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Yukon River Coho Salmon microsatellite baseline

Final Report for Study 14-206

Blair Flannery and Randal Loges

U.S. Fish and Wildlife Service
Conservation Genetics Laboratory
1011 E. Tudor Rd.
Anchorage, Alaska 99503
U.S.A.

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Abstract

Yukon River coho salmon exhibit a high degree of geographically based genetic structure (G_{ST}=0.078), with a strong genetic disjunction between lower and upper river populations. Analyses involving simulated and real mixtures indicate that this level of divergence can be used to accurately (95%–100%) apportion coho salmon to regions and areas. Stock composition estimates for the test fishery indicated that the spawning migration was evenly divided (50:50) between the lower and upper river populations. Upper river populations generally had earlier migration timing, comprising 66% of the mixture in the beginning and 33% at the end. There was variability within region to the general statement. For example, coho salmon from the Porcupine River arrived at the end of the migration. The largest component of the upper river region was Tanana at 44%, followed by the Nenana at 5%, and the Porcupine at 1%.

Key Words: coho salmon, Yukon River, mixed-stock analysis, microsatellites.

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Introduction

Implicit in fisheries management is a thorough knowledge of the biology of the species being harvested. Most Pacific salmon (*Oncorhynchus* spp.) are harvested when populations are mixed together, which creates problems for fisheries managers who attempt to achieve sustained yields by balancing harvest and escapement across populations. Knowledge of the population composition in many fisheries is imprecise and not directly measured. If exploitation is significant, then harvest without accounting for genetic consequences can change population parameters through differential harvest within and among populations and result in lost genetic diversity and decreased production (Allendorf et al. 1987). Long term sustained yield, ultimately the goal of fishery management, can only be accomplished through conservation of genetic resources to maintain diversity and a population's adaptive potential in the face of a fluctuating environment (Altukhov and Salmenkova 1987; Nelson and Soule 1987). To bring about effective conservation, the population structure and productivity of the species must be known in order to regulate fisheries to allow optimum escapement of each population. This is a difficult proposition, given the multi-population nature of the fisheries, but one that is possible with genetic mixed-stock analysis (MSA; Pella and Milner 1987).

Coho salmon are distributed in North America from Monterey, California to Point Hope, Alaska and in Asia from North Korea to the Anadyr River in Russia (Sandercock 1991). Like all Pacific salmon, coho salmon are anadromous, philopatric, and spawn semelparously. Fry emerge in the spring and spend one to two years in freshwater before migrating to saltwater to mature. The majority of coho salmon north of British Columbia return to spawn at age four whereas in the south age three is typical (Sandercock 1991). Most coho salmon spawn in coastal streams after short upstream migrations, but in large rivers they are known to migrate extensively, which has led to two migratory phenotypes, coastal and interior. The coastal type has a larger body and fins while the interior type has a fusiform shape that is more efficient for long distance swimming. Although coho salmon do not have the broadest distribution, they exhibit a wide variety of life histories, which enables them to occupy the most variable spawning habitat of all salmon. Many small streams throughout the range support coho salmon. For example, within Southeast Alaska there are 5,000 known salmon streams, and coho salmon are in 4,000 of them, the most of all the salmon species, whereas Chinook salmon are in only 200 of the streams (Halupka et al. 2003). Colonizing marginal habitats can be risky and precludes many of the populations from attaining large census size, but the ability to adapt to and colonize new habitats, such as found in Glacier Bay, Alaska (Milner et al. 2000), and the sheer number of streams that coho salmon occupy appears to be a strategy to offset risk.

Coho salmon spawn throughout the Yukon River drainage, with known concentrations located in tributaries of the lower Yukon and Tanana rivers (McBride et al. 1983) and in the Canadian section of the Porcupine River (JTC 2011). Coho are believed to be negligible in the upper Yukon River due to lack of harvest in aboriginal, commercial, test, and recreational fisheries (JTC 2011; Elizabeth MacDonald, Department of Fisheries and Oceans Canada, personal communication). The late migration timing and onset of winter may prevent detection of coho salmon in the upper Yukon River. However, extensive collections of juvenile salmon from the upper Yukon River have failed to turn up any coho salmon (Wilmot et al. 1992; Daum 1994; Daum and Flannery 2011a; Daum and Flannery 2011b; Daum and Flannery 2012).

Coho salmon begin entering the Yukon River in late July to early August, largely coinciding with fall chum salmon. The similar run timing of coho and fall chum salmon complicates their management. The run size and subsistence demand for fall chum salmon is greater than coho salmon. Consequently, management focus is placed on fall chum salmon, and coho salmon are largely unmanaged and mostly taken as bycatch (Bue 2004). Data scarcity is a problem for Yukon River coho salmon. Escapement goals have only been set for the Delta Clearwater, with limited monitoring conducted in the Tanana River and at Pilot Station sonar. Moreover, with the recent decline in abundance of Yukon River Chinook salmon, the exploitation rate for coho salmon has increased dramatically, potentially subjecting coho salmon to differential harvest rates. From 1997−2010, an average of 29% of the Yukon River coho salmon run (as estimated by mainstem sonar) has been harvested, whereas since 2011, the average harvest has increased to 86% of the run (JTC 2014). The current lack of escapement, run timing, and stock composition data for coho salmon in the face of increased pressure is problematic.

Recent genetic studies (Olsen et al. 2004, 2011) of Yukon River coho salmon indicate that populations are highly divergent on a limited geographic scale, and that populations are generally small with little gene flow occurring among them, which can exacerbate the harmful effects of unmanaged harvests. These studies only analyzed eight microsatellite loci of inherently low variability, an average of four alleles per locus. Power for mixed-stock analysis (MSA) is directly related to the number of independent alleles (Kalinowski 2004). Therefore, we assayed variation at 19 microsatellite loci to: 1) evaluate patterns of genetic diversity within and among 14 putative coho salmon populations distributed throughout the Yukon River drainage; 2) provide estimates of the power of genetic data for use in MSA of Yukon River coho salmon; and 3) estimate the stock composition for Yukon River coho salmon from test fishery samples.

Methods

Sample collection and genetic analysis.—Fin clips were collected from 14 putative coho salmon populations within the Yukon River to form a genetic baseline (Table 1, Figure 1). Fin clips were also collected from coho salmon caught in the test fishery for the sonar project while on their spawning migration up the Yukon River from July 23, 2015 to August 31, 2015 (Table 1, Figure 1). The baseline included populations from the lower Yukon River, Tanana River, and Canadian Porcupine River (Figure 1, Table 1), so the major groups were represented. Total genomic DNA was extracted from the tissue (~25mg) using proteinase K with the Dneasy DNA isolation kit (Qiagen Inc., Valencia, CA). Concentrations of DNA were quantified by fluorometry and diluted to 30 ng/µl. The following micosatellite loci were amplified by polymerase chain reaction and assayed for genetic variation using the Applied Biosystems 3730 Genetic Analyzer: *Ocl8* (Condrey and Bentzen 1998); *Ogo2* (Olsen et al. 1998); *Omy1011* (Spies et al. 2005); *Oke2, Oke3, Oke4* (Buchholz et al. 2001); *Oki1, Oki3, Oki11* (Smith et al. 1998); *P53* (de Fromentel et al. 1992); *One3, One13* (Scribner et al. 1996); *Ots2m* (Grieg and Banks 1999); *Ots101, Ots103* (Small et al. 1998); *Ots105* (Nelson 1998); *Ots213* (Grieg et al. 2003); *OtsG422* (Williamson et al. 2002); and *Ssa407* (Cairney et al. 2000).

Data analysis.—Hardy-Weinberg and gametic phase equilibrium were analyzed for the loci and populations using the program FSTAT 2.9.3 (Goudet 1995). Juvenile samples were analyzed for

relatedness using the Queller and Goodnight (1989) method implemented in the program IDENTIX (Belkhir et al. 2002). These tests were done to determine if the samples represent randomly mating, Mendelian populations. The alpha was corrected to maintain a type I error rate of 0.05 for multiple tests of the same hypothesis by the sequential Bonferroni method (Rice 1989). Estimates of genetic diversity including allelic richness, percentage polymorphic loci (95%), observed and expected heterozygosity, and gene differentiation (G_{ST}) were calculated for loci and populations with FSTAT 2.9.3 and GENETIX 4.05 (Belkhir et al. 2004). Microsoft Excel was used to calculate estimates of the effective number of alleles. The diversity values for populations from the lower and upper regions of the Yukon River were tested for statistical differences ($P < 0.05$) by a one-tailed Mann-Whitney test.

Chord distances (Cavalli-Sforza and Edwards 1967) were calculated among all population pairs from allele frequencies by the program POPULATIONS 1.2.32 (Langella 1999), with loci bootstrapped 1,000 times. A neighbor-joining (Saitou and Nei 1987) dendrogram was constructed from the chord distances by TreeExplorer 2.12 (Tamura 1999). Standard linear regression was conducted on pairwise matrices of genetic (F_{ST}) and geographic (river kilometer) distances to assess whether isolation-by-distance (IBD; Wright 1943) existed among the populations overall and within and between regions. The Mantel test (Mantel 1967), performed in FSTAT 2.9.3 with 10,000 randomizations, determined whether the two matrices were significantly correlated.

Homogeneity among populations within areas, among areas within regions, and between regions was examined by likelihood ratio tests of allelic frequencies (*G*-test; Sokal and Rohlf 1995). Pooling of neighboring alleles occurred when expected overall values were less than three (Sokal and Rohlf 1995). An approximate *F*-statistic was used to contrast heterogeneity in the hierarchy (Smouse and Ward 1978). Additional population pairwise tests of allelic frequency homogeneity were conducted using a Markov chain–Monte Carlo (MCMC) exact procedure in GENEPOP 4.1 (Raymond and Rousset 1995).

The relative magnitude of genetic variation resulting from population heterogeneity was assigned to the different hierarchical levels through G_{ST}-statistics (Chakraborty and Leimar 1987; Nei and Chesser 1983). The hierarchical likelihood ratio tests determined whether the G_{ST}-statistics were significantly different from zero (Chakraborty and Leimar 1987). Estimates of effective migration ($N_e m$) were calculated from G_{ST}-statistics using a hierarchical island model (Zhivotovsky et al. 1994).

The ability of the baseline to correctly apportion test fishery samples was tested through analyses of simulated and real known-origin mixtures. The program ONCOR (Kalinowski et al. 2007) was used to simulate 1000 artificial mixtures ($N = 400$) for each population and estimate the stock composition by conditional maximum likelihood (CML). The estimates for the individual population mixtures were also summed to region and area. Additional region or area 100% simulations were performed with equal contributions from populations within the region or area. The known-origin mixture analysis consisted of removing each population in turn from the baseline and using it as a mixture. The stock composition was estimated to region or area for each known-origin mixture using cBAYES (Neaves et al. 2005) and ONCOR. This enabled an evaluation of bias introduced when using an incomplete baseline to estimate fishery stock

composition. It has been shown that MCMC chains fail to converge when the baseline is missing representation from a significant genetic component (Crane et al. 2015). The program cBAYES implements Bayesian mixture modelling (Pella and Masuda 2001) with estimates derived from nine MCMC chains that were iteratively sampled 30,000 times each. Convergence of the MCMC chains was determined with the Raftery and Lewis (1996) and Gelman and Rubin (1992) diagnostics.

The test fishery samples were stratified approximately by run quartile to achieve a minimum sample size of 150 individuals per stratum. Simulations of 5% contributions from each of the regions were conducted using ONCOR to determine the minimum sample size required to produce region or area estimates with 95% confidence intervals that excluded 0. The stock compositions for the test fishery strata were estimated by cBAYES as described above. The stock composition for the entire test fishery sampling period was calculated by taking a weighted average of each stratum's estimate of stock composition based on the stratum's relative abundance for the entire period as determined from sonar passage estimates (Seeb et al. 1997).

The probability that the test fishery samples contained individuals from populations not represented in the baseline was estimated using the program HWLER (Pella and Masuda 2006). The HWLER program uses a Gibbs and split-merge MCMC sampler to partition mixture samples into Hardy-Weinberg and linkage equilibrium subsets and identifies those that originate from missing baseline populations. The MCMC sampler in HWLER was run for 392,000 iterations with the first 196,000 iterations discarded and the posterior distribution estimated from the last 196,000 iterations. Convergence of the MCMC chains was assessed as recommended by Pella and Masuda (2006).

Results

All loci and populations were in Hardy-Weinberg and gametic phase equilibrium. The mean estimates of pairwise relatedness among juvenile samples from the Clear, Old Crow and Fishing Branch populations were -0.0301, -0.0134, and 0.0002, respectively. These values were not significant ($P > 0.05$, 1000 permutations) and indicated that the samples were not related.

Diversity values for loci ranged from 2−53 for number of alleles, 1.6−21.9 for allelic richness, 1.0−13.1 for effective number of alleles, 0.032−0.919 for expected heterozygosity, 0.029−0.933 for observed heterozygosity, and 0.020−0.280 for G_{ST} (Table 2). Diversity values for the populations ranged from 79%−100% for percent polymorphic loci, 4.1−7.6 for allelic richness, 2.3−4.8 for effective number of alleles, 0.415−0.629 for expected heterozygosity, 0.406−0.634 for observed heterozygosity (Table 3). Lower Yukon River populations had significantly higher levels of diversity ($P < 0.05$).

A major subdivision between lower and upper Yukon River coho salmon was revealed from neighbor-joining analysis (Figure 2). Mean CSE and F_{ST} distances within subdivisions were 0.174 and 0.034 whereas estimates between subdivisions were 0.322 and 0.129, respectively. Further structure within these major subdivisions was evident. Within the upper region, the populations were structured into Nenana, Tanana, and Porcupine areas, while the branching of the Clear population in the lower region suggests the possibility of a distinct Koyukuk area, but

further sampling in Koyukuk River would be required to clarify. The genetic variation followed an IBD model among all populations ($r^2 = 0.57$, $P < 0.05$; Figure 3), within the lower region ($r^2 = 0.33$, $P < 0.05$), within the upper region ($r^2 = 0.58$, $P < 0.05$), and between regions ($r^2 = 0.50$, $P < 0.05$).

The populations exhibited genetic heterogeneity ($P < 0.05$) among populations within areas, among areas within regions, and between regions as measured by differences in allelic frequencies (Table 4). Due to low cell counts, *Oke4* was dropped from the analysis. The between regions component accounted for approximately 13 times more heterogeneity than within regions ($F_{53,636} = 12.6$, $P < 0.05$). The upper region populations exhibited approximately eight times the heterogeneity ($F_{371,265} = 8.4$, $P < 0.05$) than lower region populations. Significant differences were observed in 84 of 91 pairwise tests of allelic frequency homogeneity, with F_{ST} ranging from 0.006−0.179 for the significant tests (Table 5).

Individuals varying within populations accounted for 92.2% of the gene diversity while variation among populations accounted for 7.8% (Table 6). Most of the diversity among populations resulted from regional divergence (5.3%), while divergence among areas within regions and among populations within areas accounted for 1.6% and 0.8%, respectively. Likelihood ratio analysis indicated that these gene diversity estimates were significantly ($P < 0.05$) different from 0. Likelihood ratio analysis rejected the null hypothesis ($P < 0.05$) that these gene diversity estimates equaled zero. The effective number of migrants per generation ($N_e m$) was 3.0 overall, 1.1 between regions, 3.8 among areas, and 31.1 among populations within areas.

The individual population MSA simulation accuracies ranged from 26% to 94%, only apportionments to Clear and Kantishna were ≥ 90% accurate (Table 7). Misapportionment was generally to geographically proximate populations. Improvement in MSA accuracy and precision occurred when estimates for individual populations were summed to region or area (98%–100%), and when simulations were performed on region or area aggregates (99%–100%; Table 8). In the known mixture analysis, cBAYES accurately (95%–99%) estimated the region or area composition for each population removed from the baseline and used as a mixture (Table 9). The program ONCOR was not as accurate when estimating region or area composition for the Kantishna and Delta Clearwater population mixtures, with 20% to 30% misapportionment to neighboring Nenana (Table 9).

Stock composition estimates for the test fishery indicated that upper river populations comprised the majority of the samples at the start of the spawning migration with the lower river populations dominating the latter portion (Table 10). There was variability within region to this generalization, such as coho salmon from the Porcupine River arrived at the end of the migration. The composition of the spawning migration was evenly divided (50:50) between the lower and upper river populations. The largest contributor from the upper region was Tanana at 44%, followed by the Nenana at 5%, and the Porcupine at 1% (Table 10).

The posterior distribution from the HWLER analysis indicated that the number of missing baseline populations ($\hat{k}$) ranged from 0 to 2 with a maximum probability of 0.50 at 0 (Table 11). The estimated composition of the missing baseline population in the mixture was 0.3% (95% CI: 0.0%−1.3%). Ten samples out of 690 had probabilities ranging from 0.01–0.43 of belonging to a

missing baseline population, but only 2 samples had probabilities ≥ 0.07. All of these samples had higher probabilities of originating from populations located in the lower, Nenana, or Tanana rivers.

Discussion

In the Yukon River, coho salmon exhibit a high degree of geographically based genetic structure (G_{ST} = 0.078), more than has been observed for either chum (Scribner et al. 1998; Crane et al 2001; Flannery et al. 2007) or Chinook salmon (Smith et al. 2005; Templin et al. 2005). This level of divergence is similar to the estimate for coho salmon across Alaska (Olsen et al 2003) although the patterns of population structure differ. Generally, the genetic variation of coho salmon in Alaska has weak geographic associations, likely resulting from small, locally adapted populations, with little gene flow (Gharrett et al. 2001; Olsen et al. 2003). This is not the case for Yukon River coho salmon, which show strong regional structuring. However, these results are not surprising given the dimensional nature of the Yukon River. One-dimensional habitats, such as a river, wherein populations are linearly distributed and gene flow follows a stepping-stone model, are more likely to have a geographic basis for the genetic variation (Slatkin 1993; Olsen et al. 2003). Similar results have been observed for coho salmon populations within the Kenai River (Olsen et al. 2003).

Although Yukon River coho salmon exhibit regional genetic relationships, the subdivision between lower and upper region populations represents an especially strong genetic disjunction (mean pairwise F_{ST} = 0.129). Compared to upper region populations, those in the lower region maintain more genetic diversity, are more genetically similar to one another and to Western Alaskan populations, and have comparable levels of diversity to those from other Alaskan regions (Olsen et al. 2003; Olsen et al. 2011). While previous studies have observed limited genetic diversity for Yukon River coho salmon, the populations analyzed were limited to the upper river (Gharrett et al. 2001; Olsen et al. 2003), a region where populations exhibit relatively low diversity within populations and high divergence among populations.

Similar findings of genetic as well as morphometric (i.e. coastal vs. interior) disjunction and spatial differences in genetic divergence and diversity exist for Fraser River coho salmon (Taylor and McPhail 1985; Small et al. 1998; Beacham et al. 2001). Fraser River coho salmon have been extensively sampled, and no hybrid zone between lower and upper river fish has been found, with the point of disjuncture at Hell's Gate. This has led to the conclusion that based on the geologic record and similar disjunctions for sockeye and Chinook salmon that different colonizing sources and local adaptation, which prevents or severely limits gene flow between regions, are responsible for this divide (Small et al. 1998). Parallel conclusions do not yet appear possible for Yukon River coho salmon as further sampling in the middle section between the Kaltag and Tanana Rivers is required to rule out a contact zone or identify a point of disjuncture.

The strong genetic disjunction in Yukon River coho salmon as well as other genetic barriers identified for Chinook salmon and chum salmon has led to conjecture that the observed genetic divergence between coho salmon, chum salmon, and Chinook salmon from the lower and upper regions may result from secondary contact or vicariance (Olsen et al. 2011). However, for the chum salmon the secondary contact zone between the Beringia and Cascadia lineages originates

on the North Alaska Peninsula (Seeb and Crane 1999a; Petrou et al. 2013), and fragmentation of mtDNA clades was not observed for Yukon River chum salmon (Flannery et al. 2007), which would be necessary for the hypothesis of secondary contact to be valid (Templeton et al. 1995). Thus, recent divergence from a single colonizing source due to founding or bottleneck effects, which Olsen et al. (2004) suggest, may be one scenario. Another compelling scenario was posited by Garvin et al. (2013) who observed that the genetic similarity among chum salmon populations in Western Alaska, sometimes where populations much more distant than others are more similar, is the result of historical connections between the Yukon and Kuskokwim rivers during the last glacial maxima. These historical connections and subsequent instability of river channels in the lower region have engendered gene flow, genetic connectivity, and genetic diversity in the lower region populations because salmon straying is related to river stability (Quinn 2005). Conversely, the upper region habitat has been much more stable allowing populations to evolve for a longer time in greater isolation compared to populations in the lower region. Nevertheless, despite the reason for the divide, upper Yukon River coho salmon occupy habitat at the extremes of both geographic distribution and freshwater migratory distance and have a level of genetic distinction similar to upper Fraser River coho salmon, which Small et al. (1998) deem an evolutionary significant unit.

Fishery management

Two regional groups (lower and upper) of coho salmon occur within the Yukon River and should be conserved in order to preserve the species evolutionary ability. Additional substructure exists within both the lower and upper regions. In the lower region, two areas are apparent from the significant pairwise tests of allelic divergence: mainstem tributaries and Koyukuk River. However, greater baseline representation of populations from the Koyukuk River is necessary before it will be possible to apportion harvests to this area. More substructure occurs in the upper region, with three distinct areas that can be identified in mixtures, offering finer-scale conservation for upper region coho salmon.

The simulation and known-origin mixture analyses support the application of regional mixed-stock analysis. The simulation estimates exceeded 90% accuracy for all areas (Table 8), an indication that the populations are identifiable in fishery mixtures (Seeb and Crane 1999b). Moreover, the known-origin analysis demonstrates that unsampled populations will apportion to neighboring populations when there is concordance between geography and genetic variation (Table 9). This validates the potential of the baseline for regional MSA despite not having sampled all of the possible populations because misapportionment occurs among geographically proximate and genetically similar populations, precluding the need for an exhaustive baseline (Beacham et al. 2003). It further elucidates the superiority of Bayesian mixture modeling, which accurately (≥ 95%) apportioned all of the missing baseline populations back to the correct area while CML did not for populations from the Tanana River (Table 9). The poor performance of CML for apportioning missing baseline populations to the correct regional group was also observed by Crane et al. (2015).

Further evaluation of the baseline was conducted with HWLER. The comparison of the baseline to the test fishery mixture indicated that there was a 50% probability of either 0 or 1–2 missing baseline populations (Table 11). The analysis was 50:50 because the samples also had high

probabilities of originating from populations present in the baseline from the lower, Nenana, and Tanana areas, which suggests that the baseline is not missing a regional or area population group but that divergent populations within a represented population group were sampled in low proportion from the test fishery. This is to be expected as there are known baseline populations not yet sampled. The estimated proportion for the missing baseline population (0.3%) will apportion to the nearest neighbor, so it does not bias regional estimates. Therefore, based on the combined analyses, it is reasonable to conclude that the baseline is capable of estimating regional stock composition.

The analysis of the test fishery samples provides the first view of the stock composition for Yukon River coho salmon. Several insights were gleaned from this survey. First, run timing differences exist among coho salmon populations with those from the upper river generally migrating earlier than those from the lower river. Porcupine River coho salmon are the notable exception to this generalization. Second, the stock proportions indicate that the lower and upper regions comprise equal parts of the migration. However, disparity exits among the areas within the upper region with coho salmon from the Tanana River dominating the return, which concurs with the decision to monitor coho salmon escapement into the Delta Clearwater (JTC 2016). Escapement monitoring has been identified as the most important aspect of fishery management and fundamental for quantitative stock assessment (Geiger 1991). While escapement monitoring is essential for coho salmon management, it is limited by funding shortfalls. However, MSA in conjunction with sonar enumeration can provide additional information on stock-specific proportions, abundances, and migration timings (Beacham et al. 2000; Flannery et al. 2010) that can increase our knowledge and ability to manage Yukon River coho salmon.

Conclusions

1). Yukon River coho salmon exhibit a high degree of population structure.
2). Upper Yukon River coho salmon have lower levels of genetic diversity.
3). Accurate (> 90%) apportionment to areas and regions is possible with the current microsatellite baseline.

Recommendations

1). Increase sample sizes for those populations currently below 200 individuals.
2). Improve baseline representation.

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Table 1. Population, region, area, population label, sample collection years, number of fish sampled per year (*N*), and life stage of sampled Yukon River coho salmon.

Population	Region	Area	Label	Year	N	Life stage
Archuelinguk	Lower	Lower	1	2005	50	Adult
Andreafsky	Lower	Lower	2	1998	93	Adult
Anvik	Lower	Lower	3	2002	56	Adult
Rodo	Lower	Lower	4	2005	51	Adult
Kaltag	Lower	Lower	5	2007	91	Adult
Clear	Lower	Lower	6	2004	47	Juvenile
Kantishna	Upper	Tanana	7	2001	250	Adult
Delta Clearwater	Upper	Tanana	12	1997, 2011	100, 25	Adult
Glacier	Upper	Nenana	8	2010	60	Adult
17 mile slough	Upper	Nenana	9	1997, 2010	100, 51	Adult
Otter	Upper	Nenana	10	2003, 2004	50, 50	Adult
Lignite	Upper	Nenana	11	2010	51	Adult
Old Crow	Upper	Porcupine	13	1998	100	Juvenile
Fishing Branch	Upper	Porcupine	14	1998, 1999, 2000	74, 150, 200	Juvenile
Test Fishery			TF	2015	694	Adult

Table 2. Across populations for each locus: number of alleles, allelic richness (A_R), effective number of alleles (A_E), expected heterozygosity (H_E), observed heterozygosity (H_O), and G_{ST}.

Locus	Alleles	A_R	A_E	H_E	H_O	G_{ST}
Ocl8	13	6.0	2.0	0.461	0.452	0.069
Oki1	8	5.0	3.2	0.680	0.679	0.081
Omy1011	10	6.1	3.3	0.650	0.649	0.090
One13	12	6.1	2.7	0.504	0.503	0.128
Ots103	53	21.9	8.1	0.869	0.859	0.054
Ots213	21	5.3	2.4	0.569	0.556	0.032
OtsG422	42	21.1	13.1	0.919	0.933	0.028
P53	9	5.1	2.9	0.581	0.586	0.140
Oke2	3	1.9	1.2	0.107	0.119	0.130
Oke4	5	1.6	1.0	0.032	0.029	0.020
Ogo2	7	3.9	1.8	0.432	0.433	0.063
Ots2m	5	4.0	3.0	0.666	0.669	0.099
Ots101	26	13.1	8.2	0.865	0.850	0.037
Oke3	8	4.1	2.1	0.499	0.497	0.049
Ots105	2	1.9	1.2	0.117	0.123	0.104
Oki11	2	2.0	1.2	0.183	0.177	0.051
Oki3	2	2.0	1.5	0.349	0.330	0.280
One3	5	4.0	2.6	0.597	0.604	0.033
Ssa407	15	9.5	4.9	0.779	0.770	0.061

Table 3. Across loci for each population: mean sample size (*N*), percentage polymorphic loci at the 95 percent criterion (*%P*), allelic richness (A_R), effective number of alleles (A_E), expected heterozygosity (H_E), and observed heterozygosity (H_O).

Population	*N*	*%P*	A_R	A_E	H_E	H_O
Archuelinguk	41	100.0	7.3	4.3	0.615	0.608
Andreafsky	88	94.7	7.3	4.7	0.617	0.613
Anvik	54	94.7	7.5	4.6	0.622	0.627
Rodo	49	94.7	7.6	4.6	0.610	0.595
Kaltag	87	94.7	7.4	4.8	0.629	0.634
Clear	45	94.7	5.9	3.7	0.579	0.571
Kantishna	233	79.0	5.2	2.9	0.439	0.429
Delta Clearwater	116	84.2	5.4	3.0	0.444	0.444
Glacier	57	84.2	5.5	2.8	0.450	0.445
17 mile slough	142	84.2	5.6	3.0	0.479	0.479
Otter	115	84.2	5.6	3.1	0.482	0.488
Lignite	50	84.2	5.0	2.8	0.469	0.480
Old Crow	97	79.0	4.2	2.3	0.415	0.406
Fishing Branch	339	79.0	4.1	2.4	0.418	0.417

Table 4. Hierarchical tests of homogeneity using likelihood ratio analysis of allele frequencies from 18 microsatellite loci (one locus dropped due to expected counts below three) among Yukon River coho salmon populations within an area, among areas within a region, and between regions. Asterisks indicate significance at $P < 0.05$.

Source of variation		df	*G*
Lower		265	644.3*
Upper	Nenana	159	342.8*
	Tanana	53	169.7*
	Porcupine	53	51.9
Within Upper		265	564.5*
Among Upper		106	4856.3*
Total Upper		371	5420.7*
Within Regions		636	6065.1*
Between Regions		53	6370.5*
Total		689	12435.6*

Table 5. Pairwise F_{ST} estimates for Yukon River coho salmon. Values with asterisks are not significant ($P > 0.05$).

Population	Archuelinguk	Andreafsky	Anvik	Rodo	Kaltag	Clear	Kantishna	Delta	Glacier	17 mile slough	Otter	Lignite	Old Crow	Fishing Branch
Archuelinguk														
Andreafsky	0.002*													
Anvik	0.005*	0.005*												
Rodo	0.007	0.009	0.007*											
Kaltag	0.007	0.007	0.007	0.005*										
Clear	0.031	0.023	0.026	0.026	0.033									
Kantishna	0.135	0.134	0.142	0.119	0.129	0.135								
Delta	0.124	0.123	0.131	0.104	0.118	0.123	0.006							
Glacier	0.129	0.130	0.130	0.111	0.120	0.128	0.058	0.051						
17 mile slough	0.112	0.117	0.117	0.095	0.106	0.120	0.040	0.032	0.006					
Otter	0.106	0.109	0.112	0.091	0.101	0.115	0.037	0.029	0.007	0.001*				
Lignite	0.111	0.114	0.116	0.100	0.105	0.123	0.059	0.051	0.019	0.012	0.012			
Old Crow	0.156	0.165	0.165	0.142	0.151	0.175	0.059	0.050	0.088	0.065	0.063	0.083		
Fishing Branch	0.161	0.175	0.172	0.149	0.161	0.179	0.062	0.054	0.091	0.069	0.066	0.088	0.000*	

Table 6. Hierarchical gene diversity analysis of Yukon River coho salmon using 19 microsatellite loci. H_T is the total gene diversity; H_S is the gene diversity within populations; D_{SR} is the gene diversity among populations within areas; D_{RC} is the gene diversity among areas within regions; D_{CT} is the gene diversity between regions; H_S/H_T is the relative gene diversity due to variation within populations; G_{ST} is the relative gene diversity due to variation among populations; G_{RT} is the relative gene diversity due to variation among regions; G_{SR} is the relative gene diversity due to variation among populations within regions; N_em is the number of effective migrants per generation.

Source	Gene diversity	Coefficient of gene differentiation	N_em
Within populations	H_S = 0.519	H_S/H_T = 0.922	
Among populations, within areas	D_{SR} = 0.004	G_{SR} = 0.008*	31.1
Among areas, within regions	D_{RC} = 0.009	G_{RC}= 0.016*	3.8
Between regions	D_{CT} = 0.030	G_{CT}= 0.053*	1.1
Total gene diversity	H_T = 0.563	G_{ST} = 0.078*	3.0

*P<0.05 Inferred from hierarchical tests of homogeneity

Table 7. Mixed-stock analysis accuracy for 100% individual population simulations. Accuracy listed above the standard deviation.

Source of mixture	Mean apportionment by population													
Population	Archuelinguk	Andreafsky	Anvik	Rodo	Kaltag	Clear	Kantishna	Delta	Glacier	17 mile slough	Otter	Lignite	Old Crow	Fishing Br
Archuelinguk	**0.39**	0.35	0.07	0.04	0.14	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	0.03	0.03	0.02	0.02	0.03	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Andreafsky	0.07	**0.65**	0.10	0.07	0.11	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	0.02	**0.03**	0.02	0.02	0.02	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Anvik	0.04	0.26	**0.37**	0.15	0.17	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	0.02	0.03	**0.03**	0.03	0.03	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Rodo	0.02	0.20	0.18	**0.28**	0.32	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	0.01	0.03	0.03	**0.03**	0.03	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Kaltag	0.03	0.13	0.07	0.11	**0.67**	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	0.01	0.02	0.02	0.02	**0.03**	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Clear	0.01	0.04	0.02	0.02	0.00	**0.90**	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	0.01	0.01	0.01	0.01	0.00	**0.02**	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Kantishna	0.00	0.00	0.00	0.00	0.00	0.00	**0.94**	0.05	0.00	0.00	0.00	0.00	0.00	0.00
	0.00	0.00	0.00	0.00	0.00	0.00	**0.02**	0.02	0.00	0.00	0.00	0.00	0.00	0.00
Delta	0.00	0.00	0.00	0.00	0.00	0.00	0.12	**0.86**	0.00	0.01	0.01	0.00	0.00	0.00
	0.00	0.00	0.00	0.00	0.00	0.00	0.03	**0.03**	0.00	0.01	0.01	0.00	0.00	0.00
Glacier	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	**0.52**	0.23	0.25	0.00	0.00	0.00
	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	**0.04**	0.03	0.03	0.00	0.00	0.00
17 mile slough	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.03	**0.64**	0.30	0.01	0.00	0.00
	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.02	**0.04**	0.04	0.01	0.00	0.00
Otter	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.06	0.40	**0.51**	0.02	0.00	0.00
	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.02	0.04	**0.04**	0.01	0.00	0.00
Lignite	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.12	0.16	**0.72**	0.00	0.00
	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.03	0.03	**0.03**	0.00	0.00
Old Crow	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	**0.26**	0.74
	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	**0.04**	0.04
Fishing Br	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.15	**0.85**
	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.04	**0.04**

Table 8. Mixed-stock analysis accuracy for 100% individual population simulations summed to areas and for 100% area aggregate simulations. Accuracy listed above the standard deviation.

Source of mixture		Mean apportionment by area			
Area	Population	Lower	Tanana	Nenana	Porcupine
Lower		**1.00**	0.00	0.00	0.00
		0.00	0.00	0.00	0.00
	Archuelinguk	**1.00**	0.00	0.00	0.00
		0.00	0.00	0.00	0.00
	Andreafsky	**1.00**	0.00	0.00	0.00
		0.00	0.00	0.00	0.00
	Anvik	**1.00**	0.00	0.00	0.00
		0.00	0.00	0.00	0.00
	Rodo	**1.00**	0.00	0.00	0.00
		0.00	0.00	0.00	0.00
	Kaltag	**1.00**	0.00	0.00	0.00
		0.00	0.00	0.00	0.00
	Clear	**1.00**	0.00	0.00	0.00
		0.00	0.00	0.00	0.00
Tanana		0.00	**0.99**	0.01	0.00
		0.00	**0.01**	0.01	0.00
	Kantishna	0.00	**1.00**	0.00	0.00
		0.00	**0.00**	0.00	0.00
	Delta	0.00	**0.98**	0.02	0.00
		0.00	**0.01**	0.01	0.00
Nenana		0.00	0.00	**1.00**	0.00
		0.00	0.00	**0.00**	0.00
	Glacier	0.00	0.00	**1.00**	0.00
		0.00	0.00	**0.00**	0.00
	17 mile slough	0.00	0.01	**0.99**	0.00
		0.00	0.01	**0.01**	0.00
	Otter	0.00	0.01	**0.99**	0.00
		0.00	0.01	**0.01**	0.00
	Lignite	0.00	0.00	**1.00**	0.00
		0.00	0.00	**0.00**	0.00
Porcupine		0.00	0.00	0.00	**1.00**
		0.00	0.00	0.00	**0.00**
	Old Crow	0.00	0.00	0.00	**1.00**
		0.00	0.00	0.00	**0.00**
	Fishing Br	0.00	0.00	0.00	**1.00**
		0.00	0.00	0.00	**0.00**

Table 9. Mixed-stock analysis to evaluate the effects of missing baseline populations. Each population was removed from the baseline and used as a mixture. Accuracy to correct area is listed in bold, with the 95% credible (cBAYES) or confidence (ONCOR) interval below.

	cBAYES				ONCOR			
Source of Mixture	Mean apportionment by area				Mean apportionment by area			
Population	Lower	Tanana	Nenana	Porcupine	Lower	Tanana	Nenana	Porcupine
Archuelinguk	**0.99**	0.00	0.01	0.00	**1.00**	0.00	0.00	0.00
95 CI	**0.94**	0.00	0.00	0.00	**1.00**	0.00	0.00	0.00
	1.00	0.03	0.04	0.02	**1.00**	0.00	0.00	0.00
Andreafsky	**0.99**	0.00	0.00	0.00	**1.00**	0.00	0.00	0.00
95 CI	**0.97**	0.00	0.00	0.00	**0.98**	0.00	0.00	0.00
	1.00	0.01	0.02	0.01	**1.00**	0.00	0.02	0.00
Anvik	**0.99**	0.00	0.01	0.00	**1.00**	0.00	0.00	0.00
95 CI	**0.95**	0.00	0.00	0.00	**0.96**	0.00	0.00	0.00
	1.00	0.03	0.04	0.02	**1.00**	0.00	0.04	0.00
Rodo	**0.98**	0.01	0.01	0.00	**0.98**	0.02	0.00	0.00
95 CI	**0.92**	0.00	0.00	0.00	**0.93**	0.00	0.00	0.00
	1.00	0.07	0.04	0.03	**1.00**	0.06	0.03	0.00
Kaltag	**0.98**	0.01	0.00	0.00	**0.98**	0.02	0.00	0.00
95 CI	**0.95**	0.00	0.00	0.00	**0.95**	0.00	0.00	0.00
	1.00	0.05	0.02	0.01	**1.00**	0.05	0.01	0.00
Clear	**0.98**	0.01	0.01	0.00	**0.98**	0.02	0.00	0.00
95 CI	**0.93**	0.00	0.00	0.00	**0.94**	0.00	0.00	0.00
	1.00	0.05	0.04	0.03	**1.00**	0.06	0.04	0.00
Kantishna	0.01	**0.99**	0.00	0.00	0.01	**0.81**	0.19	0.00
95 CI	0.00	**0.97**	0.00	0.00	0.00	**0.68**	0.11	0.00
	0.03	**1.00**	0.01	0.01	0.02	**0.88**	0.31	0.02
Delta Clearwater	0.00	**0.95**	0.04	0.00	0.00	**0.71**	0.27	0.02
95 CI	0.00	**0.86**	0.00	0.00	0.00	**0.56**	0.17	0.00
	0.02	**1.00**	0.13	0.03	0.02	**0.80**	0.42	0.08
Glacier	0.02	0.02	**0.96**	0.00	0.02	0.01	**0.97**	0.00
95 CI	0.00	0.00	**0.89**	0.00	0.00	0.00	**0.90**	0.00
	0.08	0.08	**1.00**	0.02	0.06	0.07	**1.00**	0.00
17 mile slough	0.00	0.00	**0.99**	0.00	0.00	0.03	**0.97**	0.00
95 CI	0.00	0.00	**0.97**	0.00	0.00	0.00	**0.87**	0.00
	0.02	0.02	**1.00**	0.01	0.03	0.13	**0.99**	0.01
Otter	0.00	0.05	**0.95**	0.00	0.00	0.09	**0.91**	0.00
95 CI	0.00	0.01	**0.88**	0.00	0.00	0.03	**0.81**	0.00
	0.02	0.11	**0.99**	0.01	0.04	0.17	**0.96**	0.00
Lignite	0.01	0.00	**0.98**	0.00	0.00	0.00	**1.00**	0.00
95 CI	0.00	0.00	**0.92**	0.00	0.00	0.00	**0.86**	0.00
	0.06	0.03	**1.00**	0.03	0.06	0.11	**1.00**	0.00
Old Crow	0.00	0.00	0.00	**0.99**	0.00	0.02	0.00	**0.98**

Source of Mixture Population	cBAYES Mean apportionment by area Lower	Tanana	Nenana	Porcupine	ONCOR Mean apportionment by area Lower	Tanana	Nenana	Porcupine
95 CI	0.00	0.00	0.00	**0.96**	0.00	0.00	0.00	**0.93**
	0.02	0.03	0.02	**1.00**	0.03	0.06	0.02	**1.00**
Fishing Branch	0.00	0.00	0.00	**0.99**	0.00	0.01	0.00	**0.99**
95 CI	0.00	0.00	0.00	**0.98**	0.00	0.00	0.00	**0.96**
	0.01	0.01	0.01	**1.00**	0.00	0.03	0.02	**1.00**

Table 10. Coho salmon stock composition estimates from the test fishery operated near Pilot Station, 2015, with associated standard deviations and 95% credible intervals by stratum and management group.

	7/23-8/15				8/16-8/21			
Region/Area	Estimate	SD	95 CI		Estimate	SD	95 CI	
Lower	0.338	0.035	0.272	0.407	0.425	0.039	0.350	0.503
Upper	0.662	0.035	0.592	0.728	0.575	0.039	0.497	0.650
Tanana	0.616	0.037	0.542	0.687	0.536	0.040	0.457	0.613
Nenana	0.045	0.018	0.016	0.085	0.038	0.019	0.010	0.081
Porcupine	0.001	0.003	0.000	0.012	0.001	0.002	0.000	0.007
	8/22-8/25				8/26-8/31			
	Estimate	SD	95 CI		Estimate	SD	95 CI	
Lower	0.516	0.040	0.438	0.596	0.674	0.036	0.602	0.742
Upper	0.484	0.040	0.404	0.562	0.326	0.036	0.258	0.398
Tanana	0.394	0.041	0.315	0.474	0.251	0.034	0.187	0.319
Nenana	0.088	0.026	0.043	0.144	0.041	0.016	0.014	0.078
Porcupine	0.001	0.003	0.000	0.010	0.034	0.015	0.011	0.068
	7/23-8/31							
	Estimate	SD	95 CI					
Lower	0.497	0.019	0.461	0.534				
Upper	0.503	0.019	0.466	0.539				
Tanana	0.440	0.019	0.403	0.477				
Nenana	0.053	0.010	0.033	0.072				
Porcupine	0.010	0.004	0.002	0.019				

Table 11. Probabilities for the number of missing baseline populations ($\hat{k}$).

		$\hat{k}$				
Sample	N	0	1	2	3	4
Test Fishery	690	0.50	0.45	0.05	0.00	0.00

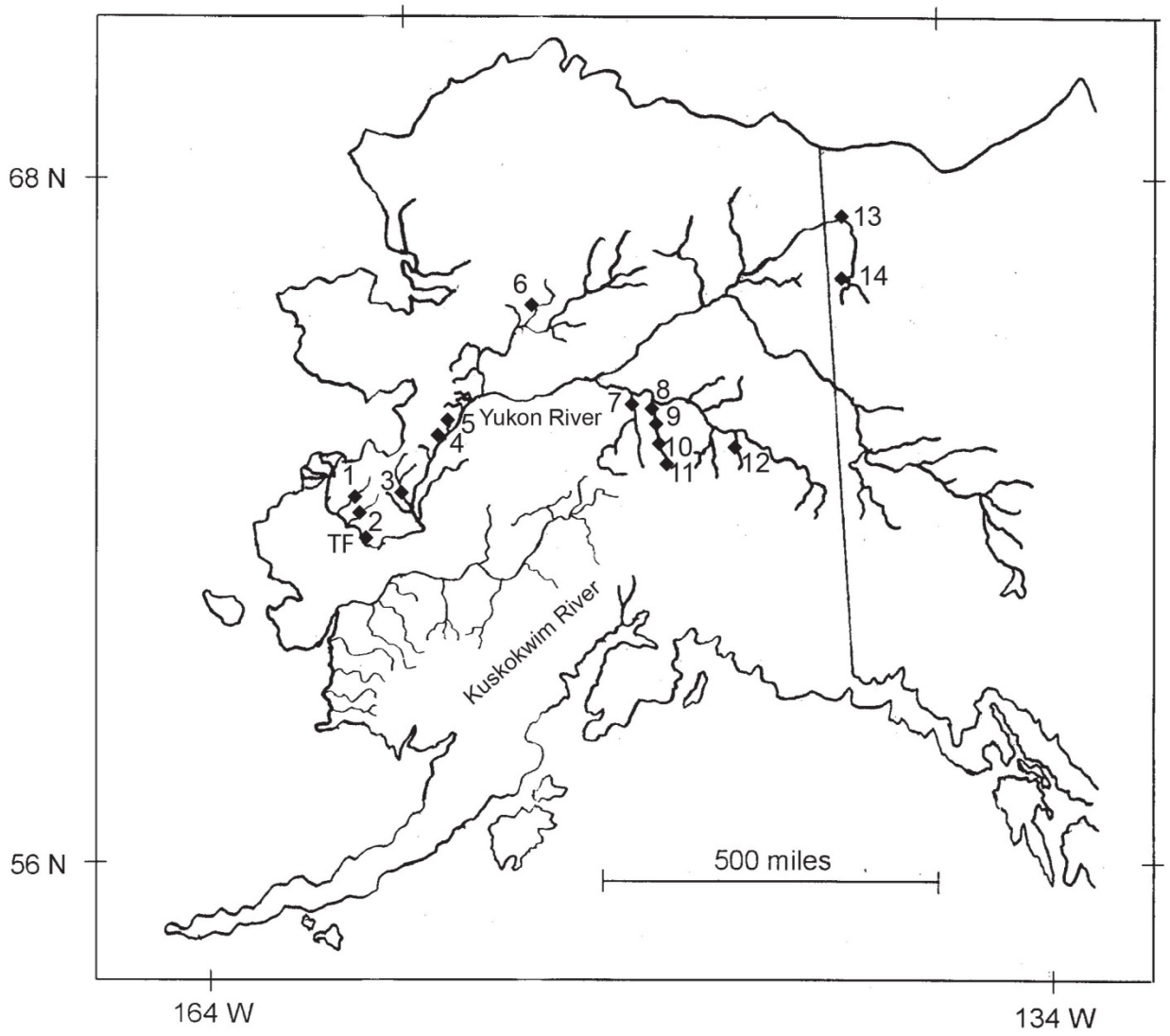

Figure 1. Sampling locations: 1 = Archuelinguk, 2 = Andreafsky, 3 = Anvik, 4 = Rodo, 5 = Kaltag, 6 = Clear, 7 = Kantishna, 8 = Glacier, 9 = 17 mile slough, 10 = Otter, 11 = Lignite, 12 = Delta Clearwater, 13 = Old Crow, 14 = Fishing Branch, TF = test fishery.

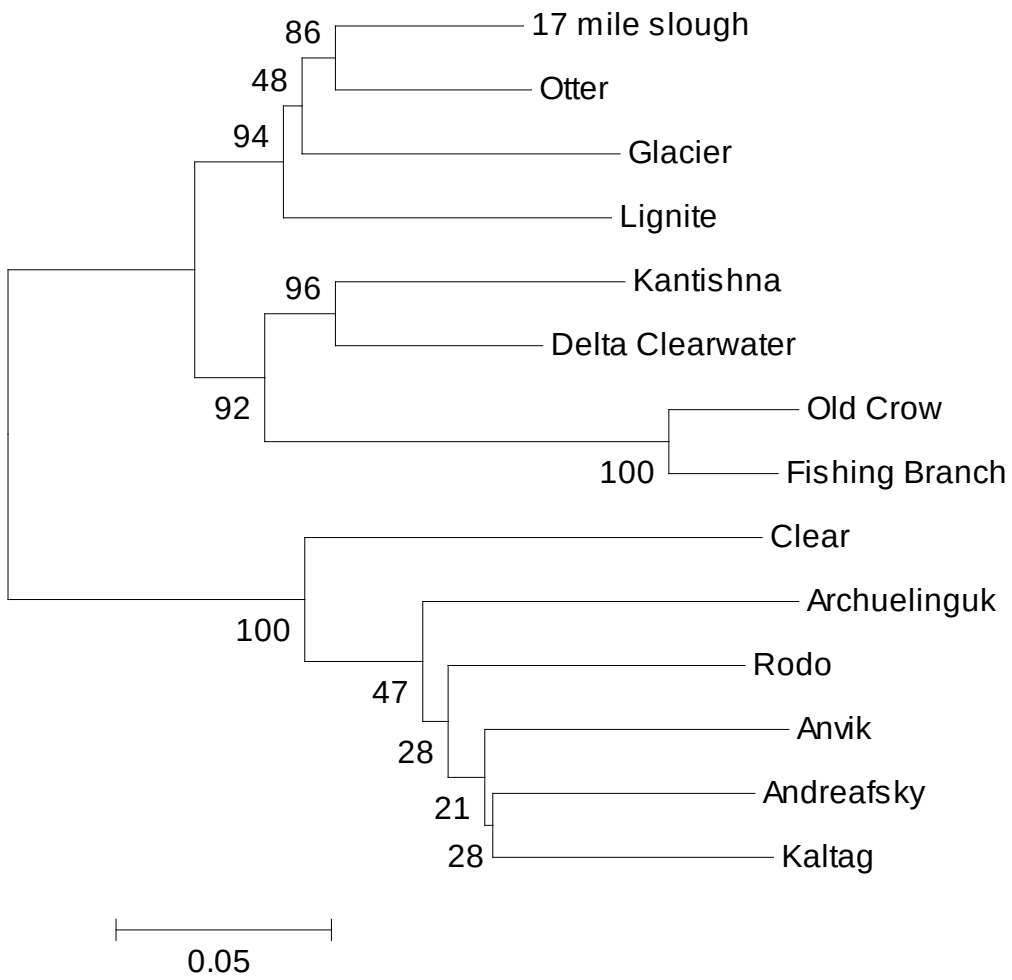

Figure 2. Neighbor-joining dendrogram of CSE distances among 14 Yukon River coho salmon populations. Bootstrap values showing support for each node are presented.

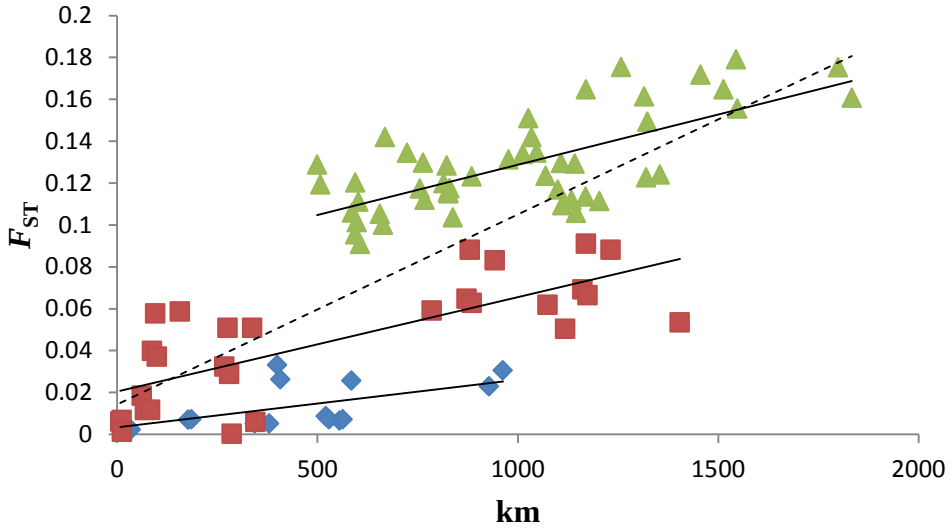

Figure 3. Scatter plot of genetic distance (F_{ST}) on geographic distance (km). Linear regression lines are shown for all populations (dashed line; y = 9 x $10^{-5}x$ + 0.014, r^2 = 0.57, P < 0.05), the upper region (squares; y = 5 x $10^{-5}x$ + 0.020, r^2 = 0.58, P < 0.05), the lower region (diamonds; y = 2 x $10^{-5}x$ + 0.003, r^2 = 0.33, P < 0.05) and between regions (triangles; y = 5 x $10^{-5}x$ + 0.081, r^2 = 0.50, P < 0.05).

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