9612	0.0006	0.0070	0.0312
*G3PDH-2**	0.9896	0.0012	0.0022	0.0070
*GPI-B1,2**	0.9983	0.0007	0.0003	0.0007
*mIDHP-1**	0.9846	0.0058	0.0027	0.0069
*sIDHP-2**	0.9865	0.0013	0.0013	0.0109
*LDH-A1**	0.9743	0.0013	0.0016	0.0228
*LDH-B2**	0.9963	0.0000	0.0025	0.0012
*sMDH-A1**	0.9874	0.0013	0.0017	0.0096
*sMDH-B1,2**	0.9940	0.0016	0.0021	0.0023
*mMEP-2**	0.9680	0.0003	0.0072	0.0246
*MPI**	0.9872	0.0007	0.0017	0.0105
*PEPA**	0.9803	0.0002	0.0013	0.0182
*PEPB-1**	0.9791	0.0015	0.0023	0.0171
*PEPLT**	0.9830	0.0014	0.0017	0.0140
*PGDH**	0.9936	0.0006	0.0006	0.0052
*TPI-1**	0.9983	0.0000	0.0000	0.0017
Overall	0.9694	0.0012	0.0050	0.0243

Table 5. Mean estimates of 100 simulations where each mixture (N=400) is composed 100% of each reporting region. Standard deviations are given in square brackets. Shaded cells should equal 100%. a. Simulation results from the updated baseline; b. Simulation results for the Wilmot et al. (1992) baseline.

a. Updated baseline

	Mixture									
Regional Allocation	Lower Summer	Middle Summer	Toklat	Upper Fall Tanana	Sheenjek/ Chandalar		Fish. Branch/ Mainstem		White	Teslin
Lower Summer	0.95 [0.03]	0.05 [0.04]	0.01 [0.02]	0.00 [0.01]	0.01	[0.01]	0.01	[0.02]	0.00 [0.00]	0.02 [0.01]
Middle Summer	0.03 [0.03]	0.85 [0.06]	0.04 [0.05]	0.01 [0.02]	0.03	[0.03]	0.01	[0.01]	0.00 [0.01]	0.01 [0.01]
Fall Tanana	0.01 [0.01]	0.04 [0.04]	0.91 [0.06]	0.93 [0.05]	0.03	[0.04]	0.01	[0.02]	0.01 [0.01]	0.00 [0.00]
Toklat	0.00 [0.01]	0.03 [0.04]	0.88 [0.08]	0.02 [0.04]	0.02	[0.03]	0.00	[0.01]	0.00 [0.00]	0.00 [0.00]
Upper Fall Tanana	0.00 [0.01]	0.01 [0.02]	0.03 [0.05]	0.91 [0.05]	0.02	[0.03]	0.01	[0.02]	0.01 [0.01]	0.00 [0.00]
Border	0.01	[0.01]	0.04 [0.04]	0.03 [0.04]	0.03 [0.04]	0.92	[0.01]	0.93	[0.00]	0.03 [0.03]	0.03 [0.03]
Sheenjek/Chandalar	0.00 [0.01]		0.02 [0.03]	0.02 [0.03]	0.01 [0.02]	0.81	[0.10]	0.09	[0.09]	0.01 [0.02]	0.00 [0.00]
Fishing Branch/Mainstem	0.00	[0.01]	0.03 [0.03]	0.01 [0.02]	0.02 [0.03]	0.11	[0.09]	0.83	[0.1]	0.02 [0.03]	0.03 [0.03]
White	0.00 [0.00]		0.01 [0.01]	0.00 [0.01]	0.02 [0.02]	0.01	[0.02]	0.02	[0.02]	0.96 [0.03]	0.00 [0.01]
Teslin	0.01 [0.01]		0.01 [0.01]	0.00 [0.01]	0.00 [0.01]	0.00	[0.01]	0.02	[0.02]	0.00 [0.00]	0.95 [0.03]

b. Wilmot et al. (1992) baseline

	Mixture								
Regional Allocation	Lower Summer	Middle Summer	Fall Tanana	Sheenjek/ Chandalar		Fish. Branch/ Mainstem		Teslin/ Kluane
Lower Summer	0.84 [0.07]	0.14 [0.08]	0.02 [0.03]	0.03	[0.03]	0.02	[0.03]	0.01 [0.01]
Middle Summer	0.11 [0.07]	0.75 [0.09]	0.03 [0.03]	0.04	[0.05]	0.02	[0.03]	0.02 [0.03]
Fall Tanana	0.02 [0.03]	0.03 [0.04]	0.88 [0.06]	0.03	[0.04]	0.06	[0.06]	0.01 [0.01]
Sheenjek/Chandalar	0.01 [0.02]	0.03 [0.03]	0.01 [0.02]	0.75	[0.11]	0.07	[0.07]	0.01 [0.03]
Fishing Branch/Mainstem	0.02 [0.02]	0.04 [0.04]	0.05 [0.06]	0.11	[0.09]	0.81	[0.11]	0.03 [0.04]
Teslin/Kluane	0.01 [0.01]	0.02 [0.02]	0.02 [0.02]	0.03	[0.03]	0.02	[0.03]	0.92 [0.05]

Table 6. Mean estimates derived from 100 simulations for simulated realistic stock compositions. Estimates for individual stock estimates were summed into three hierarchical levels.

		Observed		
Mixture 1	Expected	mean	std. dev.	c.v
Lower Summer	0.73	0.72	0.06	0.08
Middle Summer	0.16	0.15	0.07	0.46
Toklat	0.00	0.01	0.02	2.28
Upper Tanana Fall	0.00	0.01	0.02	2.04
Chandalar/Sheenjek	0.03	0.03	0.04	1.20
Fishing Branch/Mainstem	0.04	0.04	0.05	1.01
White	0.02	0.02	0.02	1.20
Teslin	0.02	0.02	0.02	1.08
Lower Summer	0.73	0.72	0.06	0.08
Middle Summer	0.16	0.15	0.07	0.46
Fall Tanana	0.00	0.02	0.03	1.49
Border	0.07	0.08	0.05	0.64
White	0.02	0.02	0.02	1.20
Teslin	0.02	0.02	0.02	1.08
Summer	0.89	0.86	0.05	0.06
Fall	0.11	0.14	0.05	0.37

		Observed		
Mixture 2	Expected	mean	std. dev.	c.v.
Lower Summer	0.09	0.10	0.03	0.36
Middle Summer	0.04	0.06	0.05	0.79
Toklat	0.01	0.02	0.03	1.72
Upper Tanana Fall	0.02	0.03	0.04	1.47
Chandalar/Sheenjek	0.30	0.32	0.13	0.39
Fishing Branch/Mainstem	0.48	0.42	0.13	0.31
White	0.03	0.03	0.03	1.01
Teslin	0.03	0.03	0.03	0.84
Lower Summer	0.09	0.10	0.03	0.37
Middle Summer	0.04	0.06	0.05	0.79
Fall Tanana	0.03	0.04	0.04	0.98
Border	0.78	0.74	0.07	0.10
White	0.03	0.03	0.03	1.01
Teslin	0.03	0.03	0.03	0.83
Summer	0.13	0.15	0.05	0.34
Fall	0.87	0.85	0.05	0.06

		Observed		
Mixture 3	Expected	mean	std. dev.	c.v.
Lower Summer	0.03	0.03	0.02	0.71
Middle Summer	0.01	0.04	0.04	1.04
Toklat	0.06	0.05	0.06	1.12
Upper Tanana Fall	0.16	0.16	0.08	0.47
Chandalar/Sheenjek	0.36	0.35	0.13	0.38
Fishing Branch/Mainstem	0.36	0.33	0.14	0.42
White	0.01	0.02	0.03	1.36
Teslin	0.01	0.02	0.02	1.34
Lower Summer	0.03	0.03	0.02	0.71
Middle Summer	0.01	0.04	0.04	1.04
Fall Tanana	0.22	0.21	0.07	0.34
Border	0.72	0.68	0.08	0.12
White	0.01	0.02	0.03	1.36
Teslin	0.01	0.02	0.02	1.34
Summer	0.04	0.07	0.04	0.57
Fall	0.96	0.93	0.04	0.04

		Observed		
Mixture 4	Expected	mean	std. dev.	c.v.
Lower Summer	0.00	0.01	0.02	1.55
Middle Summer	0.00	0.03	0.03	1.08
Toklat	0.17	0.16	0.08	0.49
Upper Tanana Fall	0.44	0.42	0.09	0.20
Chandalar/Sheenjek	0.25	0.22	0.10	0.46
Fishing Branch/Mainstem	0.13	0.14	0.10	0.73
White	0.00	0.01	0.02	1.42
Teslin	0.00	0.01	0.01	1.92
Lower Summer	0.00	0.01	0.02	1.55
Middle Summer	0.00	0.03	0.03	1.07
Fall Tanana	0.62	0.58	0.08	0.13
Border	0.38	0.36	0.07	0.20
White	0.00	0.01	0.02	1.42
Teslin	0.00	0.01	0.01	1.92
Summer	1.00	0.96	0.04	0.04
Fall	0.00	0.04	0.04	0.85

Table 6. Continued.

		Observed		
Mixture 5	Expected	mean	std. dev.	c.v.
Lower Summer	0.20	0.21	0.05	0.24
Middle Summer	0.34	0.30	0.09	0.30
Toklat	0.05	0.06	0.06	1.14
Upper Tanana Fall	0.29	0.28	0.07	0.24
Chandalar/Sheenjek	0.03	0.04	0.05	1.21
Fishing Branch/Mainstem	0.03	0.07	0.06	0.94
White	0.03	0.03	0.03	1.02
Teslin	0.03	0.03	0.03	0.88
Lower Summer	0.20	0.21	0.05	0.24
Middle Summer	0.34	0.30	0.09	0.30
Fall Tanana	0.34	0.33	0.07	0.22
Border	0.06	0.11	0.07	0.64
White	0.03	0.02	0.03	1.09
Teslin	0.03	0.03	0.03	0.88
Summer	0.54	0.50	0.08	0.15
Fall	0.46	0.50	0.08	0.15

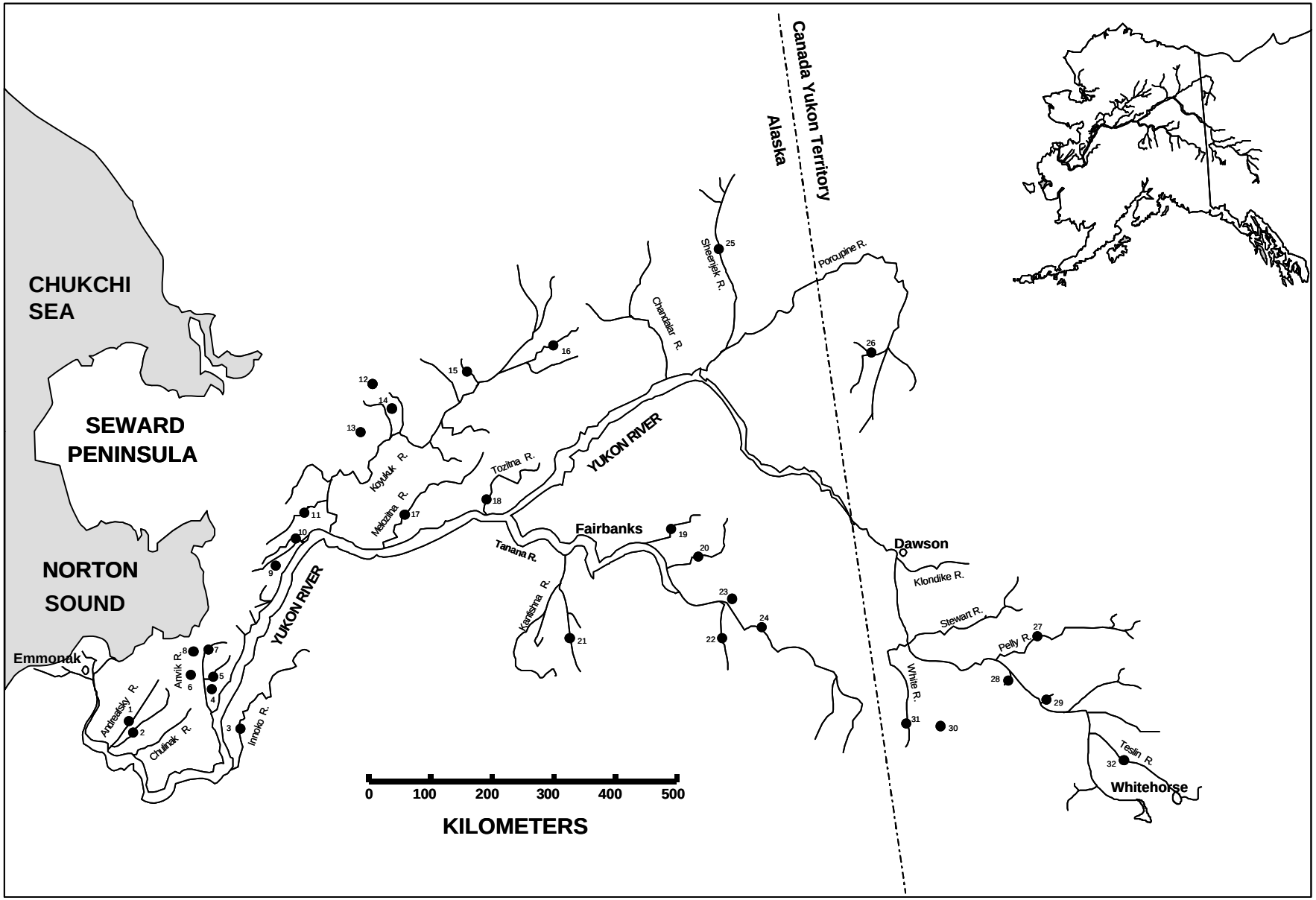

Figure 1. Approximate sampling locations of chum salmon collected in the Yukon River for genetic analysis. Numbers correspond to those in Table 1.

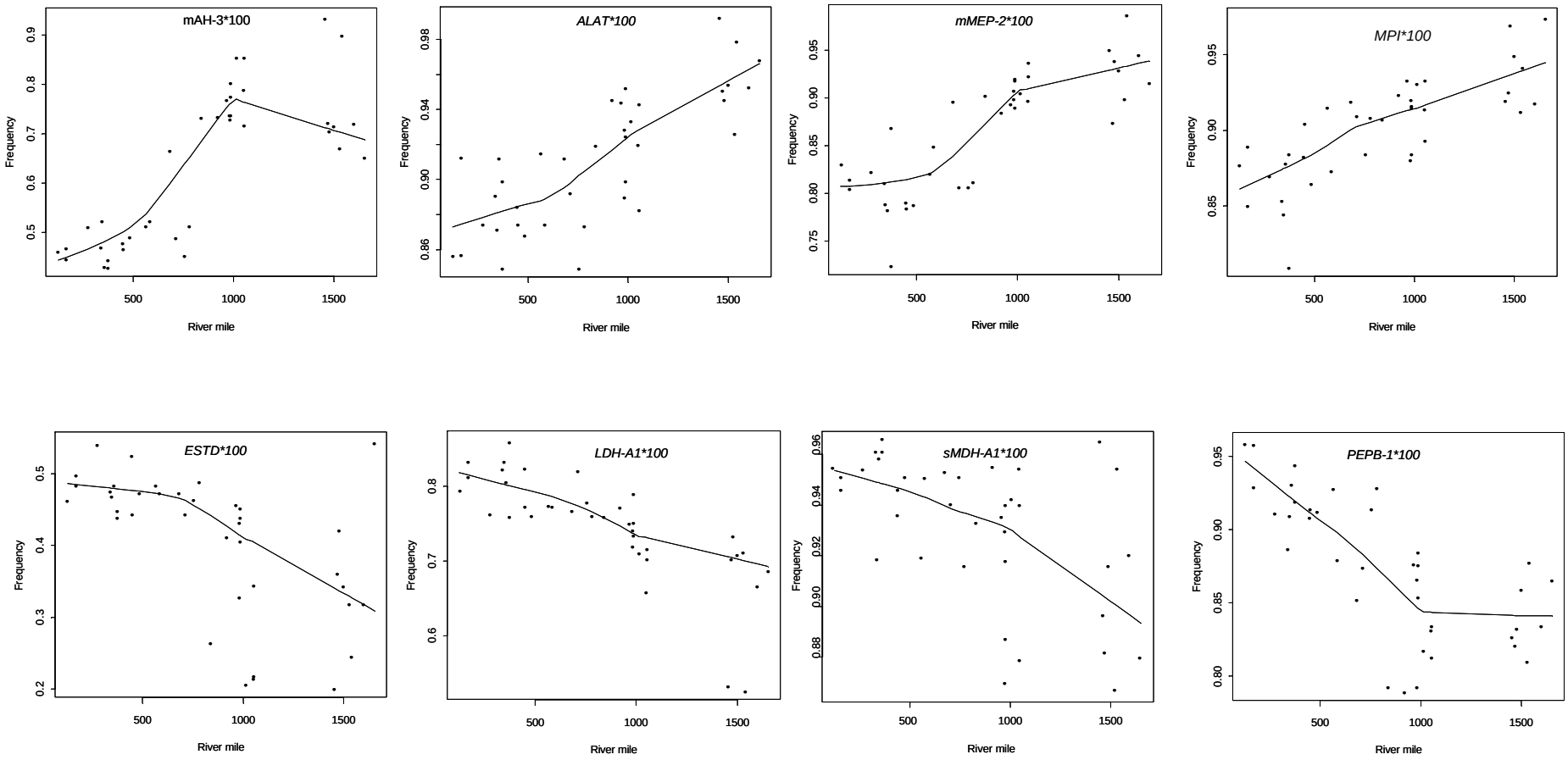

Figure 2. Relationship between rivermile and frequency of the *100 allele for eight allozyme loci surveyed in collections of chum salmon from the Yukon River.

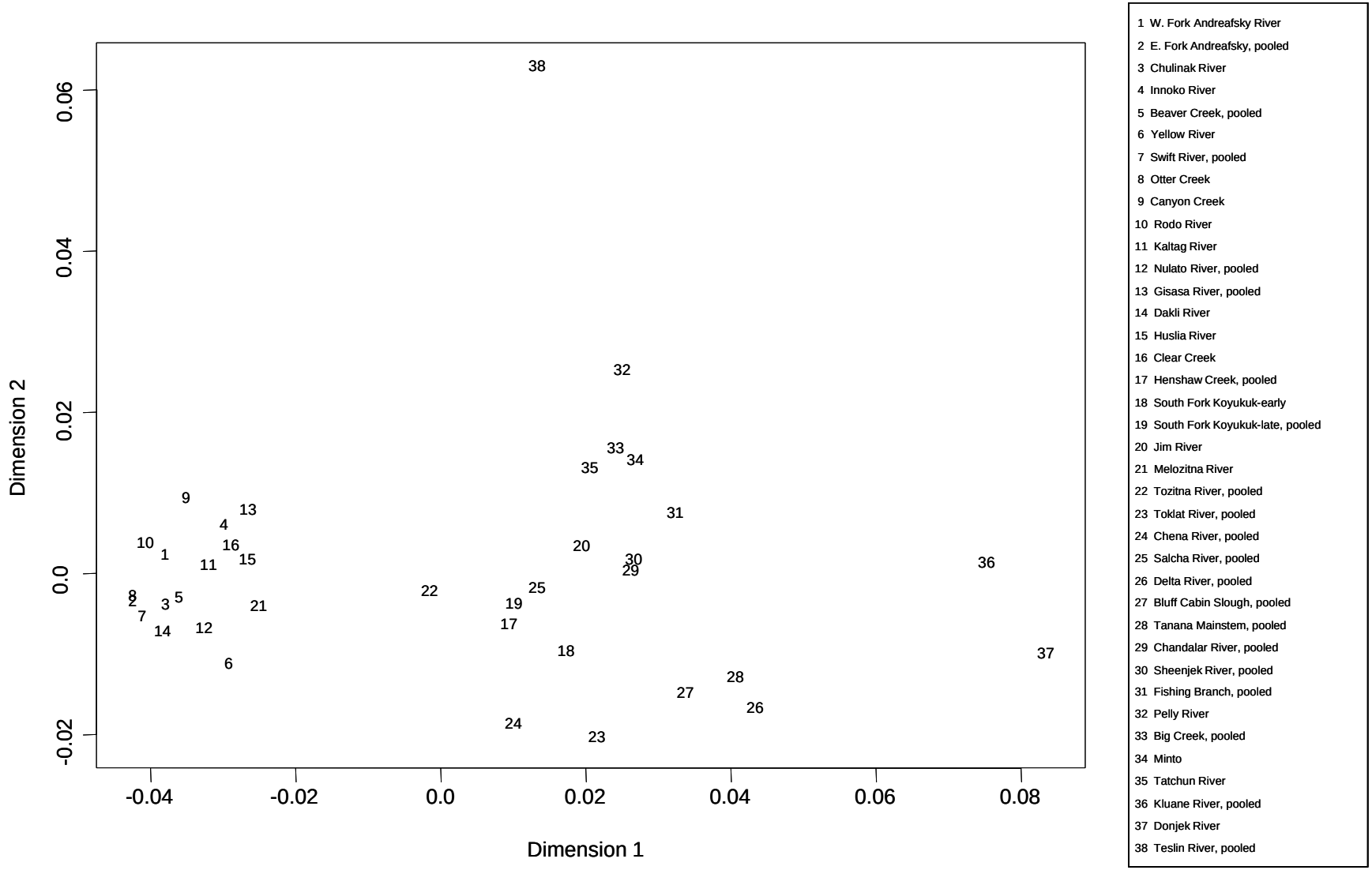

Figure 3. Metric multi dimensional scaling analysis of chum salmon populations sampled in the Yukon River. Cavalli-Sforza and Edwards chord distances (Cavalli-Sforza and Edwards 1967) were used.

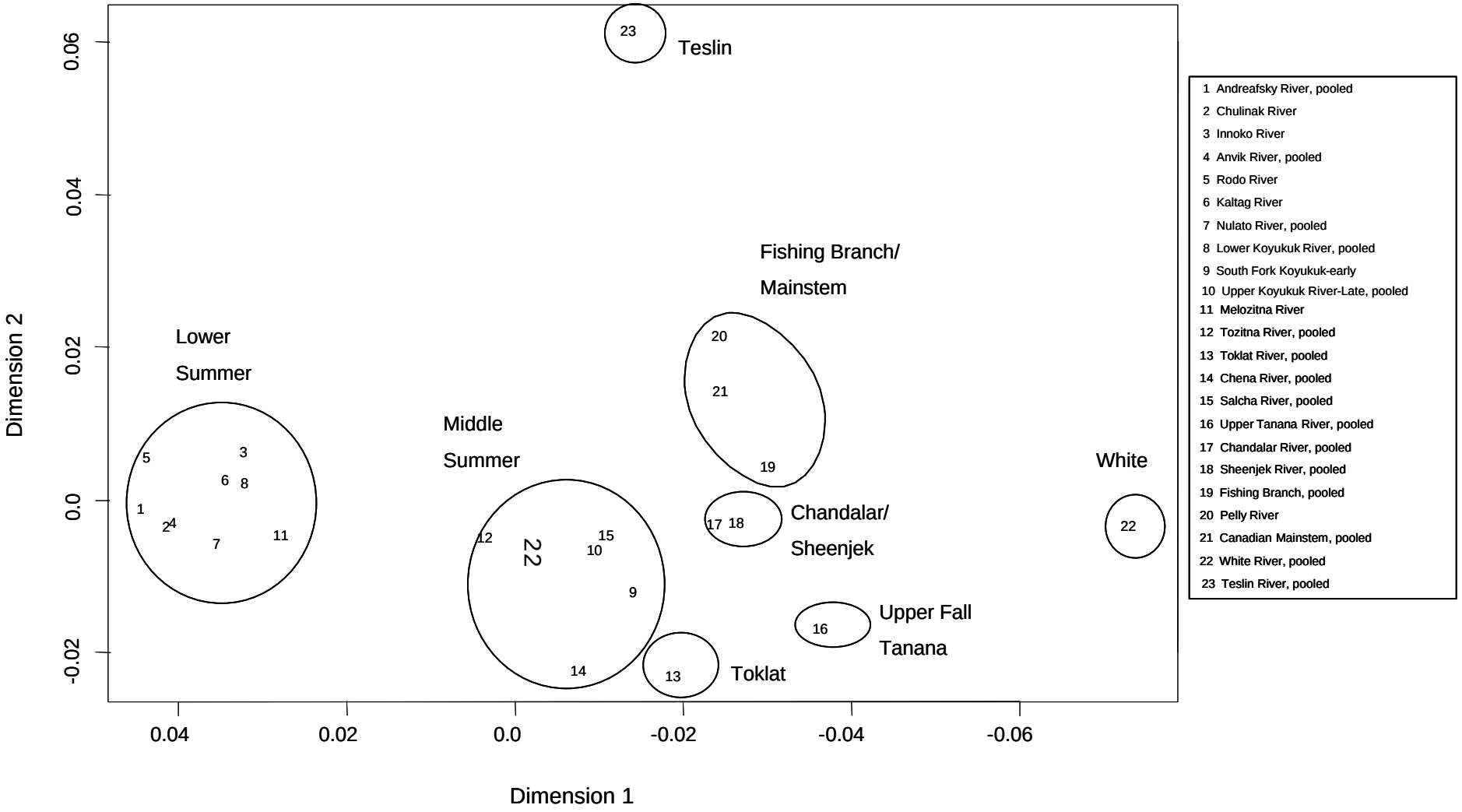

Figure 4. Metric multidimensional scaling analysis of updated chum salmon baseline used to select reporting regions for simulation studies.