U.S. Fish and Wildlife Service

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Genetic Variation Among Coho Salmon Populations From the Kuskokwim Region and Application to Stock-Specific Harvest Estimation

Penny Crane[1], Doug Molyneaux[2], Cara Lewis[1], and John Wenburg[1]

ABSTRACT

Genetic variation at 15 microsatellite loci was surveyed in coho salmon *Oncorhynchus kisutch* sampled from 12 locations in the Kuskokwim region. These data were combined with data from a previous study to survey genetic variation of coho salmon in the region. Genetic diversity patterns showed: 1) populations from the Goodnews, Kanektok and Arolik rivers were genetically distinct from Kuskokwim River populations, and 2) South Fork Kuskokwim River and Highpower Creek in the upper Kuskokwim River were extremely divergent from populations lower in the drainage. Simulation studies indicated that five population aggregates could be identified in mixtures: Kuskokwim Bay (Middle Fork Goodnews, Arolik, and Kanektok rivers); lower-middle Kuskokwim (Kwethluk, Kisaralik, Tuluksak, Salmon, George, Kogrukluk, and Tatlawiksuk rivers); Takotna River; South Fork Kuskokwim River; and Highpower Creek. Data were applied to estimate the stock contribution of a catch sample made from the commercial fishery on August 13, 2001, and the majority of fish originated from the lower and middle Kuskokwim River (87%), with smaller contributions from Kuskokwim Bay and upper Kuskokwim River.

INTRODUCTION

The largest subsistence harvest of coho salmon *Oncorhynchus kisutch* in Alaska occurs in the Kuskokwim region (ADF&G 2002, 2003a, 2003b, 2005; Fall et al. 2007), which encompasses the Kuskokwim River and rivers draining into Kuskokwim and Goodnews bays. Within the Kuskokwim region, coho salmon comprise 15 to 18% of the total subsistence salmon harvest. Coho salmon are often harvested for subsistence use in greater numbers in years of poor Chinook *O. tshawytscha* and chum *O. keta* salmon returns (Whitmore et al. 2005).

Commercial fishing provides an important source of revenue for residents of the Kuskokwim region to purchase fuel and supplies for subsistence harvests activities (Coffing 1991; Coffing et al. 2001). Coho salmon are the dominant species in the Kuskokwim region commercial catches, both in numbers harvested and in value (Whitmore et al. 2005). The average number of coho salmon harvested in commercial fisheries from 1993–2002 was 426,505 with an average exvessel value of $1,243,390. Subsistence and commercial harvests are made mostly using gillnets deployed from open skiffs and occur in three distinct geographic areas (Figure 1):

Authors: [1]Conservation Genetics Laboratory, U.S. Fish and Wildlife Service, 1011 East Tudor Road, Anchorage, AK 99503, U.S.A.; [2]Division of Commercial Fisheries, Alaska Department of Fish and Game, 333 Raspberry Road, Anchorage, AK 99518, U.S.A.

- District W5 where fishers target salmon returning to the Goodnews River drainage through harvest mostly limited to the nearly occluded estuarine waters;
- District W4 where fishers target salmon returning to the Kanektok River, and to a lesser degree the smaller Arolik River, by fishing in marine waters near the terminus of the river, though the openness of these marine waters and their proximity to the Kuskokwim River create question as to the degree of non-Kanektok-Arolik river salmon being intercepted by District 4 fishers;
- Districts W1, 2, and 3 in the Kuskokwim River where fishers, particularly those in the more intensive fisheries of the lower Kuskokwim River, target salmon returning to a wide variety of tributary spawning streams found throughout the Kuskokwim River drainage.

Of these three geographic areas, District W5 has the smallest coho salmon fishery with average subsistence and commercial harvests of 853 and 18,377; followed by District W4 with average harvests of 2,427 and 51,963; and the Kuskokwim River with average harvests of 34,804 and 356,165 (Whitmore et al. 2005). Coho salmon fisheries typically begin in late July and continue through the end of August or early September, although the tail of the coho salmon run often continues into late fall.

Spawning escapement of coho salmon in the Kuskokwim region is monitored through a series weirs (Molyneaux and Brannian 2006; Figure 1): Middle Fork Goodnews River weir in District W5; Kanektok River weir in District W4; the Kwethluk (rm 216), Tuluksak (rkm 248), George (rkm 453), Tatlawiksuk (rkm 568), Kogrukluk (rkm 710), and Takotna (rkm 835) river weirs in the Kuskokwim River. In addition to weir projects, a mark-recapture study operating from 2001 to 2005 produced total run abundance estimates for Kuskokwim River coho salmon ranging from 603,719 to 1,510,603 with total exploitation rates ranging from 20% to 47% (Pawluk et al. 2006). Unlike for Chinook salmon, aerial stream surveys are not used to provide a broader assessment of coho salmon escapements because of practical restraints in executing such surveys during the coho salmon season. Among the weir projects, only the Middle Fork Goodnews and Kogrukluk rivers have formalized escapement goals for coho salmon.

Management of salmon fisheries in the Kuskokwim region is particularly challenging, in part because of the large size of the Kuskokwim River watershed that comprises the bulk of the region, and because harvest occurs in mixed-stock fisheries. Specific management concerns include the potential for differential exploitation of stocks within the Kuskokwim River due to run timing variation and the potential interception of Kuskokwim River salmon in District W4 fisheries.

Coho salmon returning to the Goodnews, Kanektok, and Arolik rivers have a relatively short distance to travel to spawning grounds because the headwaters of these streams are less than 160 km distant from marine waters of Kuskokwim Bay. Kuskokwim River coho salmon, however, have much more variable distances to travel, with spawning grounds located from a few tens of kilometers to over 1,000 km from Kuskokwim Bay. Tagging studies show a tendency for upper Kuskokwim River spawning populations to pass through the lower

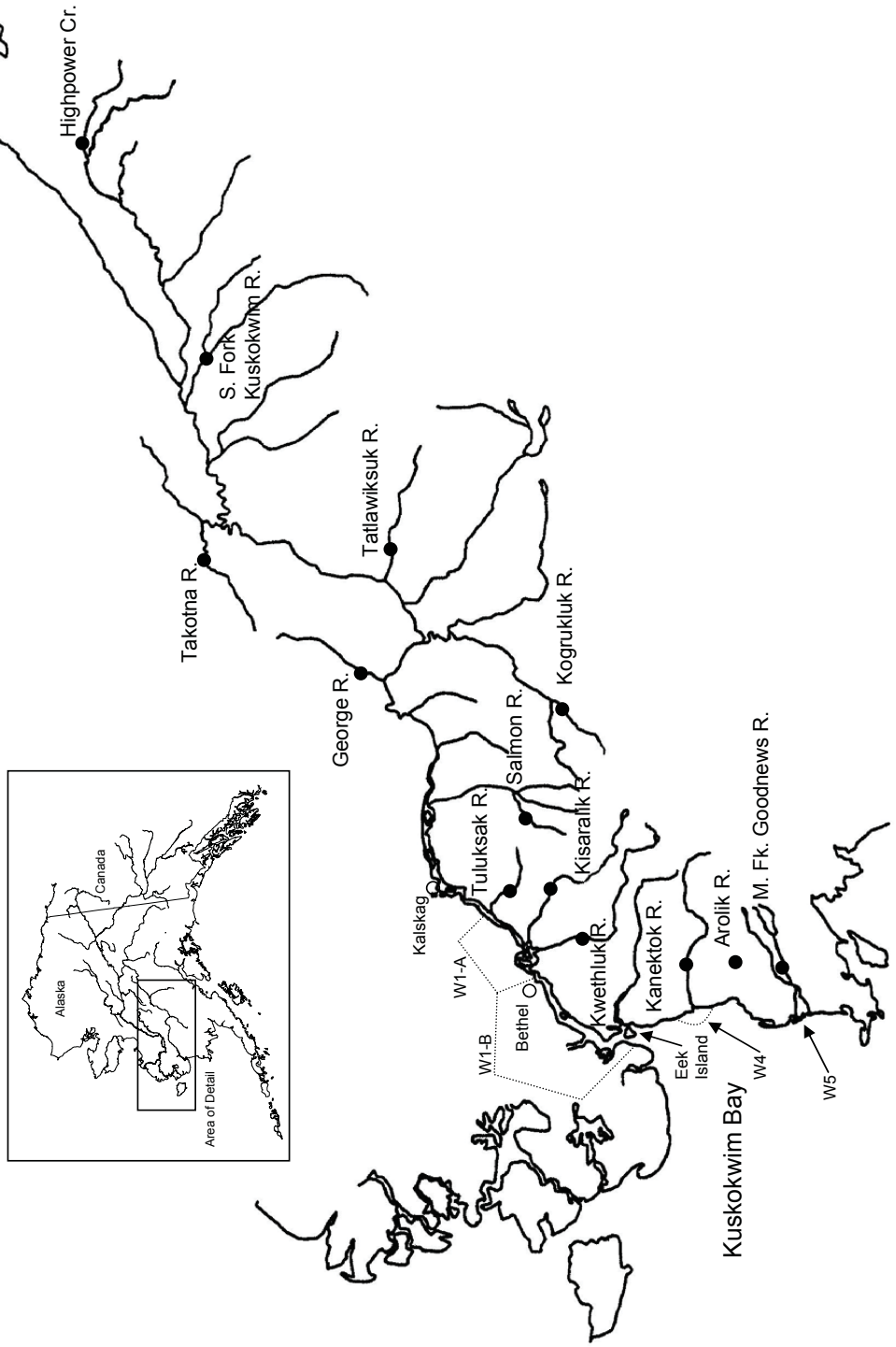

Figure 1. Sampling locations of coho salmon collected for genetic analysis in the Kuskokwim region and major commercial fishing districts.

Kuskokwim River early in the season with progressively later run timing for populations with less distant spawning grounds (Pawluk et al. 2006; Figure 2).

Variation in run timing between stocks or spawning aggregates is a management concern because there is typically limited information to assess salmon run abundance early in the fishing season, thus there is a greater risk of over harvesting these early running salmon stocks. Should over harvest occur, there are scant resources to assess the impacts on escapements because few escapement monitoring projects exist in the upper Kuskokwim River, especially for coho salmon as the Takotna River serves as the only indicator for the adequacy of escapement.

The northern boundary of District W4 was moved 3 miles south, away from the Kuskokwim River, from 2001–2003 due to concern that Kuskokwim River Chinook and chum salmon were being intercepted in the District W4 fishery (Burkey et al. 2000a, 2000b). Kuskokwim River Chinook and chum salmon were considered "Stocks of Concern" following a number of years of exceptionally low run abundance in the Kuskokwim River. A similar argument could have been made for Kuskokwim River coho salmon in the years following 1996 when coho salmon abundance in the Kuskokwim River plummeted (Whitmore et al. 2005; Molyneaux and Brannian 2006). The Alaska Board of Fisheries revoked the boundary restriction in District W4 in 2003 due to the lack of evidence that the boundary had any effect in conserving Kuskokwim River Chinook and chum salmon (Whitmore and Bergstrom 2003).

Mixed-stock analysis (MSA) using genetic characters has been suggested as a method to address the management issues describe above. Gilk et al. (2005), Seeb et al. (1997), and Templin et al. (2004) found upper Kuskokwim River chum and Chinook salmon spawning populations to be genetically distinct from locations elsewhere in the Kuskokwim region. The genetic distinctiveness of salmon spawning stocks of the upper Kuskokwim River drainage facilitates their identification in mixtures and could be used to address concern of disproportionate harvest rates between upper and lower Kuskokwim River spawning stocks. Further, Templin et al. (2004) suggested that the genetic distinction between Chinook salmon from Kuskokwim Bay and the Kuskokwim River might be used to evaluate the intercept of Kuskokwim River salmon in locations such as the District W4 commercial fishery.

Initiatives for evaluating the genetic stock structure of coho salmon have lagged behind those for chum and Chinook salmon. To address this information gap, a pilot study to survey genetic diversity of coho salmon in the Kuskokwim region was funded by the U.S. Fish and Wildlife Service Office of Subsistence Management (03-041, *Genetic variation among coho salmon populations from the Kuskokwim River region and stock-specific harvest estimation*). Results of this pilot study revealed significant allele frequency heterogeneity among samples collected from the Arolik, Kanektok, Kisaralik, George, Kogrukluk, Tatlawiksuk, and Takotna rivers (Crane et al. 2004), indicating a potential for future MSA applications.

This study expands on the pilot study of Crane et al. (2004) by increasing the number of populations surveyed in the Kuskokwim region and assaying additional loci for genetic variation. Objectives were to more completely delineate genetic population structure, particularly in the upper Kuskokwim River drainage, and delineate stock groups that can be identified in mixtures. Data were also applied to estimate the origin of coho salmon from a single mixture

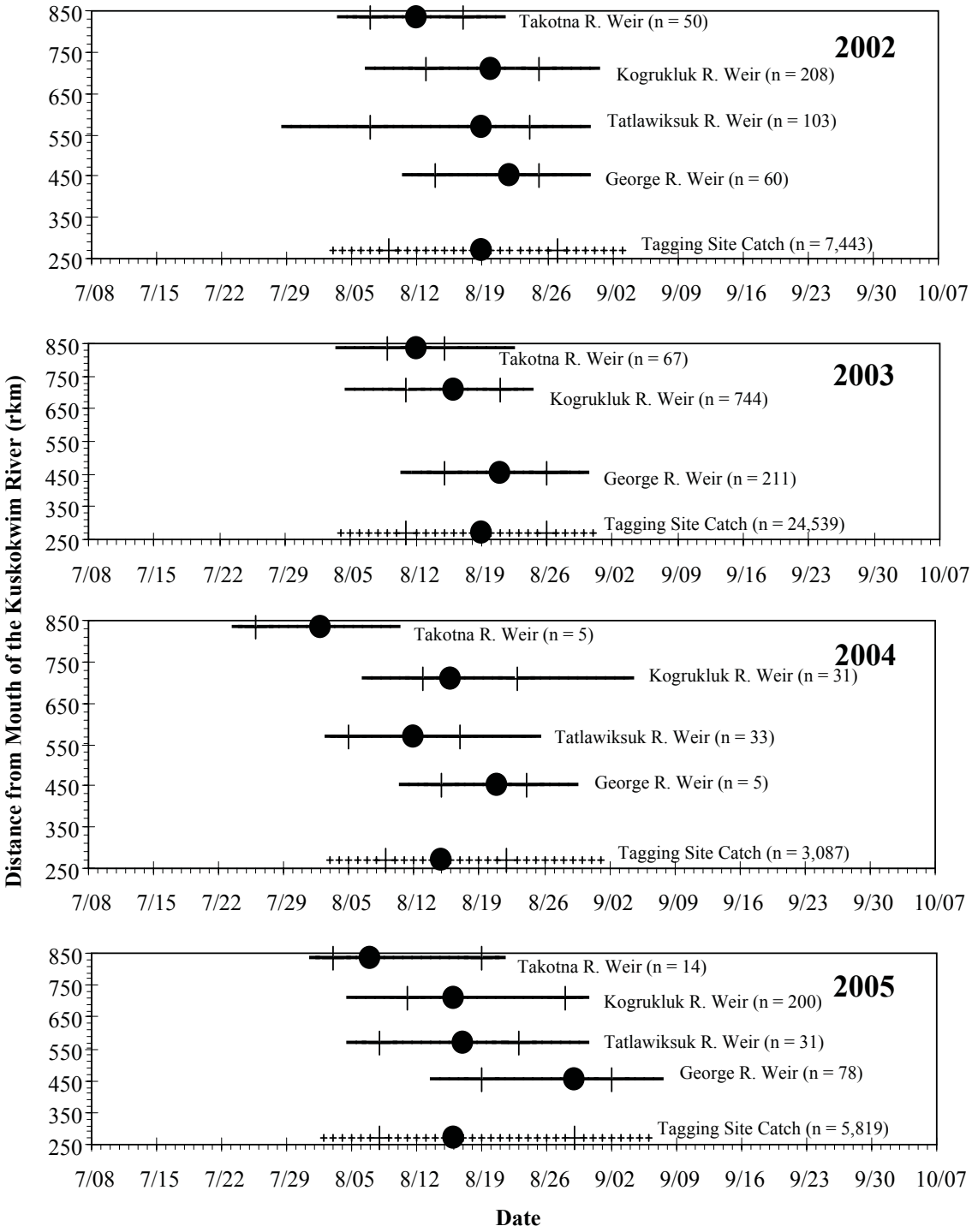

Figure 2. Run timing information for coho salmon stocks in the Kuskokwim River from Figure 16, Pawluk et al. (2006). Dates when individual coho salmon stocks pass through the Kalskag tagging site (rkm 271) based on coho salmon tagged with anchor tags. Solid lines represent the central 80%, cross-bars (+) represent the central 50%, and circles represent the median passage date for each stock.

sample collected from the District W1-B commercial fishery of the lower Kuskokwim River in 2001.

METHODS

Samples

Baseline—Fin tissue was collected from 1,520 adult coho salmon at a total of 12 locations in the Kuskokwim, Goodnews, and Kanektok river drainages in 2004 and 2005 (Table 1, Figure 1). Sampling occurred at weir sites on the Takotna, Tatlawiksuk, Kogrukluk, George, Tuluksak, Kwethluk, Kanektok, and Middle Fork Goodnews rivers, a fishwheel on the South Fork Kuskokwim River, and via hook and line near spawning areas on Highpower Creek, Salmon (Aniak) River, and Kisaralik River. Fin clips were stored in individually labeled vials filled with 90% ethanol, and sampling date and gender were recorded.

Mixture—Fin clips were collected from 250 coho salmon sampled from the District W1-B commercial catch of the lower Kuskokwim River on 13 August 2001. Fin clips were stored in 250 ml Nalgene bottles in 90% ethanol. The boundaries for District W1-B roughly include waters from Bethel downstream to the southern most tip of Eek Island (Figure 1).

Laboratory Analysis

Total genomic DNA was extracted from approximately 25 mg of fin tissue using proteinase K with the Dneasy™ DNA isolation kit (Qiagen Inc., Valencia, CA). Genetic variation was assayed at eight microsatellite loci used in a pilot study of genetic variation in Kuskokwim River coho salmon (Crane et al. 2004), plus seven new loci selected from those standardized for use in Pacific Salmon Commission Southern Boundary fisheries for coho salmon (Kassler and Young 2005; Table 2). Single-locus F_{ST} (the proportion of genetic variation among populations) estimates for two loci surveyed in Crane et al. (2004) were not significantly different from zero; therefore, more loci were incorporated to increase the potential amount of information for population discrimination. Variation at these additional loci were also assayed in archived tissue collections from the Kuskokwim region from Olsen et al. (2003) and Crane et al. (2004) (Table 1). Polymerase chain reaction amplifications of microsatellite loci were carried out in 10 µl reaction volumes (approximately 30–50 ng DNA, 1.5–2 mM $MgCl_2$, 0.8–1 mM dNTPs, 0.01–0.05 µM labeled/0.35–0.39 µM unlabeled forward primer, and 0.4 µM unlabeled reverse primer, and 1M betaine (for *One3* only) using an MJResearch thermocycler. Cycling conditions were 1 cycle of 2 min at 92°; 30 cycles of 15 sec at 92°, 15 sec at 56°–58°, and 30 sec at 72°; with a final extension for 10 min at 72°. Microsatellites were separated and visualized on 64-well denaturing polyacrylamide gels using a Li-Cor IR$^{2®}$ scanner and scored with Li-Cor Saga™ GT ver 2.0 software (Lincoln, NE). Li-Cor 50–350 base size standards were loaded in the first and last lanes and at intervals of 14 lanes or less across each gel. Positive controls consisting of two to eight alleles of predetermined size were loaded in three lanes distributed evenly across the gels to ensure consistency of allele scores. Two researchers scored alleles independently, and samples with score discrepancies between researchers were re-amplified at the loci in question and rescored.

Table 1. Sampling locations, date, and sample size of coho salmon collected from the Kuskokwim region for genetic analysis.

Location	Year	Date	*N*	Source
M. Fk. Goodnews River	2004	8/3–8/31	200	this study
Arolik River	1997	8/28–8/31	96	Olsen et al. 2003
Kanekotk River	2001	8/27	96	Crane et al. 2004
	2004	8/6–8/21	100	this study
Kwethluk River	2004	8/9–9/4	200	this study
Kisaralik River	1997	8/15/2007	96	Olsen et al. 2003
	2004	8/17	70	this study
Tuluksak River	2004	8/10–9/5	200	this study
Salmon River (Aniak River)	2004	9/14–9/18	100	this study
George River	2001	8/28–8/29	96	Crane et al. 2004
	2004	8/14–9/4	100	this study
Kogrukluk River	2001	8/24	96	Crane et al. 2004
	2004	8/12–9/3	100	this study
Tatlawiksuk River	2001	8/30–8/31	96	Crane et al. 2004
	2004	8/23 and 9/2	100	this study
Takotna River	2003	8/20–8/24	96	Crane et al. 2004
	2004	8/15–8/30	100	this study
S. Fk. Kuskokwim River	2004	9/8–10/16	200	this study
Highpower Creek	2004	9/15–10/15	21	this study
	2005	9/1	29	this study

Statistical Analysis

Baseline—Unless otherwise noted, analyses describing genetic variation within and among population samples were conducted using FSTAT ver 2.9.3 (Goudet 2001). For each locus in each sample, deviation of genotypic frequencies from Hardy-Weinberg expectation was evaluated by testing for a deficit of heterozygotes, $F_{IS}>0$. Significance was assessed through a randomization test, permuting alleles among individuals within samples. Significance of the *P*-values was evaluated by adjusting the experiment-wide $\alpha= 0.05$ for 15 (loci for each sample) and 12 (population samples for each locus) simultaneous tests using the sequential Bonferroni technique (Rice 1989).

Homogeneity of allele frequencies among temporal samples (Table 1) was tested using likelihood ratio statistics and significance was evaluated using a randomization test permuting genotypes between samples. Temporal samples were pooled for subsequent analyses

Table 2. Microsatellite loci and primer references for loci surveyed for genetic variation in coho salmon in the Kuskokwim region.

Locus	Primer sequences (5'–3')	Primer Reference	Surveyed in Crane et al. (2004)
Ocl8	F: Tag TgT TTC gTgTTC gCC Tg R: CCC TgT CAC CTT CCA TCT CT	Condrey and Bentzen 1998	
Oke2	F: Agg gCC AGA gAA AAg TCT CAC TAT R: gTC AgT CCT gCC CTC TgT gTC CTA	Buchholz et al. 1999	x
Oke3	F: ACC CTg AgA gCA ATC AAC R: TCA ggg ATA TgC AgT AAA TAg TA	Buchholz et al. 1999	x
Oke4	F: Agg CCC AAA gTC TgT AgT gAA gg R: gAT gAA TCg AgA gAA TAg ggA CTg AAT	Buchholz et al. 1999	x
Oki1	F: Agg ATg gCA gAg CAC CAC T R: CAC CCA TAA TCA CAT ATT CAg A	Smith et al. 1998	x
Oki3	F: ggA gCC CCT TAT Tgg AAg g R: CTT CCA gCA gAg TgT CCC Ag	Smith et al. 1998	x
Oki11	F: TCT gAg ACA ggC AAA TgC AC R: gTT TTA AAC CTC ACC ATT gAg T	Smith et al. 1998	x
Omy1011	F: AAC TTg CTA TgT gAA TgT gC R: gAC AAA AgT gAC Tgg TTg gT	Morris et al. 1996	
One3	F: TCT CCT Tgg TCT CTC TgT CCC TT R: CTA TCA gCC AAT CgC ATC Agg AC	Scribner et al. 1996	x
*Ots2M**	F: gCC TTT TAA ACA CCT CAC ACT TAg R: TTA TCT gCC CTC CgT CAA g	Grieg and Banks 1999	
Ots101	F: ACg TCT gAC TTC AAT gAT gTT T R: TAT TAA TTA TCC TCC AAC CCA g	Small et al. 1998	
Ots105	F: gAg gAT CTA TCA ACA TTA TC R: gCA gCA CCA gCT TCC C	Nelson 1998	x
Ots213	F: CCC TAC TCA TgT CTC TAT TTg gTg R: AgC CAA ggC ATT TCT AAg TgA C	Grieg et al. 2003	
Ssa407	F: TgT gTA ggC Agg TgT ggA C R: CAC TgC TgT TAC TTT ggT gAT TC	Cairney et al. 2000	

*Two groups of alleles were amplified using the *Ots2M* primers. No evidence of linkage was detected between the two groups, and they were treated as two separate loci, *Ots2MA* and *Ots2MB,* for analysis.

following the recommendation of Waples (1990). Expected heterozygosity and allelic richness, number of alleles adjusted for sample size, were calculated to describe within-sample diversity. Cavalli-Sforza and Edwards chord distances (Cavalli-Sforza and Edwards 1967) were calculated between each pair of populations using Phylip ver 3.5c (Felsenstein 1995). Distances were used in a multidimensional scaling (MDS) analysis in S-PLUS 6.0 (Insightful, Inc.; Seattle, WA) to visualize spatial genetic relationships among populations.

The proportion of genetic variation at different hierarchical levels was estimated with AMOVA in Arlequin version 1.1 (Schneider et al. 2000). Two different hierarchies were used. The first partitioned genetic variation into among- and within-region components. Regions were identified from the MDS. For this analysis, all population samples and loci were used. The second partitioned genetic variation into among- and within-population (temporal) components; for this analysis, only those populations with temporal replicates and the loci surveyed in Crane et al. (2004) were used. Isolation by distance (IBD) among populations was tested by plotting pairwise F_{ST} and closest waterway/shoreline distance to identify barriers to gene flow and patterns of gene flow and genetic drift. Pairwise F_{ST} values were calculated following the method of Weir and Cockerham (1984). Geographic distances were measured using a U.S. Geological Survey Alaska Topographic 1:5,840,000 map and a Scalex mapwheel. Significance of the correlation between genetic and geographic distance was evaluated through a Mantel test with 1000 permutations using GENEPOP ver 3.4 (Raymond and Rousset 1995).

Evaluation for mixed-stock analysis—Conditional maximum likelihood estimation of simulated mixtures was used to delineate identifiable populations or population aggregates of coho salmon in the Kuskokwim region. Prior to the simulation analysis, alleles in the baseline populations were binned using the program OptiBin (Bromaghin 2006) to reduce the effects of sampling error and rare alleles. For each locus, exact tests of homogeneity were used to test if allele pairs were similarly distributed across populations, with Monte Carlo simulation to estimate significance, to determine the binning strategy. Log-likelihood ratios were used as the test statistic and the binning procedure executed until $P<0.25$. For the simulation analysis, for each population under study, 1000 artificial mixtures of 400 genotypes were randomly constructed using Hardy-Weinberg expectations from the baseline allele frequencies. The program SPAM ver 3.7b (Debevec et al. 2000) was used for the simulation analysis. Bayesian estimates of baseline allele proportions (Rannala and Mountain 1997) were used to further reduce the effects of sampling error in the baseline allele frequencies. Mean contribution estimates for the population under study should approximate 100%. Populations were aggregated until mean contribution estimates exceeded 90%, which is generally considered suitable for mixture analysis (Teel et al. 1999; Kondzela et al. 2002). When populations were aggregated, mixtures were comprised of genotypes from each population contributing equally.

Lower Kuskokwim River mixture sample—Stock compositions for the District W1-B commercial catch sample from the lower Kuskowkwim River were estimated using Bayesian mixture modeling (Pella and Masuda 2001; Neaves et al. 2005). The initial proportion for the chains (N=5; 5,000 samples each) was 95% from a randomly selected population, with 5% distributed evenly among remaining populations. Values for genetic prior parameters were determined as described in Pella and Masuda (2001). The Raftery and Lewis (1996) diagnostic was used to verify that chain lengths were sufficiently long. Convergence was determined using the Gelman and Rubin (1992) diagnostic. The mean, standard deviaiton, and posterior quantiles of sample stock compostion estimates were generated after a burn-in of 4,000 samples.

Conditional power analyses following the procedure described in Reynolds (2001) were conducted using SPAM ver 3.7b to determine sample sizes required for detection of small contributions. Stock contributions are often judged as significantly greater than zero if the lower bounds of the 95% confidence interval is greater than zero (Reynolds and Templin 2004). Simulated mixtures of N=100, 200, 300, 400, 500, 600, 700, and 800 with contributions of each population or population aggregate equal to the estimates from the District W1-B sample as estimated above, were created to evaluate the effects of mixture sample size on detection and bias.

RESULTS

Baseline

A deficit of heterozygotes was detected at *Oke3* for George River 2004; *Oki1* for Goodnews River; *Oki3* for Highpower Creek 2004, George River 2004, Salmon River, and Goodnews River; *One3* for Tatlawiksuk River 2004; *Ssa407* for George River 2004; *Ocl8* for Highpower Creek 2004; *Omy1011* for Highpower Creek 2004; *Ots105* for Kogrukluk River 2001; *Ots2MA* for Takotna River 2004; and *Ots213* for Takotna River 2004 and Kanektok River 2004 (Appendix 1). Within samples, a deficit of heterozygotes was detected for George River 2004 and Kanektok River; however, after adjusting for multiple tests for comparisons within loci and within samples, no deviation was deemed significant.

Homogeneity of allele frequencies from temporal samples from new and archived collections from the Kanektok River, Kisaralik River, George River, Kogrukluk River, Tatlawiksuk River, Takotna River, and Highpower Creek (Table 1) was tested using likelihood ratio statistics. Allele frequency differences were detected for temporal samples from the Kisaralik River (P=0.044), Kogrukluk River (P=0.009), and Takotna River (P=0.001). Only the comparison for Takotna River was deemed significant after adjusting for multiple tests. Temporal samples within tributaries were pooled for subsequent analyses.

Expected heterozygosity ranged from 0.42 in Highpower Creek to 0.59 in Goodnews River and allele richness, based on a minimum sample size of 37 individuals, ranged from 4.11 in Highpower Creek to 7.17 in Goodnews River (Appendix 2). There was a decreasing trend in both expected heterozygosity and allele richness from Kuskokwim Bay populations and populations further upstream in the Kuskokwim River (Appendix 2).

Multidimensional scaling of pairwise Cavalli-Sforza and Edwards chord distances (Cavalli-Sforza and Edwards 1967) showed spatial clustering: the samples collected furthest upstream in the Kuskokwim River (South Fork Kuskokwim River and Highpower Creek) were clearly distinct from each other and all remaining populations (Figure 3). Populations from Goodnews River, Arolik River, and Kanektok River were somewhat distinct from Kuskokwim River collections. The proportion of genetic variation for two hierarchies, one exploring among- and within-region variation, and one exploring among population and temporal variation within populations was estimated using AMOVA. The first AMOVA indicated that 95% of the observed genetic variation was due to within-population variation, 5% was due to among-region variation, and 0.4% was due to within-region (Table 3). The second AMOVA indicated that spatial variation among populations (1.2%) exceeded temporal varia-

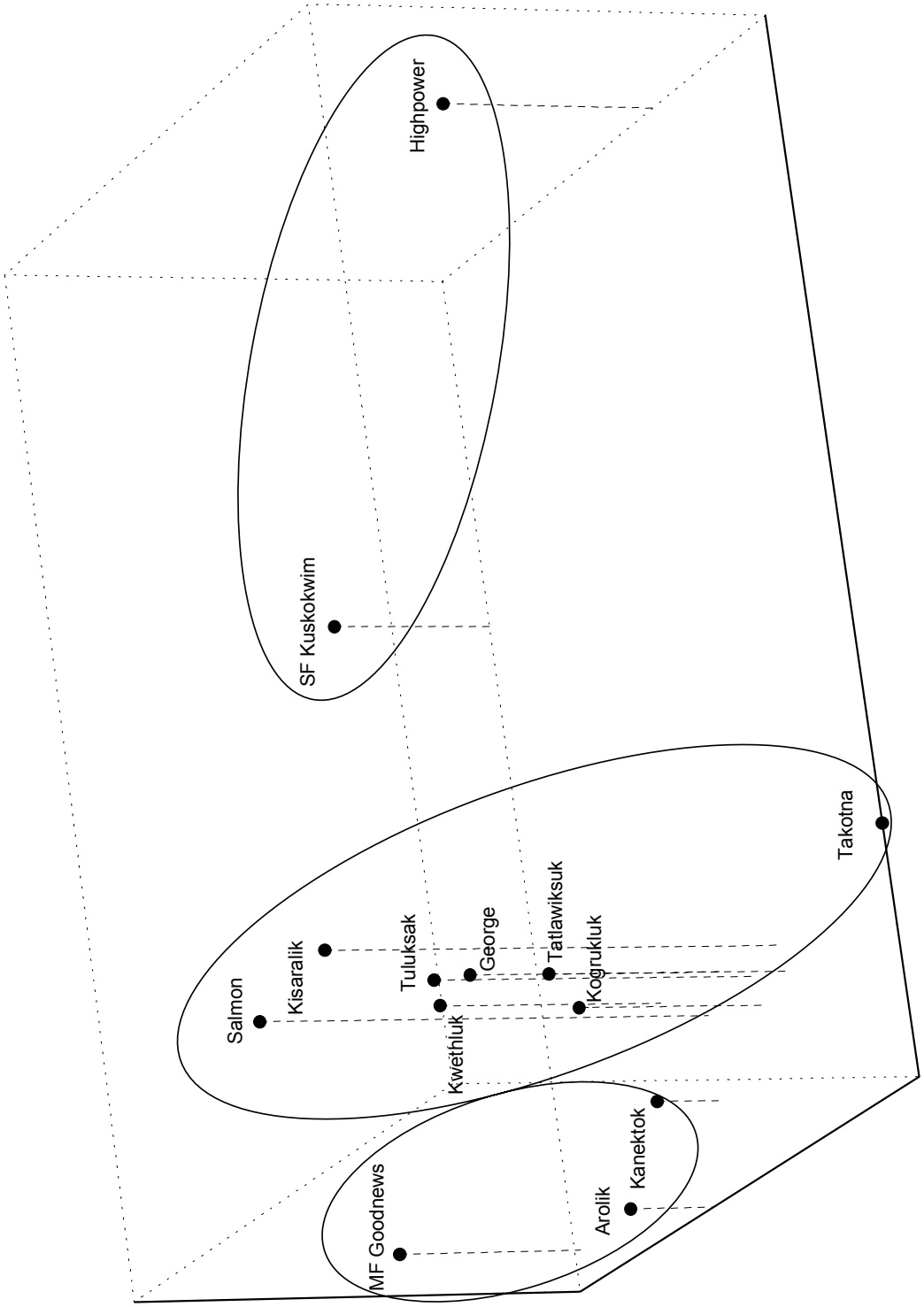

Figure 3. Multidimensional scaling analysis of Cavalli-Sforza and Edwards (Cavalli-Sforza and Edwards 1967) chord distances between populations of coho salmon sampled from the Kuskowkim region. Circles depict regions used in AMOVA.

tion within samples (0.17%) (Table 3). Though temporal variation was a small, it was significant.

A weak but significant correlation (Spearman's R=0.52; P<0.001) was found between pairwise genetic and geographic distances. The scatterplot shows a strong genetic distinction between the South Fork Kuskokwim River and Highpower Creek and all other samples (Figure 4). Two distinct clusters were apparent in the scatterplot; one comprising pairwise values including Highpower Creek and South Fork Kuskokwim River at F_{ST}>0.08, and a second cluster comprising all other comparisons at F_{ST}<0.02.

Table 3. Proportion of variation due to spatial and temporal components of coho salmon sampled from the Kuskokwim region.

Component	Proportion of Variation
1. Regional Variation	
Among region	4.72
Among populations within region	0.38
Within population	94.9
2. Temporal Variation	
Among populations	1.21
Among samples within population	0.17
Within samples	98.62

Evaluation for Mixed-Stock Analysis

Mean estimates for artificial mixtures composed of randomly generated genotypes from individual populations ranged from 0.70 for the Kisaralik River to 0.99 for the South Fork Kuskokwim River (Table 4). Populations were grouped into larger stock aggregates until mean estimates were 90% or greater: Kuskokwim Bay (0.94), Kwethluk to Tatlawiksuk River (0.95), Takotna (0.90), South Fork Kuskokwim (0.99), Highpower Creek (0.93) (Figure 5). Simulations were conducted with the original eight loci to determine if the addition of new loci increased accuracy and precision of mixture estimates. For all stock groups, the addition of new loci both increased the accuracy of the estimates and also shrank the 90% confidence intervals (Figure 6).

District W1-B Mixture Sample

Markov chain Monte Carlo estimates of stock contributions indicated that 87% of the 250 coho salmon sampled from District W1-B commercial catches on 13 August 2001 originated from tributaries of the lower and middle Kuskokwim River (Table 5). A smaller proportion originated from Kuskokwim Bay (7%). Small proportions occurred from Highpower Creek (2%), South Fork Kuskokwim River (1%), and Takotna River (3%), but zero was contained within the 95% probability interval. When Highpower Creek and South Fork Kuskokwim River were combined into a single reporting group, zero was not included within the 95% probability interval, indicating the presence of coho salmon from the upper drainage in the mixture sample.

In the power analysis, regardless of sample size, small contributions of Highpower Creek, and Highpower Creek/South Fork Kuskokwim River combined, were slightly underestimated (Figure 7). Contributions of Kuskokwim Bay were consistently overestimated, while Takotna River was overestimated in mixture sample sizes of less than N=300. Using the criterion of the lower limit of the 95% confidence interval to infer non-zero contributions, sample sizes

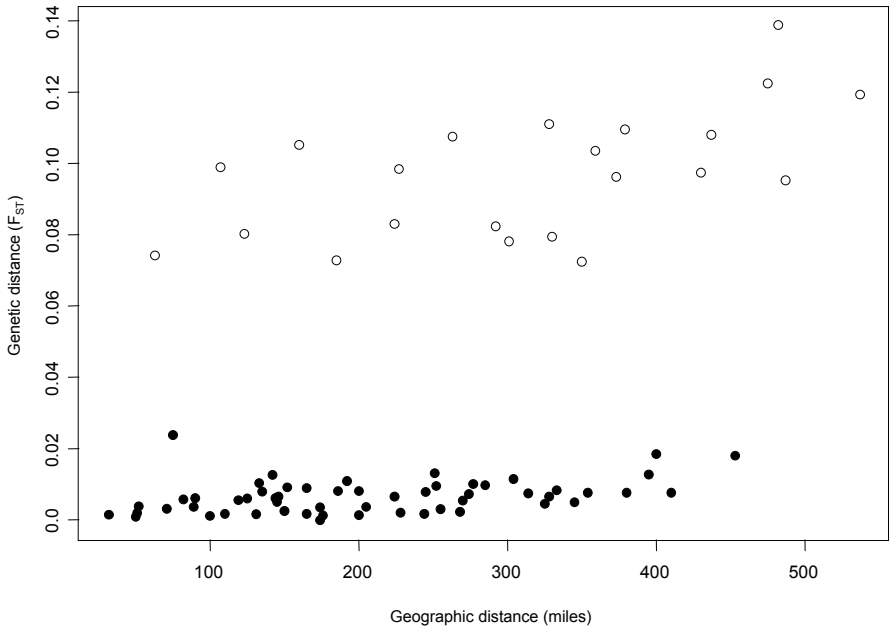

Figure 4. Scatter plot of pairwise geographic versus genetic distances for populations of coho salmon sampled from the Kuskokwim region. Open circles are pairwise comparisons including Highpower Creek and South Fork Kuskokwim River, and closed circles are all other comparisons.

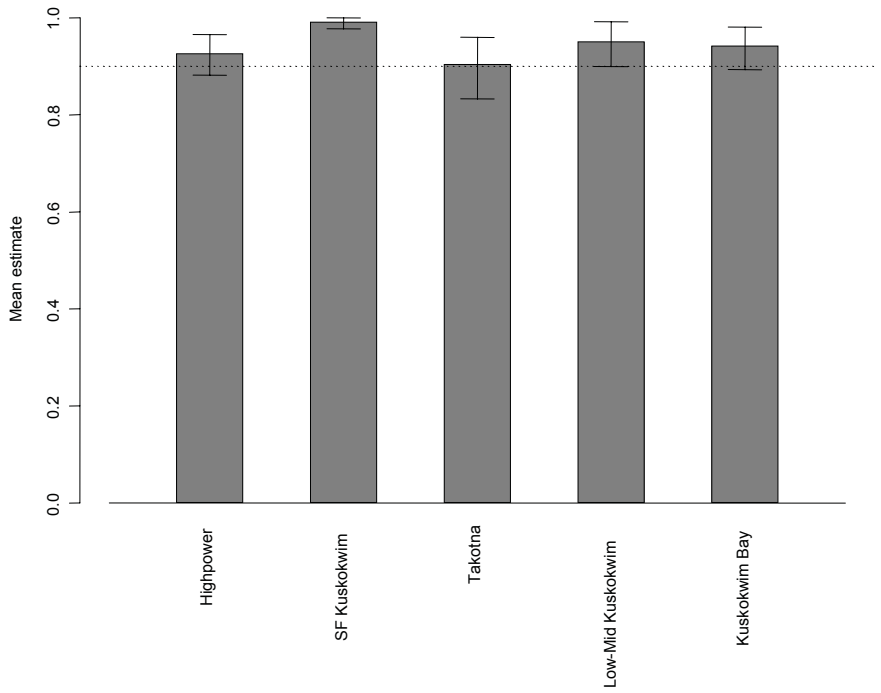

Figure 5. Mean estimates and 90% confidence intervals from simulations created from 1000 simulated mixtures composed of individual stock aggregates. Stock aggregates with mean estimates exceeding 90% (dotted line) are generally considered acceptable for mixed-stock analysis.

Table 4. Mean estimates and standard deviations of population contributions from analysis of 1000 simulated mixtures of coho salmon from individual populations in the Kuskokwim region. Mean estimates in shaded cells should approximate 100%.

	Mixture Source												
Contribution	**MFG**	**Aro**	**Kan**	**Kwe**	**Kis**	**Tul**	**Ani**	**Geo**	**Kog**	**Tat**	**Tak**	**SFK**	**Hig**
MF Goodnews	0.94	0.01	0.02	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	0.0251	0.0269	0.0251	0.0113	0.0067	0.0048	0.011	0.012	0.0159	0.0146	0.0031	0.0011	0.001
Arolik	0.05	0.86	0.07	0.00	0.00	0.00	0.01	0.00	0.01	0.00	0.00	0.00	0.00
	0.0123	0.0426	0.0232	0.0073	0.005	0.0058	0.0088	0.0053	0.0085	0.009	0.0033	0.0007	0.0004
Kanekotk	0.04	0.03	0.85	0.01	0.01	0.01	0.01	0.01	0.02	0.01	0.00	0.00	0.00
	0.0172	0.0328	0.0435	0.0096	0.0166	0.0073	0.0117	0.012	0.027	0.0227	0.0115	0.0007	0.0008
Kwethluk	0.01	0.01	0.01	0.79	0.02	0.08	0.03	0.03	0.01	0.02	0.01	0.00	0.00
	0.0121	0.0073	0.0126	0.0559	0.0544	0.0455	0.0463	0.0391	0.0331	0.0404	0.017	0.0022	0.0026
Kisaralik	0.00	0.00	0.02	0.13	0.70	0.04	0.01	0.07	0.01	0.01	0.01	0.00	0.00
	0.0049	0.004	0.0089	0.0179	0.0593	0.0063	0.0083	0.0174	0.0095	0.0056	0.0075	0.0012	0.0012
Tuluksak	0.00	0.00	0.00	0.08	0.00	0.83	0.02	0.03	0.01	0.01	0.00	0.00	0.00
	0.0056	0.0072	0.0137	0.0418	0.0323	0.0513	0.0456	0.0308	0.0364	0.0376	0.0186	0.0013	0.002
Aniak	0.01	0.01	0.01	0.09	0.01	0.10	0.74	0.01	0.01	0.02	0.00	0.00	0.00
	0.007	0.0084	0.011	0.0239	0.0134	0.019	0.053	0.0108	0.0222	0.0232	0.0033	0.0013	0.0017
George	0.01	0.00	0.01	0.06	0.02	0.04	0.01	0.81	0.04	0.01	0.01	0.00	0.00
	0.0069	0.0054	0.0128	0.0248	0.0436	0.0245	0.0134	0.0528	0.0309	0.0128	0.0157	0.0018	0.0025
Kogrukluk	0.02	0.01	0.04	0.04	0.01	0.05	0.02	0.04	0.74	0.02	0.02	0.00	0.00
	0.0077	0.0093	0.018	0.0167	0.017	0.0183	0.0143	0.0319	0.0537	0.0241	0.0179	0.0013	0.0015
Tatlawiksuk	0.02	0.01	0.03	0.06	0.00	0.06	0.03	0.01	0.02	0.76	0.01	0.00	0.00
	0.006	0.0078	0.0141	0.0194	0.0106	0.0132	0.0219	0.0109	0.0209	0.0543	0.0129	0.0008	0.0008
Takotna	0.00	0.00	0.01	0.02	0.01	0.02	0.00	0.01	0.02	0.01	0.90	0.00	0.00
	0.0028	0.0029	0.0062	0.0094	0.0087	0.0076	0.0022	0.0083	0.015	0.0106	0.0312	0.0016	0.0024
SF Kuskokwim	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.99	0.00
	0.0006	0.0004	0.0005	0.0011	0.001	0.0007	0.0007	0.0008	0.0007	0.0007	0.0011	0.006	0.0207
Highpower	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.07	0.93
	0.0002	0.0002	0.0002	0.0004	0.0004	0.0003	0.0003	0.0003	0.0002	0.0003	0.0004	0.0045	0.0211

Table 5. Markov chain Monte Carlo means, standard deviations (S.D.), and posterior quantiles for stock proportions for 250 coho salmon sampled from the W-1B fishery on 13 August 2001.

			Posterior Quantiles		
Group	**Mean**	**S.D.**	**2.50%**	**Median**	**97.50%**
Highpower Creek	2.0	1.2	0.0	1.9	4.8
South Fork Kuskokwim River	0.8	1.1	0.0	0.2	3.9
Takotna River	3.3	3.3	0.0	2.6	11.1
Tatlawiksuk to Kwethluk River	86.6	4.7	76.4	86.9	94.5
Kuskokwim Bay	7.4	3.3	2.0	7.1	14.7
Highpower Creek to South Fork Kuskokwim River	2.8	1.2	1.0	2.6	5.6
Takotna River to Kwethluk River	89.8	3.5	82.3	90.0	95.7
Kuskokwim Bay	7.4	3.3	1.9	7.1	14.5

of approximately 300–600 will be needed to identify the contribution of individual stocks in the upper Kuskokwim River; however, smaller sample sizes may suffice for estimates for a single, Highpower Creek/South Fork Kuskokwim River stock aggregate (Figure 7).

DISCUSSION

Population Structure

The majority of genetic variation in Kuskokwim region coho salmon occurs within populations (95%). This value falls within the range of values reported from similar geographic regions (90%, Yukon River, Flannery et al. 2006; 97.5%, Oregon Coast, Ford et al. 2004). Patterns of within-population variation for Kuskokwim River coho salmon follow that described for Chinook salmon (Templin et al. 2004) in that Kuskokwim Bay and lower Kuskokwim River populations show more within-population diversity than in populations further upstream. For coho salmon, mean heterozygosity and allele richness were highest in Kuskokwim Bay populations, with a decreasing trend in these diversity measures with geographic distance from the river mouth.

Of the remaining variation, genetic differences among regions accounted for more variation than among populations within regions. Though allele frequency differences were detected between temporal samples collected from Kisaralik, Kogrukluk, and Takotna rivers, among-population variation was a far greater component of overall variation.

Both the MDS and IBD analysis indicated a genetic discontinuity between the Takotna River and the South Fork of the Kuskokwim River. Pairwise F_{ST} estimates between Highpower Creek and South Fork Kuskokwim River in the upper Kuskokwim with samples from the Takotna River to the river mouth were approximately 0.1, a value indicative of strong genetic divergence (e.g., Faubet et al. 2007). This discontinuity has been reported at approximately the same geographical location for other salmon species (chum salmon: Takotna River and Big River, Gilk et al. 2005, Seeb et al. 1997; Chinook salmon: Takotna River and Pitka Fork, Templin et al. 2004). Vicariance is often implicated when barriers to gene flow are detected,

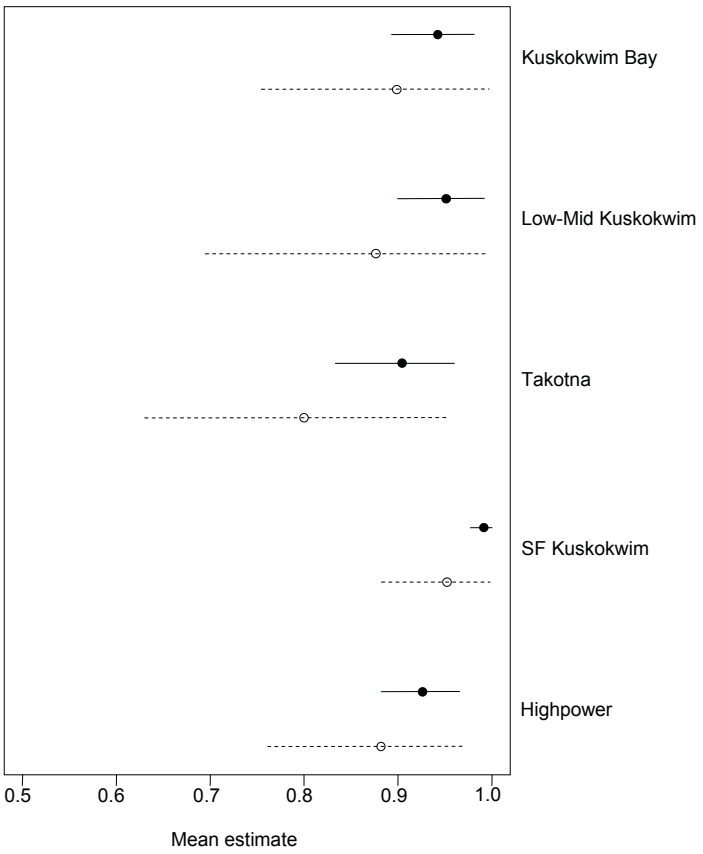

Figure 6. Mean estimates and 90% confidence intervals from simulations created from 1000 simulated mixtures composed of individual stock aggregates. Solid circles and lines are simulations using data from 15 microsatellite loci; open circles and dashed lines are simulations using eight microsatellite loci reported in Crane et al. (2004).

especially when such barriers are observed in multiple species (Avise 1994). It is possible that salmon in the upper Kuskokwim River drainage shared a separate and distinct refuge during the Pleistocene from salmon that now inhabit the lower Kuskokwim River and coastal rivers. A similar pattern exists in the Yukon River, where populations of Chinook salmon and coho salmon in the upper drainage are genetically distinct from more homogenous populations in the lower Yukon River. Patterns of genetic diversity in the Yukon River may represent secondary contact between upper river populations that are remnant from those inhabiting the Yukon River during the Pleistocene and lower populations extant from colonizers from coastal streams of the Bering Land Bridge (Flannery et al. 2006; Olsen et al. submitted).

Differences in spawning or run timing can also produce barriers to gene flow and produce patterns such as the IBD observed in this study (e.g., Olsen et al. 2006). Run timing has been used to explain genetic differences observed in upper versus lower river populations of Kuskokwim River chum salmon (Seeb et al. 1997; Templin et al. 2004). Coho salmon spawning in the upper Kuskokwim River may represent some of the longest freshwater migrations known for this species. Coho salmon typically do not migrate more than 240 km upstream

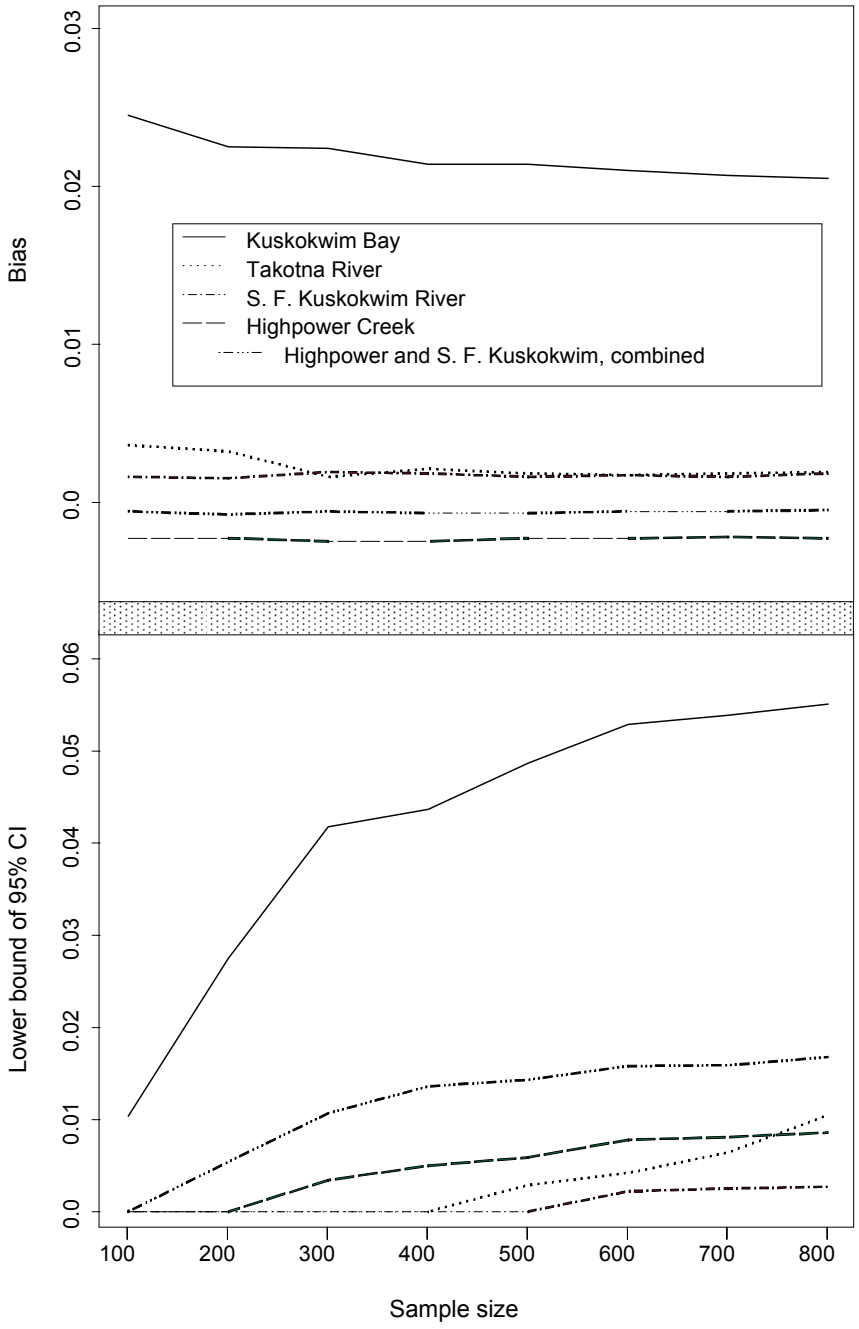

Figure 7. Bias estimates and lower limit of 95% bootstrap confidence intervals for varying mixture sample sizes. True stock contributions were based on small (<10%) stock contributions estimated from a W1-B fishery sample, as follows: Kuskokwim Bay, 7%; Takotna River, 3%; South Fork Kuskokwim River, 1%; and Highpower Creek, 2%.

in large river systems; migrations of over 1,000 km have only been reported for the Yukon River (Sandercock 1991). Coho salmon spawning in the upper reaches of the Kuskokwim River travel distances of 1,100 to 1,500 km from the river mouth (Whitmore et al. 2005). Time of entry from marine waters for upstream spawners is typically earlier than for lower river spawners (Sandercock 1991), a life history attribute also observed in the Kuskokwim River. Mark-recapture data show that coho salmon bound for the Takotna River were among the first to migrate passed the tagging site in the lower Kuskokwim River, and that fish tagged earlier had slower travel times (Pawluk et al. 2006; Figure 2). The central 50% of the run monitored at weir sites in the region are earlier for the Takotna and Tatlawiksuk rivers than for weir sites further down stream or in Kuskokwim Bay drainages (e.g.; Shelden et al. 2005; Costello et al. 2006a, 2006b; Jones and Linderman 2006a, 2006b). Regardless of the origin of genetic differentiation in the Kuskokwim River drainage, South Fork Kuskokwim River and Highpower Creek and populations from the Kwethluk to Takotna rivers represent distinct diversity groups.

Mixed-Stock Fishery Applications

Reliable estimation of the stock composition of mixtures is dependent, in part, on adequate sampling of the genetic diversity of baseline populations contributing to the mixture (Shaklee and Phelps 1990). Although our collections represent a wide geographic array, we were unsuccessful in collecting coho salmon spawning in the Eek River and Stony River, as originally intended. For estimation of the origin of Kuskokwim Bay coho salmon, sampling of the Eek River, located at the mouth of the Kuskokwim River, may be warranted to determine if these fish are genetically more similar to Kuskokwim Bay or Kuskokwim River coho salmon. Sampling of fish from the Stony River may be less important, given that fish from the Tatlawiksuk River, immediately upstream of the Stony River, were more similar to lower river populations than to the Takotna River. Improved understanding of the distribution and relative contribution of tributaries, perhaps through radio-telemetry studies, would provide better insight as to where additional baseline sampling is needed.

The addition of more loci clearly improved both the accuracy and precision of mixture estimates in our simulation study (Figure 6). Increasing the number of loci used in mixture analyses can often improve stock composition estimates providing that new loci add novel information (e.g., Scribner et al. 1998; Winans et al. 2004), and may be especially useful when low levels of genetic diversity exist among stocks (Faubet et al. 2007). When large numbers of loci are available for stock composition estimation, a variety of methods have been suggested for finding the most parsimonious set of loci to address a mixture problem, e.g., ranking loci according to information content indicated by number of alleles (e.g., Beacham et al. 2006), or searches of combinations of loci (e.g., Bromaghin 2007). Though not evaluated in this study, these methods could improve the cost effectiveness of mixture analysis by reducing the number of loci needed to estimate regional groups.

Simulation analyses indicated that the following five stock groups could be identified in mixtures comprising coho salmon from the populations sampled in this study: Kuskokwim Bay (Goodnews, Arolik, and Kanektok rivers); lower-middle Kuskokwim (Kwethluk, Kisaralik, Tuluksak, Salmon, George, Kogrukluk, and Tatlawiksuk rivers); Takotna River; South Fork Kuskokwim River; and Highpower Creek. These stock groupings suggest two areas where

genetic data may be useful in mixed-stock fishery applications: 1) separation of Kuskokwim Bay from Kuskokwim River populations, and 2) separation of coho salmon spawning in the upper reaches of the Kuskokwim River from remaining populations. Concern about disproportionate exploitation rates on upper Kuskokwim River coho salmon populations can be addressed through mixed-stock analysis of samples from the Bethel test fishery and/or commercial fishery of District W1 collected throughout the duration of the coho salmon run to estimate the relative proportion and timing of upriver populations which currently receive little monitoring. Similarly, the efficacy of boundary changes for reducing the catch of salmon bound for the Kuskokwim River in the District W4 fishery could be evaluated through MSA (Templin et al. 2004; Fisheries Resource Monitoring Plan 2005, http://alaska.fws.gov/asm/fisdetails.cfm?choose=5). The boundaries for the District W4 fishery were modified by the Alaska Board of Fisheries to reduce suspected interception by Kuskokwim Bay fishers of Chinook and chum salmon bound for Kuskokwim River (Burkey et al. 2000a, 2000b). The measure was reversed in January 2004 because of the lack of evidence that the boundary change had any effect in conserving Kuskokwim River salmon (Whitmore and Bergstrom 2003). A better understanding of the migration patterns of coho salmon stocks through Kuskokwim Bay could be important in years when this species is in low abundance in the Kuskokwim River.

District W1-B Mixture Sample

The majority of fish sampled from the W1-B mixture sample originated from tributaries in the lower and middle portion of the Kuskokwim River, with smaller proportions originating from Kuskokwim Bay drainages (7%) and tributaries of the upper Kuskokwim River (Highpower Creek, South Fork Kuskokwim River, 3%). The conditional power analysis, given the stock proportions in the W1-B mixture estimate, indicated that small contributions of Kuskokwim Bay are generally overestimated, while contributions from the upper Kuskokwim River are close to their true proportions (Figure 6). Though a proportion of the estimate for Kuskokwim Bay may be misallocation between Kuskokwim Bay and lower-middle Kuskokwim River stocks, District W1-B includes the Kuskokwim River mouth and is entirely under tidal influence and other in-river mixture studies have detected fish from other drainages, perhaps due to "nosing-in". For example, Robertson (1984), using scale-pattern analyses and coded-wire tagging, found sockeye salmon originating from the Wood River in mixture samples collected in the Nushagak River 50 km upstream from the river mouth.

The detection of small contributions to mixtures presents a statistical challenge (Reynolds and Templin 2004); however, the genetic distinctiveness of coho salmon of South Fork Kuskokwim River and Highpower Creek in the upper Kuskokwim River may permit the estimation of very small proportions, even in relatively small mixture samples (Figure 6) and suggests that for small proportions, fishery sampling error may be more of a concern than genetic error in mixture analysis. Further, their genetic distinctiveness may also support individual-based analyses. Cornuet et al. (1999) found that for F_{ST} approximating 0.1, the accuracy of identifying the origin of individuals should be close to 100%. The posterior assignment probabilities of genotypes in the Bayesian mixture analysis used in this study indicated that five of the 242 individuals from the mixture analysis were likely to have originated from South Fork Kuskokwim River/Highpower Creek.

CONCLUSIONS

- A database of microsatellite allele frequencies and a tissue archive of baseline samples are available for use in future mixture- or population-level analyses.
- Significant genetic population structure exists in coho salmon in the Kuskokwim region.
- A strong genetic discontinuity occurs between populations located from the Takotna River downstream and populations further upstream in the Kuskokwim River, a pattern similar to that observed previously in chum and Chinook populations.
- Populations in the lower Kuskokwim River have more within-population variability and less among population variability than populations in the upper Kuskokwim River.
- Analysis of artificial mixtures indicated that the following groups can be identified in mixtures comprising the populations sampled in this study: Kuskokwim Bay (Goodnews, Arolik, and Kanektok rivers); lower-middle Kuskokwim (Kwethluk, Kisaralik, Tuluksak, Salmon, George, Kogrukluk, and Tatlawiksuk rivers); Takotna River; South Fork Kuskokwim River; and Highpower Creek.
- The genetic distinctiveness of coho salmon in South Fork Kuskokwim River and Highpower Creek should permit estimation of very small mixture proportions even in relatively small mixture samples.

RECOMMENDATIONS

The following recommendations could be implemented in order to address management concerns detailed above:

- Continue sampling of coho salmon populations for genetic analysis on opportunistic basis, especially the Eek River, Stony River, and tributaries in the upper Kuskokwim River drainage, as well as other Bering Sea basin stocks that may potentially pass through the Kuskokwim region.
- Use radio-telemetry deployment on coho salmon to better define the distribution and relative contribution of coho salmon spawning streams in the Kuskokwim River drainage, and use the findings to target genetic sampling of additional populations.
- Collect a temporal array of mixed-stock coho salmon samples from the lower Kuskokwim River (District W1) to assess run timing of genetically identifiable aggregates through the commercial fishing district.
- Collect a temporal array of mixed-stock coho salmon samples from District W4 to assess potential interception of Kuskokwim River coho salmon in that fishery through the commercial fishing district.

- Collect a temporal array of mixed-stock coho salmon samples from District W5 to assess potential interception of Kuskokwim River coho salmon in that fishery through the commercial fishing district.

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Appendix 1. Sample size, allele frequency estimates, and *P* (F_{is}>0) for coho salmon collected from the Kuskokwim region. Bold *P*-values indicate a significant deficit of heterozygotes.

Locus/*N*/ Allele		*Hig04*	*Hig05*	*SFK04*	*Tak03*	*Tak04*	*Tat01*	*Tat04*	*Kog01*	*Kog04*	*Geo01*	*Geo04*	*Sal04*	*Tul04*	*Kis97*	*Kis04*	*Kwe04*	*Kan01*	*Kan04*	*Aro97*	*Goo04*
Oke2	*N*	26	21	200	161	99	96	100	96	100	95	100	100	198	81	54	200	96	99	86	193
	170	1.000	1.000	0.885	0.829	0.914	0.891	0.875	0.885	0.905	0.916	0.855	0.870	0.874	0.914	0.898	0.903	0.943	0.854	0.977	0.891
	172	0.000	0.000	0.115	0.171	0.086	0.109	0.125	0.115	0.095	0.084	0.145	0.130	0.126	0.086	0.102	0.098	0.057	0.146	0.023	0.109
	P	NA	NA	1	0.1388	1	0.294	1	1	0.6095	0.4942	0.9105	0.52	0.6362	1	1	1	1	1	1	0.3898
Oke3	*N*	22	17	194	160	97	96	96	95	99	96	96	93	192	73	53	197	96	94	93	199
	250	0.000	0.000	0.005	0.034	0.036	0.063	0.036	0.079	0.025	0.031	0.057	0.022	0.068	0.062	0.047	0.063	0.026	0.037	0.011	0.018
	254	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.003	0.000	0.000	0.000	0.000
	256	0.045	0.059	0.013	0.041	0.005	0.005	0.000	0.011	0.020	0.021	0.010	0.016	0.005	0.048	0.000	0.015	0.005	0.011	0.000	0.015
	260	0.000	0.029	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
	262	0.000	0.000	0.003	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.003	0.000	0.000	0.000	0.000
	264	0.091	0.176	0.193	0.203	0.232	0.255	0.318	0.200	0.268	0.224	0.234	0.161	0.211	0.123	0.217	0.135	0.266	0.277	0.339	0.286
	268	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.005	0.000	0.000	0.000	0.000	0.000	0.000	0.000
	272	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.005	0.000	0.003
	274	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.026	0.016	0.000	0.003	0.000	0.000	0.000	0.000	0.000	0.000	0.003
	276	0.705	0.647	0.606	0.588	0.644	0.583	0.495	0.642	0.556	0.547	0.495	0.683	0.547	0.568	0.528	0.581	0.615	0.564	0.651	0.510
	278	0.159	0.088	0.180	0.134	0.082	0.094	0.151	0.068	0.131	0.151	0.188	0.118	0.161	0.199	0.208	0.201	0.089	0.106	0.000	0.166
	P	0.2245	0.4953	0.2877	0.8703	0.9378	0.3442	0.6475	0.6358	0.9492	0.8575	**0.021**	0.8492	0.3605	0.98	0.6125	0.355	0.8537	0.0848	0.9775	0.5548
Oke4	*N*	20	17	182	155	98	93	99	96	100	90	99	97	196	81	52	199	95	99	87	200
	234	0.000	0.000	0.000	0.000	0.010	0.005	0.000	0.000	0.015	0.006	0.000	0.005	0.015	0.000	0.000	0.010	0.000	0.000	0.006	0.000
	238	0.000	0.000	0.005	0.023	0.020	0.016	0.020	0.036	0.025	0.044	0.091	0.026	0.023	0.012	0.019	0.010	0.063	0.030	0.046	0.078
	242	1.000	1.000	0.995	0.977	0.969	0.978	0.980	0.964	0.960	0.939	0.904	0.964	0.962	0.988	0.981	0.980	0.937	0.970	0.948	0.918
	244	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.011	0.005	0.005	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.005
	P	NA	NA	1	1	1	1	1	1	1	1	0.5688	1	1	1	1	1	1	1	0.196	1
Oki1	*N*	26	20	200	158	99	91	99	96	100	96	99	98	197	87	54	199	94	99	88	200
	92	0.000	0.000	0.003	0.000	0.000	0.000	0.000	0.000	0.005	0.026	0.005	0.000	0.000	0.000	0.000	0.000	0.011	0.005	0.006	0.000
	96	0.019	0.000	0.015	0.013	0.035	0.033	0.005	0.026	0.020	0.047	0.020	0.036	0.020	0.011	0.019	0.020	0.021	0.010	0.017	0.035
	100	0.250	0.325	0.243	0.519	0.505	0.423	0.480	0.453	0.565	0.500	0.475	0.459	0.477	0.494	0.361	0.430	0.436	0.515	0.426	0.460
	104	0.327	0.375	0.175	0.127	0.091	0.143	0.162	0.089	0.115	0.135	0.126	0.122	0.107	0.080	0.074	0.163	0.154	0.162	0.142	0.215
	108	0.385	0.300	0.473	0.133	0.202	0.132	0.111	0.135	0.075	0.109	0.162	0.133	0.162	0.201	0.231	0.138	0.101	0.106	0.080	0.095
	112	0.019	0.000	0.075	0.203	0.157	0.269	0.237	0.281	0.200	0.177	0.202	0.250	0.221	0.201	0.278	0.236	0.261	0.187	0.295	0.153
	116	0.000	0.000	0.018	0.006	0.010	0.000	0.005	0.016	0.020	0.005	0.010	0.000	0.013	0.006	0.028	0.013	0.016	0.015	0.017	0.023
	120	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.006	0.009	0.000	0.000	0.000	0.000	0.005
	124	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.017	0.013
	132	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.003
	P	0.7213	0.9947	0.9598	0.8768	0.6798	0.9975	0.1288	0.8408	0.6138	0.734	0.9247	0.1163	0.7725	0.983	0.5612	0.2438	0.8177	0.3615	0.8647	**0.029**

Continued

Appendix 1. Continued.

Locus/*N*/ Allele		*Hig04*	*Hig05*	*SFK04*	*Tak03*	*Tak04*	*Tat01*	*Tat04*	*Kog01*	*Kog04*	*Geo01*	*Geo04*	*Sal04*	*Tul04*	*Kis97*	*Kis04*	*Kwe04*	*Kan01*	*Kan04*	*Aro97*	*Goo04*
Oki3	*N*	21	17	187	153	99	96	91	96	97	84	98	98	197	85	52	196	94	100	87	199
	64	0.000	0.000	0.003	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
	67	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.010	0.000	0.000	0.000	0.000	0.000	0.000	0.000
	70	0.810	0.765	0.655	0.281	0.379	0.276	0.302	0.328	0.242	0.250	0.306	0.250	0.256	0.306	0.260	0.293	0.223	0.170	0.132	0.183
	73	0.190	0.235	0.342	0.719	0.621	0.724	0.698	0.672	0.758	0.750	0.694	0.750	0.731	0.688	0.740	0.704	0.777	0.830	0.868	0.817
	76	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.003	0.006	0.000	0.003	0.000	0.000	0.000	0.000
	P	**0.006**	1	0.8542	0.9228	0.9403	0.9945	0.4395	0.0628	0.3007	0.6492	**0.016**	**0.033**	0.7425	0.3718	0.4748	0.1702	0.7437	0.5677	0.8092	**0.013**
Oki11	*N*	28	20	200	162	98	96	99	96	100	96	99	98	199	89	53	200	92	98	90	200
	82	0.000	0.000	0.000	0.003	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
	84	1.000	1.000	0.980	0.827	0.837	0.839	0.828	0.849	0.850	0.839	0.869	0.832	0.791	0.831	0.774	0.813	0.772	0.811	0.800	0.773
	86	0.000	0.000	0.000	0.000	0.000	0.000	0.005	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
	88	0.000	0.000	0.020	0.167	0.163	0.161	0.162	0.135	0.145	0.146	0.121	0.153	0.198	0.169	0.198	0.173	0.228	0.189	0.194	0.225
	90	0.000	0.000	0.000	0.003	0.000	0.000	0.005	0.016	0.005	0.016	0.010	0.015	0.010	0.000	0.028	0.015	0.000	0.000	0.006	0.003
	P	NA	NA	1	0.995	0.4915	0.9475	0.1143	0.8733	0.3757	0.9108	0.8093	0.533	0.5787	0.7612	0.3578	0.9138	0.0505	0.7112	0.248	0.9998
One3	N	24	18	199	149	99	96	99	95	99	96	98	98	198	58	54	197	91	99	90	200
	173	0.542	0.556	0.583	0.483	0.455	0.464	0.414	0.384	0.439	0.370	0.439	0.398	0.455	0.397	0.528	0.409	0.445	0.404	0.389	0.318
	175	0.229	0.250	0.284	0.151	0.116	0.193	0.152	0.274	0.172	0.276	0.194	0.250	0.179	0.224	0.139	0.193	0.176	0.177	0.194	0.210
	177	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.005	0.000	0.000	0.000	0.000	0.003	0.000	0.000	0.000	0.000	0.000	0.000	0.003
	179	0.229	0.167	0.106	0.292	0.298	0.203	0.247	0.205	0.227	0.208	0.240	0.204	0.197	0.224	0.157	0.254	0.181	0.242	0.194	0.208
	181	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.009	0.000	0.000	0.000	0.000	0.000
	183	0.000	0.028	0.028	0.074	0.131	0.141	0.187	0.132	0.162	0.146	0.128	0.148	0.167	0.155	0.167	0.145	0.198	0.177	0.222	0.263
	P	0.9665	0.1743	0.0935	0.335	0.553	0.8482	**0.013**	0.3923	0.3897	0.3895	0.2318	0.5878	0.6617	0.6698	0.1525	0.2055	0.6453	0.7077	0.2285	0.2822
Ots105	*N*	26	18	170	162	99	96	98	95	98	96	97	99	197	61	52	199	96	98	90	200
	129	1.000	0.944	0.929	0.806	0.909	0.839	0.847	0.842	0.806	0.802	0.845	0.884	0.845	0.852	0.865	0.842	0.745	0.770	0.789	0.798
	133	0.000	0.056	0.071	0.194	0.091	0.161	0.153	0.158	0.194	0.198	0.155	0.116	0.155	0.148	0.125	0.158	0.255	0.230	0.211	0.203
	137	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.010	0.000	0.000	0.000	0.000	0.000
	P	NA	1	0.5788	0.3923	0.579	0.7602	1	**0.049**	0.7627	0.9313	0.3983	0.1157	0.7267	0.7757	0.5718	0.773	0.9265	0.8123	0.8247	0.428

Continued

Appendix 1. Continued.

Locus/*N*/ Allele		*Hig04*	*Hig05*	*SFK04*	*Tak03*	*Tak04*	*Tat01*	*Tat04*	*Kog01*	*Kog04*	*Geo01*	*Geo04*	*Sal04*	*Tul04*	*Kis97*	*Kis04*	*Kwe04*	*Kan01*	*Kan04*	*Aro97*	*Goo04*
Omy1011	*N*	29	21	183		98		97		99		100	96	184		53	191		100	84	193
	179	0.397	0.190	0.221		0.362		0.268		0.263		0.345	0.219	0.242		0.349	0.275		0.305	0.244	0.238
	183	0.517	0.786	0.607		0.189		0.155		0.162		0.160	0.104	0.147		0.094	0.157		0.180	0.196	0.228
	187	0.086	0.024	0.066		0.204		0.263		0.278		0.165	0.250	0.253		0.189	0.225		0.170	0.226	0.171
	191	0.000	0.000	0.000		0.000		0.000		0.005		0.000	0.005	0.003		0.000	0.000		0.000	0.000	0.000
	195	0.000	0.000	0.000		0.000		0.000		0.000		0.000	0.000	0.000		0.000	0.000		0.000	0.000	0.010
	199	0.000	0.000	0.000		0.051		0.015		0.015		0.035	0.021	0.011		0.000	0.024		0.025	0.030	0.049
	203	0.000	0.000	0.000		0.000		0.000		0.000		0.000	0.000	0.003		0.000	0.003		0.005	0.006	0.005
	207	0.000	0.000	0.025		0.077		0.067		0.076		0.075	0.063	0.079		0.038	0.097		0.080	0.077	0.083
	211	0.000	0.000	0.057		0.087		0.129		0.131		0.160	0.255	0.168		0.208	0.162		0.160	0.155	0.153
	215	0.000	0.000	0.014		0.010		0.021		0.025		0.010	0.036	0.049		0.038	0.031		0.030	0.018	0.003
	219	0.000	0.000	0.011		0.020		0.082		0.035		0.045	0.042	0.038		0.085	0.024		0.045	0.048	0.052
	223	0.000	0.000	0.000		0.000		0.000		0.010		0.000	0.005	0.005		0.000	0.003		0.000	0.000	0.008
	231	0.000	0.000	0.000		0.000		0.000		0.000		0.000	0.000	0.003		0.000	0.000		0.000	0.000	0.000
	235	0.000	0.000	0.000		0.000		0.000		0.000		0.005	0.000	0.000		0.000	0.000		0.000	0.000	0.000
	P	**0.047**	0.5535	0.2183		0.0662		0.198		0.3345		0.4693	0.9435	0.0743		0.1195	0.0643		0.2045	0.9775	0.9897
Ssa407	*N*	26	21	184		98		97		98		100	96	184		54	193		100	81	182
	152	0.000	0.000	0.000		0.000		0.005		0.000		0.000	0.000	0.000		0.000	0.000		0.000	0.000	0.000
	156	0.038	0.048	0.082		0.260		0.175		0.153		0.190	0.141	0.174		0.120	0.140		0.130	0.160	0.146
	160	0.000	0.000	0.024		0.031		0.000		0.010		0.020	0.000	0.000		0.028	0.010		0.020	0.019	0.025
	164	0.000	0.000	0.000		0.000		0.026		0.010		0.010	0.005	0.005		0.000	0.008		0.000	0.000	0.036
	168	0.000	0.000	0.030		0.092		0.124		0.102		0.085	0.130	0.120		0.074	0.163		0.120	0.105	0.162
	172	0.115	0.262	0.049		0.276		0.340		0.337		0.250	0.281	0.293		0.296	0.280		0.415	0.346	0.308
	176	0.115	0.095	0.079		0.117		0.108		0.117		0.165	0.177	0.111		0.222	0.135		0.125	0.179	0.124
	180	0.000	0.000	0.000		0.005		0.010		0.005		0.025	0.010	0.030		0.046	0.023		0.000	0.012	0.005
	184	0.000	0.000	0.003		0.000		0.000		0.000		0.000	0.021	0.003		0.000	0.003		0.000	0.000	0.000
	188	0.038	0.000	0.068		0.000		0.000		0.015		0.005	0.000	0.000		0.000	0.003		0.000	0.000	0.008
	192	0.019	0.048	0.109		0.000		0.021		0.010		0.025	0.010	0.024		0.028	0.034		0.015	0.031	0.025
	196	0.096	0.048	0.117		0.056		0.062		0.036		0.075	0.094	0.054		0.093	0.065		0.050	0.037	0.047
	200	0.423	0.310	0.231		0.082		0.082		0.082		0.090	0.063	0.106		0.056	0.070		0.080	0.062	0.038
	204	0.154	0.167	0.068		0.026		0.041		0.056		0.045	0.052	0.071		0.019	0.052		0.025	0.012	0.016
	208	0.000	0.024	0.049		0.051		0.000		0.041		0.010	0.000	0.005		0.000	0.008		0.000	0.000	0.008
	212	0.000	0.000	0.022		0.000		0.000		0.000		0.000	0.000	0.000		0.000	0.000		0.005	0.012	0.027
	216	0.000	0.000	0.024		0.000		0.005		0.005		0.005	0.005	0.003		0.019	0.008		0.000	0.019	0.014
	220	0.000	0.000	0.046		0.005		0.000		0.000		0.000	0.010	0.000		0.000	0.000		0.000	0.006	0.003
	224	0.000	0.000	0.000		0.000		0.000		0.020		0.000	0.000	0.000		0.000	0.000		0.010	0.000	0.005
	228	0.000	0.000	0.000		0.000		0.000		0.000		0.000	0.000	0.000		0.000	0.000		0.005	0.000	0.003
	P	0.353	0.586	0.2512		0.9785		0.8262		0.2947		**0.043**	0.926	0.8697		0.5727	0.116		0.884	0.9903	0.9108

Continued

Appendix 1. Continued.

Locus/*N*/ Allele		*Hig04*	*Hig05*	*SFK04*	*Tak03*	*Tak04*	*Tat01*	*Tat04*	*Kog01*	*Kog04*	*Geo01*	*Geo04*	*Sal04*	*Tul04*	*Kis97*	*Kis04*	*Kwe04*	*Kan01*	*Kan04*	*Aro97*	*Goo04*
Ocl8	*N*	29	21	199		96		97		98		99	94	196		51	194		98	86	198
	95	0.000	0.000	0.000		0.000		0.000		0.000		0.000	0.000	0.000		0.010	0.000		0.000	0.000	0.000
	97	0.000	0.000	0.000		0.000		0.000		0.000		0.000	0.000	0.003		0.000	0.000		0.000	0.000	0.000
	99	0.017	0.000	0.048		0.089		0.052		0.102		0.081	0.080	0.082		0.069	0.085		0.077	0.081	0.013
	101	0.000	0.000	0.000		0.000		0.000		0.000		0.000	0.000	0.000		0.000	0.000		0.000	0.000	0.003
	103	0.000	0.000	0.003		0.005		0.000		0.005		0.020	0.011	0.013		0.010	0.021		0.015	0.017	0.058
	105	0.000	0.000	0.000		0.068		0.005		0.020		0.010	0.000	0.010		0.020	0.008		0.020	0.017	0.020
	107	0.793	0.762	0.781		0.708		0.680		0.556		0.646	0.644	0.625		0.618	0.647		0.628	0.622	0.591
	109	0.000	0.000	0.023		0.047		0.144		0.168		0.116	0.128	0.128		0.147	0.111		0.117	0.087	0.134
	111	0.069	0.024	0.083		0.010		0.010		0.005		0.000	0.005	0.013		0.000	0.013		0.000	0.012	0.018
	113	0.000	0.000	0.000		0.000		0.000		0.000		0.005	0.000	0.005		0.000	0.005		0.000	0.000	0.000
	115	0.000	0.000	0.000		0.000		0.000		0.000		0.000	0.000	0.000		0.000	0.000		0.000	0.000	0.003
	117	0.000	0.024	0.000		0.000		0.000		0.000		0.000	0.000	0.003		0.000	0.000		0.000	0.000	0.000
	121	0.121	0.190	0.028		0.026		0.067		0.087		0.066	0.080	0.079		0.078	0.049		0.056	0.047	0.045
	125	0.000	0.000	0.000		0.000		0.000		0.015		0.025	0.005	0.005		0.000	0.005		0.000	0.006	0.000
	127	0.000	0.000	0.000		0.005		0.000		0.000		0.000	0.000	0.000		0.000	0.000		0.000	0.000	0.003
	137	0.000	0.000	0.000		0.000		0.005		0.000		0.000	0.000	0.000		0.000	0.000		0.000	0.000	0.008
	139	0.000	0.000	0.008		0.000		0.000		0.000		0.000	0.005	0.000		0.020	0.008		0.000	0.000	0.005
	141	0.000	0.000	0.000		0.000		0.000		0.000		0.000	0.000	0.000		0.000	0.005		0.000	0.000	0.008
	143	0.000	0.000	0.028		0.042		0.036		0.041		0.030	0.043	0.036		0.029	0.039		0.082	0.110	0.093
	145	0.000	0.000	0.000		0.000		0.000		0.000		0.000	0.000	0.000		0.000	0.003		0.005	0.000	0.000
	147	0.000	0.000	0.000		0.000		0.000		0.000		0.000	0.000	0.000		0.000	0.003		0.000	0.000	0.000
	P	**0.006**	1	0.7318		0.501		0.9018		0.9973		0.8555	0.37	0.2427		0.552	0.764		0.0917	0.1527	0.8022
Ots2MA	*N*	29	21	199		97		99		98		98	98	196		52	191		98	87	198
	133	0.379	0.381	0.214		0.072		0.025		0.036		0.061	0.056	0.061		0.077	0.060		0.026	0.000	0.033
	135	0.500	0.452	0.442		0.299		0.303		0.265		0.291	0.276	0.253		0.231	0.285		0.255	0.236	0.255
	137	0.017	0.048	0.128		0.222		0.247		0.347		0.316	0.214	0.237		0.375	0.275		0.250	0.293	0.295
	139	0.103	0.119	0.173		0.402		0.424		0.342		0.327	0.449	0.441		0.317	0.369		0.439	0.431	0.386
	141	0.000	0.000	0.043		0.000		0.000		0.010		0.005	0.005	0.008		0.000	0.010		0.031	0.040	0.030
	145	0.000	0.000	0.000		0.005		0.000		0.000		0.000	0.000	0.000		0.000	0.000		0.000	0.000	0.000
	P	0.9797	0.935	0.0513		**0.03**		0.2657		0.8392		0.918	0.7645	0.7752		0.7165	0.4317		0.1163	0.972	0.7595

Continued

Appendix 1. Continued.

Locus/*N*/ Allele		*Hig04*	*Hig05*	*SFK04*	*Tak03*	*Tak04*	*Tat01*	*Tat04*	*Kog01*	*Kog04*	*Geo01*	*Geo04*	*Sal04*	*Tul04*	*Kis97*	*Kis04*	*Kwe04*	*Kan01*	*Kan04*	*Aro97*	*Goo04*
Ots2MB	*N*	29	20	194		96		97		98		95	95	194		48	192		99	86	196
	161	0.069	0.000	0.057		0.026		0.021		0.020		0.063	0.032	0.034		0.104	0.036		0.091	0.087	0.079
	163	0.000	0.000	0.003		0.000		0.000		0.000		0.000	0.000	0.000		0.000	0.000		0.005	0.000	0.000
	165	0.000	0.000	0.008		0.005		0.000		0.000		0.000	0.005	0.015		0.000	0.003		0.000	0.000	0.000
	167	0.000	0.000	0.000		0.000		0.000		0.000		0.000	0.000	0.003		0.000	0.000		0.000	0.000	0.000
	169	0.000	0.000	0.000		0.000		0.000		0.000		0.026	0.005	0.015		0.010	0.008		0.000	0.000	0.010
	171	0.707	0.725	0.619		0.370		0.454		0.429		0.384	0.511	0.448		0.344	0.427		0.318	0.331	0.337
	173	0.000	0.000	0.000		0.010		0.010		0.000		0.011	0.011	0.003		0.021	0.005		0.005	0.006	0.008
	175	0.086	0.125	0.113		0.130		0.242		0.204		0.216	0.232	0.204		0.188	0.242		0.308	0.250	0.194
	177	0.000	0.000	0.023		0.219		0.103		0.117		0.089	0.063	0.116		0.104	0.083		0.061	0.076	0.069
	179	0.000	0.000	0.000		0.000		0.005		0.000		0.000	0.000	0.003		0.000	0.003		0.010	0.006	0.010
	181	0.000	0.000	0.008		0.021		0.021		0.026		0.011	0.016	0.008		0.021	0.016		0.040	0.017	0.051
	185	0.086	0.050	0.036		0.016		0.021		0.000		0.021	0.032	0.034		0.021	0.036		0.000	0.047	0.020
	207	0.000	0.000	0.000		0.000		0.000		0.000		0.000	0.000	0.000		0.000	0.000		0.000	0.000	0.008
	211	0.000	0.000	0.005		0.000		0.000		0.000		0.000	0.000	0.000		0.000	0.000		0.005	0.000	0.000
	213	0.000	0.025	0.111		0.036		0.026		0.020		0.016	0.005	0.008		0.021	0.013		0.061	0.029	0.046
	215	0.000	0.000	0.000		0.016		0.005		0.005		0.011	0.005	0.005		0.010	0.008		0.000	0.017	0.013
	217	0.052	0.075	0.018		0.146		0.093		0.163		0.147	0.084	0.106		0.156	0.115		0.091	0.122	0.140
	219	0.000	0.000	0.000		0.000		0.000		0.005		0.005	0.000	0.000		0.000	0.000		0.000	0.000	0.003
	221	0.000	0.000	0.000		0.005		0.000		0.010		0.000	0.000	0.000		0.000	0.000		0.005	0.012	0.013
	223	0.000	0.000	0.000		0.000		0.000		0.000		0.000	0.000	0.000		0.000	0.003		0.000	0.000	0.000
	225	0.000	0.000	0.000		0.000		0.000		0.000		0.000	0.000	0.000		0.000	0.003		0.000	0.000	0.000
	P	0.3252	0.8503	0.7673		0.3682		0.3798		0.4272		0.2717	0.2233	0.8945		0.3035	0.6977		0.0623	0.6848	0.4827
Ots213	*N*	29	20	188		95		99		98		98	95	189		52	181		100	86	186
	151	0.431	0.650	0.330		0.442		0.444		0.367		0.388	0.368	0.402		0.375	0.398		0.355	0.378	0.382
	155	0.534	0.250	0.604		0.384		0.303		0.337		0.378	0.368	0.362		0.404	0.367		0.315	0.355	0.266
	159	0.034	0.000	0.019		0.026		0.030		0.071		0.046	0.053	0.045		0.087	0.050		0.065	0.023	0.051
	163	0.000	0.000	0.000		0.000		0.000		0.000		0.000	0.000	0.000		0.000	0.000		0.010	0.012	0.000
	223	0.000	0.000	0.000		0.000		0.000		0.000		0.000	0.000	0.000		0.000	0.000		0.000	0.000	0.005
	227	0.000	0.000	0.000		0.000		0.015		0.020		0.015	0.026	0.019		0.000	0.017		0.035	0.023	0.038
	231	0.000	0.050	0.000		0.005		0.005		0.026		0.010	0.005	0.005		0.000	0.000		0.005	0.006	0.027
	235	0.000	0.000	0.000		0.011		0.000		0.005		0.000	0.000	0.011		0.010	0.017		0.005	0.012	0.005
	239	0.000	0.000	0.011		0.000		0.010		0.010		0.005	0.000	0.008		0.010	0.014		0.040	0.029	0.040
	243	0.000	0.000	0.000		0.000		0.030		0.010		0.005	0.011	0.011		0.019	0.011		0.015	0.029	0.040
	247	0.000	0.000	0.008		0.000		0.000		0.000		0.031	0.000	0.008		0.000	0.008		0.005	0.000	0.000

Continued

Appendix 1. Continued.

Locus/*N*/ Allele		*Hig04*	*Hig05*	*SFK04*	*Tak03*	*Tak04*	*Tat01*	*Tat04*	*Kog01*	*Kog04*	*Geo01*	*Geo04*	*Sal04*	*Tul04*	*Kis97*	*Kis04*	*Kwe04*	*Kan01*	*Kan04*	*Aro97*	*Goo04*
	251	0.000	0.000	0.000		0.021		0.000		0.010		0.005	0.005	0.016		0.000	0.000		0.015	0.012	0.005
	255	0.000	0.000	0.021		0.000		0.000		0.000		0.000	0.037	0.000		0.000	0.011		0.000	0.000	0.024
	259	0.000	0.000	0.000		0.016		0.045		0.010		0.010	0.016	0.016		0.000	0.025		0.005	0.006	0.011
	263	0.000	0.000	0.005		0.032		0.030		0.061		0.046	0.032	0.008		0.048	0.019		0.040	0.017	0.013
	267	0.000	0.050	0.000		0.011		0.035		0.015		0.026	0.016	0.013		0.010	0.008		0.035	0.029	0.040
	271	0.000	0.000	0.000		0.000		0.025		0.015		0.000	0.000	0.003		0.010	0.011		0.015	0.017	0.016
	275	0.000	0.000	0.000		0.000		0.005		0.000		0.000	0.026	0.003		0.010	0.006		0.005	0.006	0.005
	279	0.000	0.000	0.000		0.005		0.000		0.005		0.005	0.000	0.000		0.000	0.000		0.010	0.017	0.005
	283	0.000	0.000	0.000		0.021		0.015		0.005		0.015	0.021	0.045		0.010	0.014		0.020	0.000	0.011
	287	0.000	0.000	0.003		0.026		0.005		0.026		0.000	0.016	0.021		0.010	0.017		0.005	0.023	0.011
	291	0.000	0.000	0.000		0.000		0.000		0.005		0.015	0.000	0.005		0.000	0.008		0.000	0.006	0.000
	295	0.000	0.000	0.000		0.000		0.000		0.000		0.000	0.000	0.000		0.000	0.000		0.000	0.000	0.003
	P	0.9383	0.2782	0.2167		**0.045**		0.5445		0.6723		0.2608	0.8243	0.3407		0.2038	0.5838		**0.05**	0.8985	0.2325
Ots101	*N*	29	21	179		97		94		99		99	97	186		49	196		100	87	180
	96	0.000	0.000	0.000		0.000		0.005		0.000		0.000	0.000	0.000		0.000	0.000		0.000	0.000	0.000
	104	0.000	0.000	0.003		0.000		0.005		0.000		0.000	0.000	0.000		0.000	0.003		0.030	0.023	0.014
	108	0.000	0.000	0.000		0.005		0.027		0.025		0.010	0.036	0.008		0.010	0.008		0.015	0.017	0.028
	112	0.000	0.000	0.000		0.010		0.005		0.000		0.000	0.000	0.000		0.000	0.000		0.030	0.011	0.000
	124	0.000	0.000	0.000		0.000		0.000		0.000		0.000	0.015	0.005		0.000	0.003		0.000	0.006	0.003
	128	0.000	0.000	0.000		0.000		0.000		0.000		0.000	0.010	0.000		0.000	0.000		0.010	0.011	0.006
	132	0.000	0.000	0.000		0.005		0.000		0.010		0.010	0.000	0.000		0.010	0.015		0.010	0.034	0.031
	136	0.000	0.000	0.000		0.000		0.005		0.005		0.005	0.031	0.013		0.000	0.005		0.020	0.006	0.019
	140	0.000	0.000	0.014		0.036		0.069		0.056		0.051	0.021	0.032		0.010	0.031		0.035	0.017	0.064
	144	0.000	0.000	0.025		0.082		0.090		0.116		0.116	0.093	0.099		0.071	0.097		0.075	0.063	0.106
	148	0.000	0.024	0.050		0.108		0.074		0.056		0.111	0.021	0.056		0.102	0.061		0.050	0.034	0.047
	152	0.000	0.000	0.008		0.015		0.048		0.056		0.061	0.077	0.099		0.041	0.066		0.060	0.069	0.086
	156	0.000	0.000	0.022		0.015		0.037		0.035		0.035	0.052	0.027		0.051	0.051		0.045	0.052	0.067
	160	0.069	0.024	0.003		0.015		0.021		0.005		0.000	0.005	0.000		0.010	0.013		0.010	0.034	0.039
	164	0.224	0.143	0.078		0.010		0.000		0.005		0.005	0.010	0.011		0.031	0.013		0.045	0.040	0.025
	168	0.000	0.071	0.045		0.000		0.011		0.000		0.000	0.010	0.008		0.000	0.010		0.000	0.052	0.008
	172	0.052	0.071	0.087		0.216		0.133		0.051		0.056	0.041	0.046		0.071	0.074		0.060	0.034	0.022
	176	0.069	0.071	0.059		0.067		0.027		0.071		0.086	0.041	0.083		0.122	0.046		0.060	0.046	0.050
	180	0.069	0.095	0.073		0.103		0.048		0.051		0.076	0.057	0.110		0.061	0.079		0.085	0.092	0.053
	184	0.052	0.071	0.156		0.067		0.138		0.121		0.101	0.124	0.089		0.153	0.130		0.045	0.075	0.108
	188	0.138	0.143	0.165		0.041		0.074		0.096		0.066	0.093	0.051		0.041	0.041		0.090	0.040	0.064

Continued

Appendix 1. Continued.

Locus/*N*/ Allele		*Hig04*	*Hig05*	*SFK04*	*Tak03*	*Tak04*	*Tat01*	*Tat04*	*Kog01*	*Kog04*	*Geo01*	*Geo04*	*Sal04*	*Tul04*	*Kis97*	*Kis04*	*Kwe04*	*Kan01*	*Kan04*	*Aro97*	*Goo04*
	192	0.310	0.286	0.134		0.052		0.048		0.096		0.111	0.067	0.086		0.133	0.097		0.090	0.069	0.064
	196	0.000	0.000	0.039		0.036		0.074		0.071		0.076	0.103	0.056		0.041	0.079		0.055	0.126	0.047
	200	0.017	0.000	0.017		0.093		0.032		0.040		0.010	0.067	0.070		0.020	0.054		0.050	0.023	0.022
	204	0.000	0.000	0.022		0.021		0.016		0.015		0.015	0.021	0.027		0.020	0.020		0.020	0.000	0.014
	208	0.000	0.000	0.000		0.000		0.000		0.015		0.000	0.005	0.019		0.000	0.003		0.005	0.011	0.008
	212	0.000	0.000	0.000		0.000		0.005		0.005		0.000	0.000	0.000		0.000	0.000		0.005	0.006	0.000
	216	0.000	0.000	0.000		0.000		0.000		0.000		0.000	0.000	0.003		0.000	0.000		0.000	0.006	0.006
	220	0.000	0.000	0.000		0.000		0.005		0.000		0.000	0.000	0.000		0.000	0.003		0.000	0.000	0.000
	P	0.7843	0.8173	0.1038		0.0782		0.2407		0.5558		0.0867	0.6307	0.4457		0.089	0.7458		0.0857	0.2085	0.0232
	P	0.1973	0.9082	0.1845	0.8773	0.1985	0.9952	0.1067	0.2502	0.7975	0.8595	**0.033**	0.4273	0.6735	0.9655	0.0625	0.1865	0.792	**0.022**	0.9905	0.5062

Appendix 2. Sample size (*N*), allele richness (*AR*), and expected heterozygosity (H_e) for coho salmon collected from the Kuskokwim region.

		Population												
Locus		Hig	SFK	Tak	Tat	Kog	Geo	Sal	Tul	Kis	Kwe	Kan	Aro	Goo
Oke2	*N*	47	200	260	196	196	195	100	198	135	200	195	86	193
	AR	1.00	2.00	2.00	2.00	2.00	2.00	2.00	2.00	2.00	2.00	2.00	1.90	2.00
	H_e	0.00	0.20	0.24	0.21	0.19	0.21	0.23	0.22	0.17	0.18	0.19	0.05	0.19
Oke3	*N*	39	194	257	192	194	192	93	192	126	197	190	93	199
	AR	4.95	4.19	4.83	4.18	4.71	5.52	4.66	4.89	4.91	5.09	4.60	2.64	4.85
	H_e	0.51	0.57	0.57	0.61	0.58	0.65	0.50	0.63	0.63	0.60	0.57	0.46	0.63
Oke4	*N*	37	182	253	192	196	189	97	196	133	199	194	87	200
	AR	1.00	1.37	2.10	1.97	2.39	2.67	2.68	2.57	1.73	2.13	1.98	2.42	2.34
	H_e	0.00	0.01	0.05	0.04	0.07	0.15	0.07	0.07	0.03	0.04	0.09	0.10	0.15
Oki1	*N*	46	200	257	190	196	195	98	197	141	199	193	88	200
	AR	4.61	5.66	5.29	4.98	5.81	6.13	4.97	5.46	5.87	5.46	5.92	6.84	6.95
	H_e	0.68	0.68	0.67	0.70	0.66	0.69	0.70	0.69	0.70	0.72	0.69	0.71	0.71
Oki3	*N*	38	187	252	187	193	182	98	197	137	196	194	87	199
	AR	2.00	2.20	2.00	2.00	2.00	2.00	2.00	2.75	2.27	2.19	2.00	2.00	2.00
	H_e	0.34	0.46	0.44	0.41	0.41	0.41	0.38	0.40	0.42	0.42	0.32	0.23	0.30
Oki11	*N*	48	200	260	195	196	195	98	199	142	200	190	90	200
	AR	1.00	1.81	2.29	2.38	2.57	2.65	2.76	2.56	2.60	2.71	2.00	2.41	2.19
	H_e	0.00	0.04	0.28	0.28	0.26	0.25	0.29	0.34	0.31	0.31	0.33	0.32	0.35
One3	*N*	42	199	248	195	194	194	98	198	112	197	190	90	200
	AR	3.88	3.90	4.00	4.00	4.19	4.00	4.00	4.19	4.33	4.00	4.00	4.00	4.19
	H_e	0.61	0.57	0.66	0.70	0.71	0.71	0.72	0.70	0.70	0.71	0.71	0.73	0.75
Ots105	*N*	44	170	261	194	193	193	99	197	113	199	194	90	200
	AR	1.98	2.00	2.00	2.00	2.00	2.00	2.00	2.00	2.33	2.00	2.00	2.00	2.00
	H_e	0.05	0.13	0.26	0.27	0.29	0.29	0.21	0.26	0.25	0.27	0.37	0.34	0.32
Omy1011	*N*	50	183	98	97	99	100	96	184	53	191	100	84	193
	AR	3.00	6.14	7.46	7.62	8.61	7.92	8.58	8.50	6.99	8.03	8.20	8.21	8.56
	H_e	0.51	0.58	0.78	0.81	0.81	0.80	0.81	0.82	0.79	0.81	0.81	0.82	0.83
Ssa407	*N*	47	184	98	97	98	100	96	184	54	193	100	81	182
	AR	8.73	13.64	9.60	10.13	12.15	11.59	10.49	9.90	10.74	11.15	9.84	11.19	13.10
	H_e	0.79	0.89	0.82	0.82	0.83	0.85	0.84	0.84	0.84	0.85	0.77	0.81	0.84
Ocl8	*N*	50	199	96	97	98	99	94	196	51	194	98	86	198
	AR	4.48	6.27	7.28	6.34	7.35	7.68	6.80	7.88	8.29	8.78	6.99	7.73	9.02
	H_e	0.37	0.38	0.48	0.51	0.65	0.56	0.56	0.58	0.59	0.56	0.58	0.59	0.62

Continued

Appendix 2. Continued.

		Population												
Locus		Hig	SFK	Tak	Tat	Kog	Geo	Sal	Tul	Kis	Kwe	Kan	Aro	Goo
Ots2MA	*N*	50	199	97	99	98	98	98	196	52	191	98	87	198
	AR	3.98	4.97	4.38	3.91	4.58	4.38	4.37	4.46	4.00	4.57	4.85	3.98	4.86
	H_e	0.62	0.71	0.70	0.67	0.69	0.71	0.68	0.68	0.71	0.71	0.68	0.68	0.70
Ots2MB	*N*	49	194	96	97	98	95	95	194	48	192	99	86	196
	AR	5.75	8.05	9.68	8.86	7.98	9.83	8.86	9.18	10.34	9.36	9.08	10.10	11.34
	H_e	0.47	0.59	0.78	0.72	0.74	0.78	0.68	0.73	0.81	0.74	0.78	0.80	0.82
Ots213	*N*	49	188	95	99	98	98	95	189	52	181	100	86	186
	AR	4.83	5.24	9.33	10.93	12.16	10.85	11.35	11.41	9.90	11.94	13.41	13.72	13.78
	H_e	0.56	0.53	0.66	0.71	0.74	0.70	0.72	0.70	0.69	0.70	0.77	0.73	0.77
Ots101	*N*	50	179	97	94	99	99	97	186	49	196	100	87	180
	AR	10.46	14.85	16.06	18.38	17.43	15.28	18.81	17.25	16.88	17.80	20.76	21.93	20.40
	H_e	0.84	0.90	0.90	0.93	0.93	0.92	0.93	0.93	0.92	0.93	0.95	0.94	0.94
Average	*AR*	4.11	5.48	5.89	5.98	6.40	6.30	6.29	6.33	6.21	6.48	6.51	6.74	7.17
	H_e	0.42	0.48	0.55	0.56	0.57	0.58	0.55	0.57	0.57	0.57	0.57	0.55	0.59