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Genetic Stock Identification of Chum Salmon (*Oncorhynchus keta*) from the Yukon River District 5 Subsistence Fishery

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Abstract: We evaluated the feasibility of using genetic stock identification methods in a midriver mixed stock fishery to resolve patterns of stock composition, run timing, and bank orientation. Chum salmon were collected during August and September 1992, from the subsistence fishery in the Yukon River below the confluence of the Tanana River and assayed for 19 protein-coding loci. We used a chum salmon genetic baseline developed in a previous study that consisted of six U.S. origin and six Canadian origin spawning stocks. Genetic relationships resolved three stock aggregates: 1) a Tanana River stock group; 2) a U.S.-Canada Border stock group comprising the Chandalar and Sheenjek River stocks in the U.S., and Fishing Branch River, Big Creek, Minto, and Tatchun River stocks in Canada; and 3) Kluane and Teslin River stocks in the upper Yukon River in Canada. We partitioned the mixed stock fishery data by calendar week and river bank (north versus south) and performed stock composition analyses using a maximum likelihood computer program. Precision of the estimates was evaluated using the coefficient of variation of the mean. Precision was highest with analyses based on the three-stock aggregate grouping. When we integrated a country-of-origin component into the analyses precision declined, due primarily to the necessary split in the U.S.-Canada Border group to achieve country-of-origin. Run timing patterns suggested that non-Tanana River stocks migrated through the study area during August and September and the Tanana River stocks were present in September. Bank orientation was distinct, with non-Tanana River stocks occurring primarily in the north bank catch and Tanana River stocks occurring almost exclusively in the south bank catch. Our results supported the findings of an earlier tagging study performed by the Alaska Department of Fish and Game.

Introduction

The Yukon River is divided into six fishing districts, with some districts further divided into subdistricts (Figure 1). Commercial fishing occurs along the entire mainstem and the lower 220 miles of the Tanana River, while subsistence fishing occurs throughout the entire Yukon River drainage. An estimated 1,500 households composing about 40 communities of approximately 11,000 people (excluding Fairbanks) harvest salmon for subsistence use in the Yukon River drainage. Generally, most of the commercial fall chum salmon harvest has occurred in Districts 1 and 2 of the lower river, while most of the subsistence harvest has occurred further upstream in Districts 4, 5, and 6. The Alaska State Legislature

has designated subsistence as the highest priority use of the fish resources. (ADFG 1993)

Regulations restricting harvest were implemented by Alaska Department of Fish and Game (ADFG) in response to below target escapements of fall chum salmon in the early 1980s except for spawning stocks in the Toklat River, Fishing Branch River, and Canadian Yukon River mainstem. To improve escapements of fall chum salmon drainagewide, Yukon River Districts 1-5 and lower Tanana River Subdistrict 6a were closed to commercial fishing during the fall season of 1992, however subsistence fishing was permitted (except for the taking of fall chum salmon from the Kantishna River; ADFG 1993). Fishery managers attempt to manage for optimum sustained yield, however



FIGURE 1. Map of the Yukon River showing Alaska Department of Fish and Game fishing districts, fishwheel sites, and baseline sample locations.

adequate information is not always available to support that goal. Execution of mixed-stock fisheries may result in the under- or over-harvest of individual stocks in relation to their abundance due to an inability to identify and manage for individual stocks (ADFG 1993). The weak chum salmon runs of 1993 and the associated fishing closures (Bergstrom et al. 1995), emphasize the need for additional management tools. Genetic stock identification (GSI) is one of a number of methods that are being evaluated to improve the information base from which management decisions are made (ADFG 1993).

Fisheries managers could potentially use GSI before, during, or after the fishing season to achieve harvest objectives or stock conservation goals. How the genetic information is used depends in large part on the achievable level of discrimination among stocks or stock aggregates. Well defined and predictable patterns of run timing and stock composition could be used before the season to set seasons and time-specific harvest objectives. If the patterns are less predictable, but still well defined, GSI information could be used during the season to support management decisions. Complex patterns of run timing and stock composition may require post season evaluation of the stock composition of the catch.

Wilmot et al. (1992) reported the results of an evaluation of GSI methods applied in the chum and chinook salmon commercial and test fisheries at the mouth of the Yukon River (District 1) during 1987-1990. That study was performed by the U.S. Fish and Wildlife Service (USFWS) with the cooperation of Canada Department of Fisheries and Oceans (CDFO) and ADFG. That study involved two related components, 1) the establishment of genetic baselines of spawning stocks and 2) the genetic characterization of samples from the mixed-stock fisheries. Genetic profiles of spawning stocks were developed to create separate genetic baseline databases of chum and chinook salmon in the Yukon River watershed. In each year 1987-1990, samples were collected from the District 1 commercial and test fisheries throughout the fishing season. Wilmot et al. (1992) found the GSI methods permitted discrimination among regional chinook salmon stock groups and resulted in precise estimates by country-of-origin. Five stock groups for chum salmon were identified: lower and midriver summer-run groups and three fall-run groups. Apparent genetic similarities among fall-run stocks in the vicinity of the U.S. and Canada border prevented precise discrimination by country-of-origin.

Knowledge of stock composition, run timing, and migratory behavior could be used by fisheries managers to direct the harvest at various points along a migration route. ADFG used tagging methods to identify patterns of run timing and bank orientation in Yukon River fall chum salmon (Buklis 1981). Results indicated that non-Tanana River stocks migrated mostly along the north bank of the Yukon River while Tanana River stocks migrated mostly along the south bank in the Galena-Ruby area. Apparent differences in run timing were observed, as indicated by fish wheel catches at Galena, where the north bank catches peaked August 10 and 24, and south bank catches peaked August 24 and September 20. Subsequently, the Alaska Board of Fisheries divided fishing districts in the vicinity by bank to account for bank orientation behavior (e.g., Subdistricts 4b, 4c, 5a, and 5b; L. Buklis, ADFG, Anchorage, Alaska, personal communication).

We initiated this study in 1992 to test the feasibility of applying GSI methods in a midriver mixed-stock fishery to determine stock composition and identify patterns of run timing and bank orientation. We applied the chum salmon baseline developed and described by Wilmot et al. (1992) to provide continuity with their pioneering GSI work on the Yukon River and permit comparisons with their results. We performed stock composition analyses using three different stock groupings to demonstrate the effects of the various groupings on the precision of the stock composition estimates. One stock grouping was based on genetic relatedness among the stocks, while two stock groupings had country-of-origin components.

Methods

Collections

Eye, heart, liver, and skeletal muscle samples were collected from chum salmon caught in subsistence fish wheels and gill nets in the Yukon River below the confluence with the Tanana River

United	STATES		CANADA					
TANANA	Chandalar/ Sheenjek	U.SCANADA Border	Fishing Br/ Mainstem	Upper Canadian				
Salcha Toklat Delta Bluff Cabin	Chandalar Sheenjek	Chandalar Sheenjek Fishing Branch Minto	Fishing Branch Minto Tatchun Big Creek	Kluane Teslin				
		Tatchun Big Creek						

TABLE 1. Stock groupings used for analyses.

(Figure 1). The samples were placed in individually numbered vials and maintained at <-40 °C. During the collection period, samples were periodically shipped on dry ice or in liquid nitrogen to Anchorage for storage in ultracold freezers.

Subsistence fish wheels were located in the vicinity of Tanana Village along the north bank of the Yukon River during August and along the north and south banks during September. Fish wheel catches were sampled almost daily, with a target of 50 fish per day. Gill nets were periodically deployed along the south bank in August to check for the presence of chum salmon. From August 4 to September 23 a total of 2,353 chum salmon was collected, 2,191 of which were used in our analysis for this study (Appendix 1). We considered the samples representative of the subsistence harvest due to the distribution of sampling effort throughout the season and we assumed that the fish wheel catches were representative of the stock composition of the run.

Laboratory processing

Protein electrophoresis methods generally followed those described by Aebersold et al. (1987) and Gall et al. (1989). Gene nomenclature followed the recommendations of Shaklee et al. (1990). The loci used for analysis are described in Appendix 2. Isoloci were scored to account for all four alleles, however variation was assigned to a single locus pair for analyses to be consistent with Wilmot et al. (1992).

The genetic baseline

A subset of the chum salmon baseline described by Wilmot et al. (1992) was used for the stock composition analyses (Appendix 2). We used this baseline because the performance properties of it have been thoroughly described and to permit comparisons with the results reported by Wilmot et al. (1992). The Wilmot baseline consisted of 26 Yukon River chum salmon stocks from throughout the Yukon River watershed that were scored for 19 proteincoding loci. The subset of the baseline that we used consisted of six U.S. origin and six Canadian origin spawning stocks. Stocks from below the confluence of the Tanana River were not used for these analyses as we assumed that they would not contribute to the catch in the study area. The UNITED STATES group comprised the Chandalar, Sheenjek, and four Tanana River stocks (Salcha, Toklat, Delta, and Bluff Cabin; Table 1; Figure 1). The summer-run Salcha stock, because of its geographic proximity to the Tanana River fall-run stocks, was included in the TANANA group to account for the possible presence of that stock in the fishery samples. The CANADA group comprised the Fishing Branch River in the Porcupine River drainage, the Big Creek, Minto, and Tatchun stocks from the Yukon River mainstem, and the Kluane and Teslin River stocks from the upper Yukon River. The performance properties of the baseline were described by Wilmot et al. (1992). The computer program BIOSYS-1 (Swofford and Selander 1989) was used to calculate genetic distances (Cavalli-Sforza and Edwards 1967, arc distance) and perform



FIGURE 2. Dendrogram of genetic distances (Cavalli-Sforza and Edwards 1967, arc distance) showing genetic realtionships among 12 Yukon River chum salmon stocks.

unweighted pair-group method with arithmetic averages (UPGMA; Sneath and Sokal 1973) clustering of the distances to illustrate relationships among the stocks.

Stock composition analyses

We used the same stock grouping strategy used by Wilmot et al. (1992), except for our inclusion of the summer-run Salcha River with the fall-run Tanana River stocks and our formation of a U.S.-CANADA BORDER group (Table 1) comprising U.S. and Canada origin stocks. We performed analyses with three sets of stock groups to compare precision between estimates based on stock aggregates defined by genetic stock structure versus aggregates that included a country-of-origin component (Table 1).

The mixed-stock fishery sample of 2,191 fish was stratified by calendar week and bank for analyses (Appendix 1). Only fish wheel samples from the vicinity of the Yukon-Tanana River confluence were used for analyses. Fish with missing scores from three or more loci were omitted from analyses. Stock composition estimates of the mixed-stock samples were calculated using the conditional maximum likelihood computer program, GIRLSEM (Pella and Milner 1987; Masuda et al. 1991). The program calculated the most likely combination of baseline stocks that would be required to form the observed stock mixture. Bootstrap resampling (Efron 1982) was used to provide a mean and standard error of 200 estimates of stock composition for each stock mixture. Stock composition estimates were calculated for individual stocks and then summed for each of the stock groupings (i.e., allocate and sum). The degree of precision associated with the stock composition estimates was evaluated by relative comparisons among coefficients of variation (CV) of the means, with large CVs indicating lower precision and small CVs indicating higher precision. Standard errors vielding CVs>50% result in 95% confidence intervals that include zero as one of the possible values for those stock contribution estimates. The 50% level was used as a relative reference level for comparisons among CVs (Marlowe and Busack 1995).



Time and Bank

FIGURE 3A. Stock contribution estimates by calendar week and river bank for four Yukon River drainage chum salmon stock groups. Error bars are one standard error.

Results

Stock relationships

The pattern of clustering that we observed with our 12 stock baseline (Figure 2) was similar to the clustering for the same 12 stock subcomponent of the 26 stock baseline of Wilmot et al. (1992). This suggested that the genetic relationships among the 12 stocks remained unchanged by removing them from the 26 stock aggregate, therefore the performance properties of our 12 stock baseline should have reflected those reported by Wilmot et al. (1992). Simulations performed by Wilmot et al. (1992) indicated that Chandalar and Sheenjek River stocks misallocated to Fishing Branch River and Canadian Yukon River mainstem stocks due to the genetic



Time and Bank

FIGURE 3B. Coefficients of variation for the stock contribution estimates in FIGURE 3A, with reference lines for CV=50%.

similarities among those stocks (Figure 2).

Stock Composition

The **first set** of analyses contained a countryof-origin component, using the TANANA, CHANDALAR/SHEENJEK, FISHING BR/MAINSTEM, and UPPER CANADIAN groups (Table 1). Estimated contributions of the TANANA group were highest in the south bank catch during September where estimated proportions ranged from 84-95% (Figure 3a; Appendix 3). Contributions of the TANANA group in the north bank catches were <10%. Standard errors were under 15% and generally greater for south bank estimates than for north bank estimates (Appendix 3). CVs were smallest for the south bank estimates (CV<20%) and largest for the north bank estimates (up to CV=580%; Figure 3b; Appendix 3). All of the CVs for the north bank TANANA group were >50%.



Time and Bank

FIGURE 4A. Stock contribution estimates by calendar week and river bank for three Yukon River drainage chum salmon stock groups. Error bars are one standard error.

The non-TANANA groups occurred primarily in the north bank catches, with the CHANDALAR/ SHEENJEK group contributing the largest proportions to the catch in most of the weeks. North bank stock contributions of the CHANDALAR/SHEENJEK group were generally around 50%, the FISHING BR/MAINSTEM group about 40%, and the UPPER CANADIAN group under 20% (Figure 3a; Appendix 3). Standard errors of the CHANDALAR/SHEENJEK and FISHING BR/MAINSTEM groups were 10-20% in most cases (Appendix 3). CVs for the CHANDALAR/ SHEENJEK and FISHING BR/MAINSTEM groups were <50% in the August samples, with the CVs varying more among the September catches (Figure 3b; Appendix 3). The high CVs for the September south bank catches for those two groups indicated low precision for those estimates. CVs >50% were observed in the north bank catches in September for the CHANDALAR/SHEENJEK group during Week 2 and for the FISHING BR/MAINSTEM group during Weeks 1 and 3. Proportions of the UPPER CANADIAN group were greatest in the September north bank catch, however only the estimate for Week 2 in September had a CV<50%.

The **second set** of analyses used the TANANA and UPPER CANADIAN groups plus a U.S.-CANADA BORDER group comprising CHANDALAR/SHEENJEK and FISHING BR/MAINSTEM groups (Table 1). That grouping reflected the clustering depicted in Figure 2 and yielded more precise stock contribution estimates.



FIGURE 4B. Comparison of coefficients of variation for the stock contribution estimates for the U.S.-CANADA BORDER group in FIGURE 4A versus the coefficients of variation of its component groups. Reference lines show CV=50%.

North bank estimates for the U.S.-CANADA BORDER group were 69-94%, with lower standard errors than were observed for the separate groups that composed the U.S.-CANADA BORDER group (Figure 4a; Appendix 3). The associated CVs ranged from about 8 to 21% (Figure 4b; Appendix 3). Standard errors for the south bank catches remained relatively high and CVs indicated relatively low precision.

In the **third set** of analyses, with the stocks partitioned into UNITED STATES and CANADA groups, the stock contribution estimates showed a UNITED STATES group presence on both banks due to the merging of the CHANDALAR/SHEENJEK and TANANA groups (Figure 5a; Appendix 3). The CANADA group contributed mainly to the north bank catches. Standard errors were about 15-20%, similar to the standard errors for the separate CHANDALAR/ SHEENJEK and FISHING BR/MAINSTEM groups (Appendix 3). CVs were generally under 50%, except for the UNITED STATES group in the September Week 2 north bank catch, and for the CANADA group in the September south bank catches in each of the weeks (Figure 5b; Appendix 3). The main effect of grouping by country-of-origin was to obscure the patterns of bank orientation that were evident at the finer levels of grouping.



FIGURE 5A. Stock contribution estimates by calendar week and river bank for two Yukon River drainage chum salmon stock groups. Error bars are one standard error.

Discussion

One anticipated outcome of sampling a midriver location as we did in District 5 was an improvement in stock discrimination over what Wilmot et al. (1992) obtained in the District 1 fishery at the mouth. Wilmot et al. (1992) reported misallocations (4.5-7.3%) between U.S. fall-run stocks and summer-run stocks. The District 5 sampling ensured that we had a potentially simpler stock mixture than could be obtained from District 1. Lower river stocks, stocks of the Koyukuk River, and other downstream stocks would be excluded from our mixture. With a simpler mixture to analyze, stock resolution could possibly be improved. However, we found that the baseline and behavior of the GSI model retained the performance properties observed by Wilmot et al. (1992) in District 1. Wilmot et al. (1992) reported similar standard errors of about 1020% for stock contribution estimates of the TANANA, CHANDALAR/SHEENJEK, and FISHING BR/MAINSTEM groups in District 1 fisheries. Their estimates of the UPPER CANADIAN group were also low to negligible with standard errors similar to those reported in this study.

We observed an improvement in the precision of stock contribution estimates when we combined the CHANDALAR/SHEENJEK and FISHING BR/MAINSTEM groups into a U.S.-CANADA BORDER group. This was not surprising because that stock configuration coincided with the patterns of genetic stock structuring indicated by the measure of genetic distance. Wood (1989) reported that dendrograms of genetic distance were effective for predicting the relative reliability of stock composition estimates and for determining the stock grouping strategy. He showed that allocating and summing within problem clusters (i.e., groups of genetically similar stocks)



FIGURE 5B. Coefficients of variation for the stock composition estimates in FIGURE 5A. Reference lines for CV=50% are shown.

resulted in relatively accurate contribution estimates of those stock aggregates. While precision was improved by grouping genetically similar stocks in our study, it also illustrates one of the limitations of the chum salmon baseline from Wilmot et al. (1992)—the inability to resolve individual stocks or smaller stock aggregates.

The apparent genetic relationships among the stocks have been inferred from the genetic information obtained from 19 protein-coding loci. The genetic stock structure based on those protein data may reflect the true stock relationships or may be inaccurate due to limitations associated with the nature of protein data (Utter et al. 1987). The geographic distances separating the Chandalar, Sheenjek, Fishing Branch, and Canadian Mainstem stock spawning grounds and the strong natal homing tendency of chum salmon (Salo 1991) suggest a lower level of gene flow among those stocks than was indicated by the protein data. Genetic differentiation among stocks of chum salmon (Kondzela et al. 1994) and other salmon species has been observed on smaller geographic scales (e.g.,

Adams et al. 1994; Burger et al. In press). Better stock discrimination might be achieved with the inclusion of more informative protein loci or through the application of molecular genetics methods that permit direct access to the mitochondrial and nuclear DNA molecules.

The patterns of run timing observed would require abundance estimates for thorough evaluation. However, differential run timing on the south bank could be implied from the very low numbers of fish using that corridor during August (B. Fliris and P. Moore, Tanana Village, personal communications) as was confirmed with our gillnetting efforts. Thus, our data indicate that non-Tanana River stocks along the north bank occurred earlier than the Tanana River stocks along the south bank. This coincides with the results of Buklis (1981), who reported run peaks in 1977 on the north bank in the Galena area occurring on 10 and 24 August, and on the south bank on 24 August and 20 September. Those results led Buklis (1981) to conclude that non-Tanana stocks migrated through the Galena area earlier than Tanana River stocks.

Multiple peaks in the catches along each bank reported by Buklis (1981) suggest the possibility of stock specific run timing patterns occurring in the south-bank TANANA group and the non-TANANA north bank groups. Genetic discrimination among the stocks must be improved before those patterns can be resolved and used to achieve harvest and stock conservation objectives.

The GSI methods that we used showed a clear pattern of stock-based bank orientation, with Tanana River stocks dominating the south bank catches and non-Tanana River stocks occurring primarily in the north bank catches. Observed patterns of bank orientation were similar to those of Buklis (1981), who reported bank orientation of Tanana River and non-Tanana River stocks occurring as far down river as Galena, which is approximately 266 km (165 mi) downstream from the confluence of the Tanana River. Riverine hydrodynamics over such a great distance should ensure thorough mixing of the Tanana River effluent with that of the Yukon River, leading to the conclusion that factors other than olfaction may be influencing migratory navigation. The apparent persistence of bank orientation over such a great distance suggests a genetic basis for migratory navigation and riverine orientation.

The GSI methods were most effective in detecting patterns of bank orientation in the major stock groups. Better means of stock discrimination are necessary to obtain more precise estimates of stock composition at a finer level, and to better resolve patterns of run timing. Improved performance of the chum salmon genetic baseline may be achieved by expanding the geographic coverage of the baseline and including genetic markers with better discriminatory properties. Incomplete stock representation in the baseline could depress the stock discrimination performance of a baseline and lead to inaccurate conclusions regarding genetic stock structuring in a region. Telemetry of migrating adults may be a valuable tool for pinpointing previously unknown spawning grounds and permitting the inclusion of additional stocks in the baseline. Genetic markers that yield better resolution of stocks should be evaluated to determine their utility for GSI applications. Molecular methods that permit direct access to the mitochondrial

and nuclear genomes may be more sensitive than protein-based methods for detecting genetic stock structuring.

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Date	Week	Bank	N	Date	Week	Bank	N
Aug 4	1	Ν	19	Sep 1	1	Ν	50
Aug 5	1	Ν	57	Sep 3	1	Ν	50
Aug 6	1	Ν	43	Sep 5	1	Ν	40
Aug 7	1	Ν	66	Sep 6	1	N	50
		Subtotal	185			Subtotal	190
Aug 8	2	Ν	51	Sep 2	1	S	33
Aug 9	2	Ν	48	Sep 4	1	S	40
Aug 10	2	Ν	44			Subtotal	73
Aug 11	2	Ν	63	Sep 10	2	Ν	47
Aug 12	2	Ν	41	Sep 12	2	Ν	50
Aug 13	2	Ν	35	Sep 13	2	Ν	30
Aug 14	2	N	27	Sep 14	2	Ν	50
		Subtotal	309			Subtotal	177
Aug 15	3	Ν	19	Sep 8	2	S	35
Aug 16	3	Ν	49	Sep 9	2	S	48
Aug 17	3	Ν	22	Sep 11	2	S	50
Aug 18	3	Ν	58	Sep 13	2	S	20
Aug 19	3	Ν	64			Subtotal	153
Aug 20	3	Ν	62	Sep 22	3	Ν	40
Aug 21	3	Ν	67	Sep 23	3	Ν	36
		Subtotal	341			Subtotal	76
Aug 22	4	Ν	70	Sep 17	3	S	50
Aug 23	4	Ν	30	Sep 18	3	S	30
Aug 24	4	Ν	50	Sep 21	3	S	50
Aug 25	4	Ν	60	Sep 23	3	S	37
Aug 26	4	Ν	60			Subtotal	167
Aug 27	4	Ν	50			Total	2,191
Aug 28	4	Ν	50				
Aug 29	4	Ν	50				
Aug 30	4	Ν	50				
Aug 31	4	N	50				
		Subtotal	520				

APPENDIX 1. Sample sizes (N) and data partitioning strategy by date, week, and river bank (N=north, S=south).

APPENDIX 2. Allelic frequencies at 19 polymorphic loci for chum salmon sampled from the Yukon River drainage during 1987-1990. The most common allele is designated as 100, and other alleles assigned numbers according to their mobility relative to the 100 allele. N is the sample size. Allele designations separated by a slash indicate that the data for those alleles were pooled. An allele frequency with an asterisk indicates significant deviation from Hardy-Weinberg Equilibrium (* = p < 0.05, ** = p < 0.01, and *** = p < 0.001). (Source: Wilmot et al. 1992)

		sAAT-1*				mAA	AT-1*			ALAT	*		ESTD*		
Stock	Year	Ν	100	120	N	-100	-120	-70	N	100	93	N	100	91	
United States Sum	mer Run														
Salcha	1988	48	0.958	0.042	48	0.896	0.000	0.104	50	0.950	0.050	48	0.510	0.490	
	1989	50	0.880	0.120	50	0.920	0.010	0.070	50	0.950	0.050	50	0.460	0.540	
	Pooled	98	0.918	0.082	98	0.908	0.005	0.087	100	0.950	0.050	98	0.485	0.515	
United States Fall	Run														
Toklat	1987	133	0.850	0.150	69	0.928	0.000	0.073	132	0.845	0.155*	135	0.270	0.730	
	1990	74	0.858	0.142	74	0.892	0.000	0.108	74	0.912	0.088	74	0.284	0.716	
	Pooled	207	0.853	0.147	143	0.909	0.000	0.091	206	0.869	0.131	209	0.275	0.725	
Delta-Clearwater	1987	135	0.878	0.122	129	0.919	0.004	0.078	134	0.937	0.063	135	0.196	0.804	
	1990	75	0.887	0.114	75	0.960	0.000	0.040	75	0.927	0.073	75	0.167	0.833	
	Pooled	210	0.881	0.119	204	0.934	0.003	0.064	209	0.933	0.067	210	0.186	0.814	
Bluff Cabin	1987	135	0.878	0.122	71	0.937	0.000	0.063	133	0.921	0.079	134	0.198	0.802	
Slough															
Chandalar	1987	149	0.913	0.087	148	0.878	0.000	0.122	28	0.911	0.089	145	0.341	0.659	
	1988	73	0.897	0.103	73	0.877	0.000	0.123	73	0.918	0.082	73	0.308	0.692	
	1989	75	0.867	0.133	75	0.907	0.000	0.093	75	0.947	0.053	75	0.327	0.673	
	Pooled	297	0.897	0.103	296	0.885	0.000	0.115	176	0.929	0.071	293	0.329	0.671	
Sheenjek	1987	135	0.904	0.096	79	0.911	0.000	0.089	135	0.941	0.059	135	0.344	0.656	
	1988	79	0.905	0.095	78	0.917	0.000	0.083	80	0.938	0.063	79	0.335	0.665	
	1989	80	0.888	0.113	80	0.863	0.000	0.138	80	0.913	0.088	80	0.400	0.600	
	Pooled	294	0.900	0.100	237	0.897	0.000	0.103	295	0.932	0.068	294	0.357	0.643	
Canadian Fall Run	l														
Fishing Branch	1987	128	0.938	0.063	73	0.863	0.007	0.130	128	0.941	0.059	129	0.252	0.748	
	1989	49	0.918	0.082	49	0.878	0.000	0.122	49	0.949	0.051	49	0.388	0.612	
	Pooled	177	0.932	0.068	122	0.869	0.004	0.127	177	0.944	0.057	178	0.289	0.711	
Big Creek	1987	69	0.877	0.123	37	0.960	0.000	0.041	69	0.935	0.065	69	0.283	0.717	
Tatchun	1987	75	0.893	0.107	59	0.898	0.000	0.102	75	0.927	0.073	75	0.320	0.680	
Minto	1989	100	0.930	0.070	100	0.920	0.000	0.080	100	0.955	0.045	100	0.345	0.655	
Kluane	1987	133	0.895	0.105	66	0.909	0.000	0.091	145	0.969	0.031	143	0.255	0.745	
Teslin	1989	95	0.905	0.095	95	0.868	0.005	0.126	95	0.963	0.037	95	0.568	0.432	

Appendix 2 continued.															
		(G3PDH-2	2*		bGLUA	*		mIDHP-	1*			sIDHP-	2*	
Stock	Year	Ν	100	90	N	100	64	Ν	100	60	N	100	35	85	25
United States Summer Run															
Salcha	1988	48	0.813	0.188	49	0.959	0.041	48	0.927	0.073	48	0.521	0.448	0.031	0.000
	1989	50	0.940	0.060	50	0.930	0.070	50	0.960	0.040	50	0.530	0.400	0.070	0.000
	Pooled	98	0.878	0.122	99	0.944	0.056	98	0.944	0.056	98	0.526	0.424	0.051	0.000
United States Fall I	Run														
Toklat	1987	134	0.787	0.213	75	0.920	0.080	135	0.956	0.044	135	0.633	0.304	0.063	0.000*
	1990	73	0.836	0.164	73	0.945	0.055	74	0.953	0.047	74	0.615	0.338	0.047	0.000
	Pooled	207	0.804	0.196	148	0.932	0.068	209	0.955	0.046	209	0.627	0.316	0.057	0.000
Delta-Clearwater	1987	135	0.863	0.137	117	0.966	0.034	135	0.982	0.019	135	0.533	0.407	0.059	0.000
	1990	75	0.840	0.160	74	0.932	0.068	75	0.987	0.013	75	0.540	0.440	0.020	0.000
	Pooled	210	0.855	0.145	191	0.953	0.047	210	0.983	0.017	210	0.536	0.419	0.045	0.000
Bluff Cabin	1987	134	0.843	0.157	82	0.933	0.067	135	0.985	0.015	135	0.556	0.385	0.059	0.000*
Slough															
Chandalar	1987	148	0.865	0.135	52	0.962	0.039	149	0.990	0.010	149	0.416	0.544	0.040	0.000
	1988	73	0.849	0.151	71	0.916	0.085	73	0.993	0.007	73	0.390	0.569	0.041	0.000
	1989	75	0.900	0.100	75	0.907	0.093	75	0.993	0.007	75	0.440	0.513	0.047	0.000
	Pooled	296	0.870	0.130	198	0.924	0.076	297	0.992	0.008	297	0.416	0.542	0.042	0.000
Sheenjek	1987	134	0.881	0.119	32	0.969	0.031	135	0.982	0.019	135	0.400	0.563	0.037	0.000
	1988	78	0.891	0.109	80	0.881	0.119	79	1.000	0.000	78	0.314	0.628	0.058	0.000
	1989	80	0.863	0.138	80	0.913	0.088	80	0.981	0.019	80	0.381	0.550	0.069	0.000
	Pooled	292	0.878	0.122	192	0.909	0.091	294	0.986	0.014	293	0.372	0.577	0.051	0.000
Canadian Fall Run															
Fishing Branch	1987	128	0.848	0.152	30	0.983	0.017	129	0.996	0.004	122	0.414	0.557	0.029	0.000**
															*
	1989	49	0.847	0.153	48	0.938	0.063	49	1.000	0.000	49	0.357	0.602	0.041	0.000
	Pooled	177	0.848	0.153	78	0.955	0.045	178	0.997	0.003	171	0.398	0.570	0.032	0.000
Big Creek	1987	69	0.891	0.109	31	0.968	0.032	69	1.000	0.000	69	0.406	0.573	0.022	0.000*
Tatchun	1987	74	0.892	0.108	24	0.979	0.021	75	1.000	0.000	73	0.452	0.507	0.041	0.000
Minto	1989	100	0.875	0.125	100	0.965	0.035	100	1.000	0.000	100	0.475	0.485	0.040	0.000
Kluane	1987	134	0.828	0.172	31	0.774	0.226	135	1.000	0.000	135	0.344	0.596	0.059	0.000
Teslin	1989	94	0.973	0.027	93	0.957	0.043	95	1.000	0.000	95	0.626	0.337	0.037	0.000

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		LDH-A1*			S	MDH-A	*	5	MDH-A	2*		sMDH-B1,2*			
Stock	Year	N	-100	50	N	100	200	N	100	40	N	100	72	130/50	
United States Sum	mer Run														
Salcha	1988	48	0.719	0.281	48	0.969	0.031	48	1.000	0.000	48	0.958	0.042	0.000	
	1989	50	0.790	0.210	50	0.950	0.050	48	0.990	0.010	50	0.950	0.040	0.010	
	Pooled	98	0.755	0.245	98	0.959	0.041	96	0.995	0.005	98	0.954	0.041	0.005	
United States Fall	Run														
Toklat	1987	135	0.756	0.244	135	0.930	0.070	135	0.978	0.022	135	0.985	0.015	0.000	
	1990	72	0.757	0.243	74	0.939	0.061	74	0.987	0.014	74	1.000	0.000	0.000	
	Pooled	207	0.756	0.244	209	0.933	0.067	209	0.981	0.019	209	0.990	0.010	0.000	
Delta-Clearwater	1987	135	0.704	0.296	130	0.939	0.062	135	0.993	0.007	135	1.000	0.000	0.000	
	1990	74	0.669	0.331	75	0.933	0.067	75	0.973	0.027	75	1.000	0.000	0.000	
	Pooled	209	0.691	0.309	205	0.937	0.063	210	0.986	0.014	210	1.000	0.000	0.000	
Bluff Cabin	1987	135	0.656	0.344**	135	0.944	0.056	135	0.989	0.011	135	1.000	0.000	0.000	
Slough															
Chandalar	1987	149	0.711	0.289	149	0.826	0.175	149	0.983	0.017	149	0.990	0.010	0.000	
Chandalar	1988	72	0.792	0.208	73	0.918	0.082	73	0.980	0.021	73	0.993	0.007	0.000	
	1989	75	0.673	0.327	75	0.907	0.093	75	0.967	0.033	75	1.000	0.000	0.000	
	Pooled	296	0.721	0.279	297	0.869	0.131	297	0.978	0.022	297	0.993	0.007	0.000	
Sheenjek	1987	135	0.696	0.304	135	0.870	0.130	135	0.970	0.030	135	1.000	0.000	0.000	
	1988	77	0.760	0.240*	79	0.854	0.146	79	0.956	0.044	79	1.000	0.000	0.000	
	1989	80	0.650	0.350	80	0.900	0.100	80	0.981	0.019	80	0.994	0.006	0.000	
	Pooled	292	0.700	0.300	294	0.874	0.126	294	0.969	0.031	294	0.998	0.002	0.000	
Canadian Fall Ru	n														
Fishing Branch	1987	129	0.632	0.368	129	0.930	0.070	126	0.968	0.032	129	1.000	0.000	0.000	
	1989	49	0.643	0.357	49	0.929	0.071	49	0.990	0.010	49	1.000	0.000	0.000	
	Pooled	178	0.635	0.365	178	0.930	0.070	175	0.974	0.026	178	1.000	0.000	0.000	
Big Creek	1987	69	0.696	0.304	69	0.891	0.109	69	0.957	0.044	69	1.000	0.000	0.000	
Tatchun	1987	75	0.713	0.287	71	0.866	0.134	75	0.933	0.067	75	1.000	0.000	0.000	
Minto	1989	100	0.710	0.290	100	0.915	0.085	100	0.990	0.010	100	1.000	0.000	0.000	
Kluane	1987	135	0.533	0.467	135	0.948	0.052	134	0.985	0.015	135	0.996	0.004	0.000	
Teslin	1989	95	0.700	0.300	95	0.842	0.158	94	0.957	0.043	95	1.000	0.000	0.000	

APPENDIX 2 continued.

		mMEP-2*				MPI*			PEP-LT	F *		PGDH*			
Stock	Year	Ν	100	122	Ν	100	94	N	100	85	Ν	100	92		
United States Sum	mer Run														
Salcha	1988	48	0.927	0.073	48	0.896	0.104	50	0.990	0.010	48	0.958	0.042		
	1989	50	0.850	0.150	50	0.930	0.070	50	0.980	0.020	50	0.940	0.060		
	Pooled	98	0.888	0.112	98	0.913	0.087	100	0.985	0.015	98	0.949	0.051		
United States Fall	Run														
Toklat	1987	135	0.878	0.122	135	0.937	0.063	126	0.992	0.008	135	0.959	0.041		
	1990	73	0.932	0.069	75	0.939	0.061	74	0.987	0.014	74	0.987	0.014		
	Pooled	208	0.897	0.103	209	0.938	0.062	200	0.990	0.010	209	0.969	0.031		
Delta-Clearwater	1987	135	0.907	0.093	132	0.943	0.057	134	0.963	0.037	135	0.978	0.014		
	1990	75	0.873	0.127	75	0.933	0.067	75	0.973	0.027	75	0.960	0.040		
	Pooled	210	0.895	0.105	207	0.940	0.060	209	0.967	0.034	210	0.971	0.029		
Bluff Cabin	1987	135	0.915	0.085	135	0.933	0.067	123	0.947	0.053	135	0.956	0.044		
Slough															
Chandalar	1987	149	0.909	0.091	149	0.930	0.071	146	0.969	0.031	136	0.974	0.026		
	1988	73	0.925	0.075	73	0.938	0.062	73	0.993	0.007	73	0.980	0.021		
	1989	75	0.893	0.107	75	0.887	0.113	75	1.000	0.000	75	0.973	0.027		
	Pooled	297	0.909	0.091	297	0.921	0.079	294	0.983	0.017	284	0.975	0.025		
Sheenjek	1987	135	0.911	0.089	135	0.896	0.104	124	0.980	0.020	135	0.974	0.026		
	1988	79	0.956	0.044	79	0.892	0.108	80	0.969	0.031	79	0.968	0.032		
	1989	80	0.956	0.044	80	0.856	0.144	80	0.994	0.006	80	0.969	0.031		
	Pooled	294	0.935	0.065	294	0.884	0.116	284	0.981	0.019	294	0.971	0.029		
Canadian Fall Rur	ı														
Fishing Branch	1987	128	0.934	0.066	126	0.913	0.087	23	0.935	0.065	129	0.973	0.027		
	1989	49	0.939	0.061	49	0.898	0.102	49	0.980	0.020	49	0.980	0.020		
	Pooled	177	0.935	0.065	175	0.909	0.091	72	0.965	0.035	178	0.975	0.025		
Big Creek	1987	69	0.877	0.123	69	0.949	0.051	69	0.957	0.044	69	0.949	0.051		
Tatchun	1987	75	0.900	0.100	75	0.913	0.087	75	0.967	0.033	75	0.967	0.033		
Minto	1989	100	0.930	0.070	100	0.950	0.050	100	0.970	0.030	100	0.965	0.035		
Kluane	1987	135	0.985	0.015	142	0.947	0.053	125	0.992	0.008	135	1.000	0.000		
Teslin	1989	95	0.916	0.084	95	0.968	0.032	95	0.816	0.184	95	1.000	0.000		

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APPENDIX 2 continued.												
	-	PEPB-1*				PEPB-2*			TPI-1*			
Stock	Year	Ν	-100	-156	-128	-127	N	100	132	N	-100	-50
United States Summ	ner Run											
Salcha	1988	48	0.896	0.094	0.010	0.000	48	0.885	0.115	50	1.000	0.000
	1989	50	0.910	0.060	0.030	0.000	50	0.840	0.160	50	1.000	0.000
	Pooled	98	0.903	0.077	0.020	0.000	98	0.862	0.138	100	1.000	0.000
United States Fall Run												
Toklat	1987	135	0.789	0.182	0.030	0.000	86	0.919	0.081	85	1.000	0.000
	1990	74	0.757	0.216	0.027	0.000	73	0.904	0.096	74	1.000	0.000
	Pooled	209	0.778	0.194	0.029	0.000	159	0.912	0.088	159	1.000	0.000
Delta-Clearwater	1987	135	0.796	0.182	0.022	0.000	65	0.915	0.085	135	1.000	0.000
	1990	75	0.820	0.167	0.013	0.000	75	0.913	0.087	75	1.000	0.000
	Pooled	210	0.805	0.176	0.019	0.000	140	0.914	0.086	210	1.000	0.000
Bluff Cabin	1987	135	0.852	0.130	0.019	0.000	75	0.920	0.080	135	1.000	0.000
Slough												
Chandalar	1987	149	0.785	0.191	0.024	0.000	33	0.879	0.121	150	1.000	0.000
	1988	73	0.781	0.212	0.007	0.000	73	0.829	0.171	72	1.000	0.000
	1989	75	0.820	0.173	0.007	0.000	75	0.893	0.107	75	1.000	0.000
	Pooled	297	0.793	0.192	0.015	0.000	181	0.865	0.135	297	1.000	0.000
Sheenjek	1987	135	0.830	0.163	0.007	0.000	87	0.793	0.207	87	1.000	0.000
	1988	79	0.810	0.177	0.013	0.000	78	0.859	0.141	80	1.000	0.000
	1989	80	0.756	0.231	0.013	0.000	80	0.863	0.138	80	1.000	0.000
	Pooled	294	0.804	0.185	0.010	0.000	245	0.837	0.163	247	1.000	0.000
Canadian Fall Run												
Fishing Branch	1987	129	0.845	0.151	0.004	0.000	71	0.937	0.063	127	1.000	0.000
	1989	49	0.827	0.174	0.000	0.000	49	0.867	0.133	49	1.000	0.000
	Pooled	178	0.840	0.157	0.003	0.000	120	0.908	0.092	176	1.000	0.000
Big Creek	1987	69	0.797	0.203	0.000	0.000	45	0.967	0.033	63	1.000	0.000
Tatchun	1987	74	0.811	0.182	0.007	0.000	66	0.886	0.114	66	1.000	0.000
Minto	1989	100	0.860	0.135	0.005	0.000	100	0.870	0.130	100	1.000	0.000
Kluane	1987	143	0.888	0.112	0.000	0.000	91	0.868	0.132	144	1.000	0.000
Teslin	1989	95	0.853	0.147	0.000	0.000	95	0.790	0.211	95	1.000	0.000

^				UNITED STATES		,	CANAL	DA		
					CHANDALAR/	U.SCANADA	FISHING BR/	UPPER		
Month	Week	Bank	Estimate	TANANA	Sheenjek	BORDER	MAINSTEM	CANADIAN	USA	CANADA
August	1	North	ML	9.8	42.9	89.1	46.3	1.1	52.7	47.3
			Bootstrap	16.6	42.1	78.9	36.8	4.5	58.7	41.3
			SE	9.3	13.4	10.6	14.2	4.5	14.0	14.0
			CV	94.5	31.4	11.9	30.6	430.8	26.7	29.7
	2	North	ML	3.9	64.6	94.4	29.8	1.7	68.5	31.5
			Bootstrap	8.1	63.0	87.8	24.8	4.1	71.1	28.9
			SE	6.5	15.2	8.2	14.6	4.7	14.9	14.9
			CV	166.9	23.6	8.7	49.2	277.8	21.7	47.2
	3	North	ML	0.0	52.0	92.7	40.7	7.3	52.0	48.0
			Bootstrap	2.9	54.6	87.3	32.7	9.8	57.5	42.5
			SE	3.6	14.2	7.0	14.5	5.5	13.8	13.8
			CV	_	27.3	7.6	35.7	74.6	26.5	28.7
	4	North	ML	2.2	55.2	90.4	35.2	7.4	57.4	42.6
			Bootstrap	5.3	58.5	87.1	28.6	7.6	63.8	36.2
			SE	4.7	14.7	7.2	13.7	5.8	14.0	14.0
			CV	208.8	26.6	8.0	38.8	78.3	24.4	32.9
September	1	North	ML	0.7	72.5	82.0	9.5	17.3	73.2	26.8
			Bootstrap	3.3	67.3	79.3	11.9	17.5	70.6	29.4
			SE	4.0	12.9	10.2	12.3	9.0	12.7	12.7
			CV	580.3	17.8	12.5	128.8	52.2	17.3	47.3
		South	ML	88.0	0.0	12.0	12.0	0.0	88.0	12.0
			Bootstrap	82.6	0.8	16.3	15.5	1.1	83.4	16.6
			SE	15.4	3.8	15.5	15.4	2.4	15.3	15.3
			CV	17.5	_	128.9	127.8	_	17.3	126.7
	2	North	ML	12.1	15.3	69.4	54.1	18.5	27.4	72.6
			Bootstrap	16.0	21.2	65.0	43.8	19.0	37.2	62.8
			SE	8.7	14.6	11.5	16.2	8.0	16.8	16.8

APPENDIX 3. Percent stock composition estimates (maximum likelihood, ML, and ML bootstrap) by time and bank for various stock groups with associated bootstrap standard errors (SE) and coefficients of variation (CV; calculated with ML and SE estimates).

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				Unite	ED STATES					
Month	Week	Bank	Estimate	TANANA	CHANDALAR/ Sheenjek	U.SCANADA BORDER	FISHING BR/ MAINSTEM	UPPER CANADIAN	USA	CANADA
			CV	71.9	95.8	16.6	29.9	43.1	61.5	23.2
		South	ML	84.1	2.9	15.9	12.9	0.0	87.1	12.9
			Bootstrap	74.9	6.3	24.7	18.4	0.4	81.2	18.8
			SE	12.8	7.3	12.8	13.0	0.9	12.9	12.9
			CV	15.2	249.3	80.6	100.5		14.9	100.0
	3	North	ML	9.4	41.9	77.3	35.4	13.2	51.4	48.6
			Bootstrap	19.1	40.5	65.6	25.1	15.3	59.6	40.4
			SE	13.4	20.1	16.3	19.7	11.7	20.1	20.1
			CV	141.9	47.8	21.1	55.6	88.5	39.1	41.3
		South	ML	95.5	0.0	4.5	4.5	0.0	95.5	4.5
			Bootstrap	80.4	0.9	19.1	18.2	0.5	81.4	18.7
			SE	13.6	2.8	13.6	13.5	1.2	13.5	13.5
			CV	14.2	_	301.1	299.7		14.1	299.9

APPENDIX 3 continued.