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Genetic Analysis Identifies Consistent Proportions of Seasonal Life History Types in Yukon River Juvenile and Adult Chum Salmon

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Abstract: The Yukon River is one of the largest producers of chum salmon (*Oncorhynchus keta*) in western Alaska. Management of Yukon River chum salmon is complex. One of the current concerns is overharvesting of the fall-run component. An earlier and typically more abundant summer-run type spawns in the lower to middle reaches of the drainage, whereas the genetically distinct fall-run type spawns in the middle to upper reaches in Alaska and Canada. Juvenile chum salmon migrate from the Yukon River in the spring and are found in the pelagic waters on the eastern Bering Sea shelf during summer and fall months. We genetically analyzed juvenile chum salmon caught on the eastern Bering Sea shelf during the 2003–2007 Bering-Aleutian Salmon International Surveys. Juvenile chum salmon were predominately from coastal western Alaska and upper/middle Yukon River populations. The relative proportions of fall and summer Yukon chum salmon varied considerably across years. The proportion of fall-run chum salmon in the juvenile collections was positively correlated with the proportion of fall-run chum salmon in the adult returns to the Yukon River, suggesting that the brood-year strength of Yukon River summer and fall-run chum salmon is determined early in the first year of life.

Keywords: chum salmon, Bering Sea, Yukon River, genetic stock identification

INTRODUCTION

In western Alaska, chum salmon (*Oncorhynchus keta*) are critical for subsistence, commercial, and cultural reasons. Over the last few decades, declines in chum salmon returns in some western Alaskan drainages prompted various disaster declarations by the State of Alaska and federal agencies. In addition, chum salmon fisheries on the Yukon and Kuskokwim rivers, two of the largest chum salmon production drainages in western Alaska, have been complicated in recent years by various restrictions designed to limit the take of Chinook (*O. tshawytscha*) salmon, which are currently at very low abundance (ADF&G 2013). There are two distinct Yukon River chum salmon life-history types: an earlier and typically more abundant summer run and a later fall run. Summer-run chum salmon generally spawn in the lower to middle reaches of the Yukon drainage, whereas fall-run chum salmon are typically larger and generally spawn in spring-fed regions of the middle to upper reaches in Alaska and Canada. The summer run of chum salmon averaged 1.8 million fish between 2000 and 2012, and the fall run averaged 864,000 fish over the same time period (JTC 2013), although there is variation in the two run strengths between years. Concern about low fall-run chum salmon abundance in some years has resulted in reduced subsistence fishing opportunities and has created challenges in fulfilling treaty obligations with Canada that specify escapement objectives (Bue et al. 2009).

Little is known about the survival of juvenile Yukon River chum salmon in either their freshwater or saltwater environments. Juvenile chum salmon out-migrate from the Yukon River in the spring (Hillgruber and Zimmerman 2009) and are found in the pelagic waters on the eastern Bering Sea shelf during summer and fall months (Farley et al. 2009). Juvenile chum salmon have been collected as part of annual U.S. Bering-Aleutian Salmon International Surveys (BASIS) in the eastern Bering Sea since 2002. A previous genetic analysis of the 2002 juvenile chum salmon based on allozyme loci (Farley et al. 2004) determined that a substantial proportion of juvenile chum salmon samples collected in this area were from the Yukon River; however, samples from other years remained unanalyzed.

We genetically analyzed juvenile chum salmon samples collected on the 2003–2007 BASIS cruises to address three objectives. First, we determined the extent of stock contri-

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butions of juvenile chum salmon on the eastern Bering Sea shelf off the mouth of the Yukon River and compared the distribution across years. Second, we developed a relative abundance index of summer- and fall-run Yukon River juvenile chum salmon on the eastern Bering Sea shelf. Third, we examined the potential to correlate juvenile relative abundances with adult returns for summer and fall Yukon River chum salmon runs.

MATERIALS AND METHODS

Sample and Genetic Data Collection

Juvenile chum salmon samples were collected on the eastern Bering Sea shelf during late summer-early fall from 2003 through 2007 as part of annual U.S. BASIS cruises completed by the National Marine Fisheries Service, Alaska Fisheries Science Center's (AFSC) Ecosystem Monitoring and Assessment Program at Auke Bay Laboratories (Fig. 1; Farley et al. 2005; Farley and Moss 2009). Fish were collected with a mid-

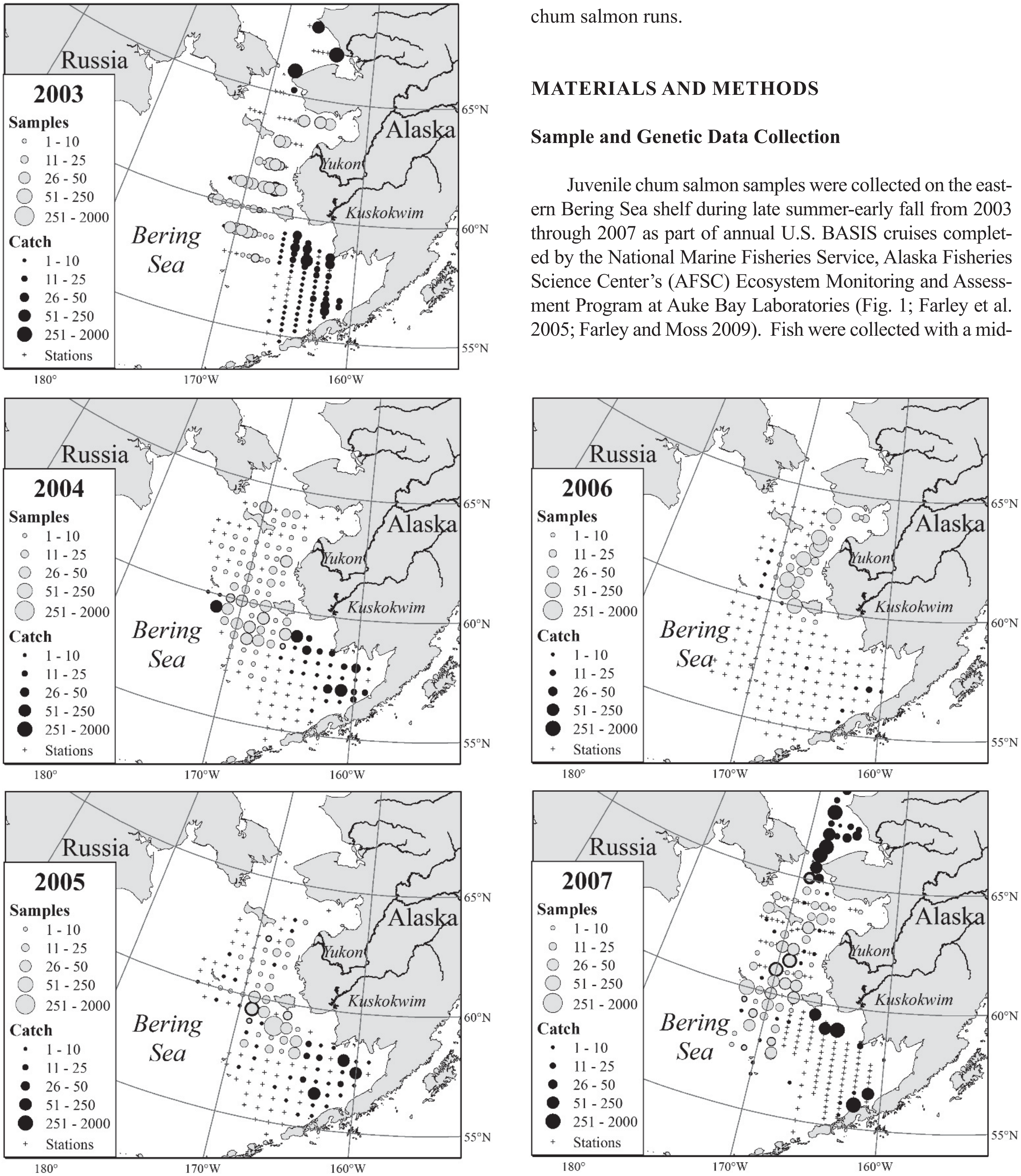

Fig. 1. Sample spatial distribution of juvenile chum salmon collected in the eastern Bering Sea from the 2003–2007 BASIS cruises. Samples that were genotyped are designated as "Samples" whereas the total catch from the survey is designated as "Catch." Stations surveyed with no juvenile salmon caught are designated with a "+".

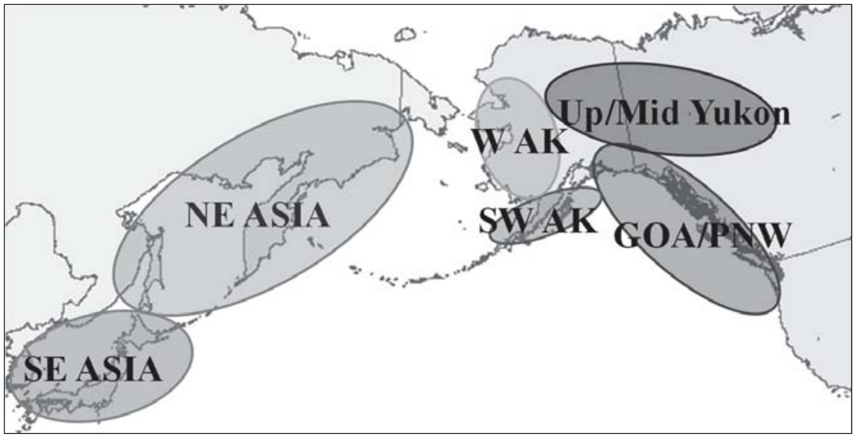

Fig. 2. The six large reporting groups of spawning chum salmon stocks from throughout the Pacific Rim: Southeast (SE) Asia; Northeast (NE) Asia; Coastal Western Alaska (W AK); Upper/Middle Yukon River (Up/Mid Yukon); Southwest Alaska (SW AK); and the Gulf of Alaska/Pacific Northwest (GOA/PNW).

water rope trawl that was towed at or near the surface during daylight hours (07:30–21:00, Alaska Daylight Savings Time); all tows lasted 30 min and covered 2.8 to 4.6 km. The genetic analysis of the 2003–2007 juvenile chum salmon focused on samples collected between approximately 58–64°N. This latitudinal range encompasses an area within which juvenile chum salmon are likely to be from the Yukon River, and relative abundances between summer- and fall-run juvenile indices may more likely correlate with adult Yukon River returns.

DNA was extracted from 5,002 juvenile chum salmon tails or opercles with DNeasy Blood and Tissue Kits (QIAGEN, Inc., Germantown, Maryland)[1] and Corbett X-tractor Gene reagents (Corbett Robotics Pty. Ltd., Mortlake, NSW, Australia) as described by the manufacturers and processed with a Corbett CAS1820 X-tractor Gene robot (Corbett Robotics Pty. Ltd., Mortlake, NSW, Australia). Extracted DNA was stored in 96-well DNA plates at -20ºC.

Genotypes of the juvenile chum salmon were obtained for 11 of the microsatellite loci represented in the coastwide chum salmon genetic baseline (Beacham et al. 2009a). The microsatellite loci were amplified with the polymerase chain reaction (PCR) in three multiplexed panels. Each PCR was conducted in a 5 µL volume containing ~10 ng of DNA, 2.5 µL QIAGEN Multiplex PCR Mastermix, 0.2 µM of each primer, and RNase-free water. Primer sequences for the 11 loci have been described in the following publications: *Oki100* (Beacham et al. 2009b), *Omm1070* (Rexroad et al. 2001), *Omy1011* (Spies et al. 2005), *One101*, *One102*, *One104*, *One114* (Olsen et al. 2000), *Ots103* (Beacham et al. 1998), *Ots3* (Greig and Banks 1999), *OtsG68* (Williamson et al. 2002), and *Ssa419* (Cairney et al. 2000). Thermal cycling for the PCR amplification of DNA fragments was performed on a dual 384-well GeneAmp PCR System 9700 (Life Technologies, Inc., Carlsbad, CA). Loci in Panel A (*Omm1070*, *Omy1011*, *One102*) were amplified with the following protocol: initial denaturation at 95ºC for 15 min, then 16 cycles at 94ºC for 30 s, 60ºC (-0.5ºC per cycle) for 90 s, and 72ºC for 1 min, then 24 cycles at 94ºC for 30 s, 52ºC for 90 s, and 72ºC for 1 min, followed by a final polymerization step at 60ºC for 30 min and then storage at 15ºC until removal from the thermocycler. Loci in Panels B (*Oki100*[2], *One101*, *Ots3*, *Ssa419*) and C (*One104*, *One114*, *Ots103*, *OtsG68*) were amplified with the following protocol: initial denaturation at 95ºC for 15 min, then 34 cycles at 94ºC for 30 s, 60ºC for 1.5 min, and 72ºC for 1 min, followed by a final polymerization step at 60ºC for 30 min and then storage at 15ºC until removal from the thermocycler.

Samples from the PCR reactions were diluted into 96-well plates for analysis with a 16-capillary, 36 cm array on the Applied Biosystems (ABI) 3130*xl* Genetic Analyzer as follows: 1 µL diluted (1:25) PCR product, 4.4 µL Hi-Di™ formamide, 4.4 µL de-ionized water, 0.2 µL GeneScan™ 600 LIZ® size standard (Life Technologies, Inc., Carlsbad, CA). Samples were denatured at 95ºC for 3 min, then cooled to 4ºC and stored until analysis on the ABI 3130*xl*. Genotypes were identified with GeneMapper® 4.0 software (Life Technologies, Inc., Carlsbad, CA). Samples genotyped for less than 8 loci were removed from analysis (Dann et al. 2009).

Quality control of sample handling and genotyping was examined by plating DNA from the samples in the bottom row of each elution plate onto 96-well plates for a total of 384 samples that were then processed for genotyping as described above. Genotypes from the quality control dataset were then compared to the genotypes of the original dataset.

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[1] Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

[2] The difficulty of genotyping *Oki100* when it was co-amplified with the other loci in Panel B led to separate amplification of this locus partway through the project. The post-PCR product was pooled with that of the other loci in Panel B prior to analysis on the ABI 3130*xl*.

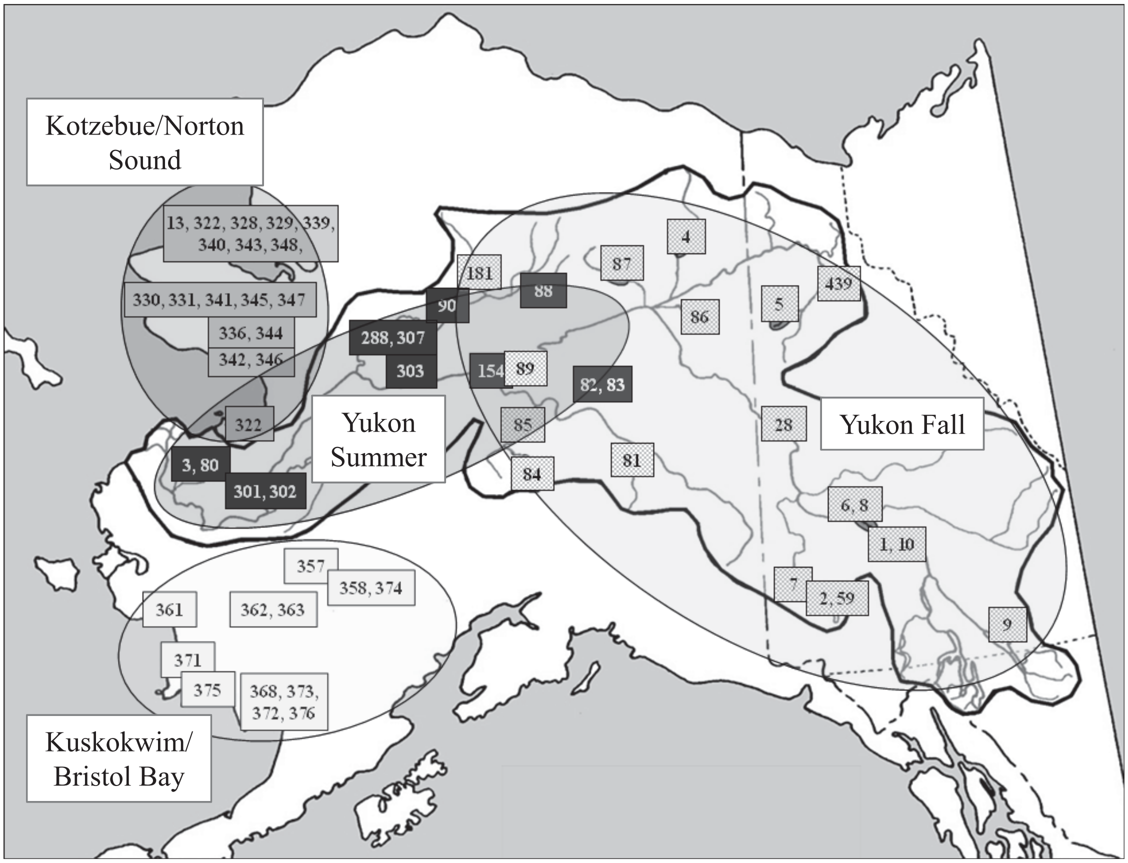

Fig. 3. Finer-scale temporal-spatial population groupings of chum salmon used for mixed-stock analysis: Yukon Summer, Yukon Fall, Kotzebue/Norton Sound, and Kuskokwim/Bristol Bay. Numbers refer to the population number in the coastwide microsatellite baseline (www.pac.dfo-mpo.gc.ca/science/facilities-installations/pbs-sbp/mgl-lgm/data-donnees/index-eng.html).

Stock Composition Analyses

Stock composition estimates were made with the data organized in two ways. First, to determine the northern and southern extent of the Yukon River juvenile chum salmon distribution in the eastern Bering Sea, and thus the optimal sampling location for estimating proportions of summer- and fall-run Yukon River chum salmon, samples were aggregated by latitude and longitude for three locations. Samples across years were combined by latitude as follows: 1,244 samples at 58–59.5°N; 2,736 samples at 60–63°N; and 296 samples at 63.5–65°N. All samples were limited to between 166.75–172.5°W. Stock composition estimates were made with the 381-population coastwide baseline for six reporting groups. Second, based on results from the first mixed-stock analyses, yearly stock composition estimates were made with the coastwide chum salmon baseline for eight reporting groups for samples collected between 166.75–172.50°W and 58–63°N.

The coastwide chum salmon microsatellite baseline (Beacham et al. 2009a) has been optimized for use in our laboratory (e.g., Vulstek et al. 2014; Whittle et al. 2015) and was used to perform stock composition analysis in this study. Baseline allele frequencies were downloaded from Fisheries and Oceans Canada's (DFO) Molecular Genetics web page (www.pac.dfo-mpo.gc.ca/science/facilities-installations/pbs-sbp/mgl-lgm/data-donnees/index-eng.html) and baseline files compatible with software programs SPAM 3.7 (ADF&G 2003) and BAYES (Pella and Masuda 2001) were created. Genetic structure of the 381-population coastwide baseline was examined with baseline simulation analyses to evaluate the effectiveness of the baseline to correctly allocate stocks to six large reporting groups: Southeast Asia, Northeast Asia, Coastal Western Alaska (summer-run), Upper/Middle Yukon River (mostly fall-run), Southwest Alaska, and the Gulf of Alaska/Pacific Northwest (Fig. 2). Simulation analyses (SPAM software) with baseline population resampling were performed by reallocating hypothetical mixtures of 400 fish from a single reporting group to determine the percentage that reallocated back to the correct reporting group. Additional baseline simulation analyses were performed with the Coastal Western Alaska group split into three groups: Kotzebue/Norton Sound, Yukon Summer, and Kuskokwim/Bristol Bay. Four of the Yukon populations (Salcha, Chena, Jim, and Koyukuk south) were moved from the Upper/Middle Yukon group to the Yukon Summer group due to run timing and genetic affinity to other summer-run

Table 1. Number of successfully genotyped (at ≥ 8 of 11 loci) juvenile chum salmon samples that were collected in the eastern Bering Sea during 2003–2007 BASIS cruises.

Year	Genotyped number	Collection date
2003	1,069	21 Aug – 8 Oct
2004	887	27 Aug – 28 Sep
2005	794	15 Aug – 5 Oct
2006	1,011	3 Sep – 20 Sep
2007	1,113	5 Sep – 6 Oct

chum salmon; the remaining upper Yukon populations were renamed the Yukon Fall group (Fig. 3).

For the mixture files, allele designations of the juvenile chum salmon genotypes were converted to match those in the baseline. Compatibility of our allele designations to the coastwide baseline was confirmed previously with a set of samples from the DFO Molecular Genetics Laboratory that was analyzed on the Auke Bay Laboratory's ABI 3130*xl* Genetic Analyzer. Genotypes from converted mixtures were then formatted into mixture files compatible with BAYES software, which uses a Bayesian algorithm to produce stock composition estimates (Pella and Masuda 2001). The stock composition estimates were the proportion of each grouping of baseline populations that contributed to the mixture of juvenile chum salmon samples of unknown origin. For all estimates, the Dirichlet prior parameters for the stock proportions were defined by reporting group to be $1/(GC_g)$, where C_g is the number of baseline populations in reporting group g, and G is the number of reporting groups. For each analysis with the 6-reporting-group baseline, six Monte Carlo chains of 10,000 iterations were run starting at disparate values of stock proportions configured such that 95% of the stocks came from one designated reporting group with weights equally distributed among the stocks of that reporting group. The remaining 5% were equally distributed among remaining stocks from all other reporting groups. The first 5,000 iterations from each chain were discarded to remove the influence of the initial values. For each analysis with the 8-reporting-group baseline, six Monte Carlo chains of 20,000 iterations were run starting at disparate values of stock proportions configured such that 95% of the stocks were equally distributed among 1/6th of the stocks in the baseline and the remaining 5% were equally distributed among the remaining 5/6th of the stocks. The first 10,000 iterations from each chain were discarded. Convergence of the chains to posterior distributions of stock proportions was assessed with Gelman and Rubin (1992) shrink statistics, which were all 1.03 or less for all the estimates, conveying strong convergence to a single posterior distribution (Pella and Masuda 2001).

Yukon River Fall-Run Component

Adult return estimates by age class for Yukon River chum salmon for years 2000–2012 were used to follow brood-year returns; the adult returns were summed for age-3 through age-6 for both summer- and fall-run fish (Estensen et al. 2015). A relative abundance index for Yukon River fall-run adult chum salmon by brood-year was then computed by dividing the proportion of fall-run chum salmon by the total Yukon River chum salmon return. For the juvenile chum salmon samples collected at sea, the yearly proportions of fall-run fish were determined by dividing the fall-run genetic composition estimate by the total Yukon River genetic composition estimate (summer plus fall). A Pearson correlation coefficient was calculated to determine whether there was a relationship between the relative proportion of Yukon River fall-run juveniles collected at sea and (1) the relative proportions of fall-run adults (escapement) that produced the juveniles, or (2) the relative proportions of fall-run adult brood-year returns.

RESULTS

Genotyping

Of the samples analyzed, 4,874 (97%) were successfully genotyped for 8 or more of the 11 loci (Table 1). Quality control of sample handling and genotyping indicated a low discrepancy rate that averaged 0.4% across loci.

Baseline Evaluation

The coastwide baseline simulation analyses reallocated stocks to six large reporting groups with a high degree of accuracy indicating that stock composition estimates derived

Table 2. Coastwide chum salmon baseline evaluation of six reporting groups with simulated mixtures in which 100% of the samples were derived from a single regional grouping (read down columns). Correct allocations highlighted. Reporting groups are as noted in Fig. 2.

Reporting group	SE Asia	NE Asia	Coastal W Alaska	Upper/Middle Yukon	SW Alaska	GOA-PNW
SE Asia	0.886	0.028	0.002	0.001	0.008	0.001
NE Asia	0.026	0.851	0.011	0.002	0.054	0.008
Coastal W Alaska	0.005	0.048	0.959	0.057	0.041	0.002
Upper/Middle Yukon	0.000	0.002	0.011	0.936	0.001	0.000
SW Alaska	0.001	0.007	0.003	0.000	0.818	0.003
GOA/PNW	0.011	0.044	0.011	0.002	0.071	0.978

Table 3. Coastwide chum salmon baseline evaluation of eight reporting groups with simulated mixtures in which 100% of the samples were derived from a single regional grouping (read down columns). Correct allocations are highlighted. Reporting groups are as noted in Figs. 2 and 3.

Reporting group	SE Asia	NE Asia	Kotzebue-Norton Sound	Yukon Summer	Yukon Fall	Kuskokwim-Bristol Bay	SW Alaska	GOA-PNW
SE Asia	0.886	0.029	0.002	0.001	0.001	0.002	0.008	0.001
NE Asia	0.026	0.852	0.013	0.004	0.002	0.011	0.055	0.008
Kotzebue/Norton Sound	0.003	0.029	0.896	0.089	0.006	0.223	0.022	0.001
Yukon Summer	0.001	0.012	0.047	0.840	0.058	0.215	0.007	0.001
Yukon Fall	0.000	0.001	0.004	0.028	0.925	0.004	0.001	0.000
Kuskokwim/Bristol Bay	0.001	0.008	0.017	0.031	0.003	0.526	0.013	0.001
SW Alaska	0.001	0.007	0.002	0.002	0.000	0.007	0.817	0.003
GOA/PNW	0.011	0.043	0.015	0.004	0.002	0.007	0.071	0.977

from the use of this baseline are highly accurate (Table 2). Similarly, baseline simulations with eight reporting groups showed that the baseline reallocated seven of the eight reporting groups with a high degree of accuracy, but there was substantial misallocation of the Kuskokwim/Bristol Bay group to other coastal western Alaska groups (Yukon Summer and Kotzebue/Norton Sound) (Table 3). Thus, stock composition analyses performed with the eight baseline reporting groups may underestimate the contribution from the Kuskokwim/Bristol Bay region.

Stock Composition Estimates by Latitude, Years Pooled

Stock composition estimates with the baseline of six reporting groups indicated that about 40% of the fish from the most northern samples were from Northeast Asia populations, with most of the remaining fish from Coastal Western Alaska (Table 4). Two-thirds to three-quarters of the fish from the two locations between 58–63°N were from Coastal Western Alaska. Nearly all of the remaining fish were from the Upper/Middle Yukon region, which is comprised mostly of fall-run populations. Given the large proportion of Northeast Asian fish and the small sample size of the most northern dataset, these samples were not analyzed further. Because the Upper/Middle Yukon fish, which are mostly fall-run, are identified with high accuracy (Table 2) and because 25–30% of the juvenile chum salmon in the two most southern areas were from this region, we focused on the samples collected between 58–63°N to investigate the relationship between the relative abundance of fall-run juvenile chum salmon and (1) the parents of the juveniles and (2) the adult brood-year returns of the juveniles.

Table 4. Stock composition estimates of juvenile chum salmon samples collected during 2003–2007 for three latitudinal ranges. Estimates with lower credible interval values > 0 are identified in bold italic font. Reporting groups are as noted in Fig. 2.

Reporting group	Proportion		
	63.5–65°N n=296	60–63°N n=2,736	58–59.5°N n=1,244
SE Asia	0.001	0.000	0.000
NE Asia	***0.408***	***0.004***	***0.019***
Coastal W Alaska	***0.479***	***0.752***	***0.673***
Upper/Middle Yukon	***0.111***	***0.244***	***0.307***
SW Alaska	0.001	0.000	0.001
GOA/PNW	0.001	0.000	0.000

Stock Composition Estimates by Year

Yearly stock composition estimates with the baseline of eight reporting groups indicated that more than 96% of the 2003–2007 juvenile chum salmon samples were from western Alaska populations (Table 5). Except in 2003 when nearly 50% of the juvenile chum salmon collected on the eastern Bering Sea shelf were from Kotzebue/Norton Sound populations, the highest proportion of juvenile chum salmon originated from the Yukon Summer populations. The Yukon Summer contribution was always higher than the Yukon Fall contribution, which averaged 20%. Typically less than 4% of the juvenile chum salmon samples originated from the Kuskokwim River/Bristol Bay populations.

Correlation of Yukon River Juvenile and Adult Chum Salmon Fall-run Proportions

The proportion of fall-run adult returns of Yukon River chum salmon based on abundance estimates varied across years (Fig. 4A). On average, 32% of the annual return between 2000 and 2012 was classified as a fall stock, with a high of 47% in 2005 and a low of 22% in 2006. A large return of age-3 and age-4 fish sometimes corresponded to a large return of age-4 and age-5 fish, respectively, the following year. The correlation coefficient between the proportion of fall-run juveniles and the parents (escapement) that produced those juveniles was not significant ($r = 0.55$, $p = 0.261$ at $\alpha = 0.05$).

The proportion of fall-run returns by brood year was also variable across years (Fig. 4B). For the 2000–2007 brood years, approximately 31% of the return was fall-run chum salmon, with a high of 42% from the 2003 brood year and a low of 24% from the 2002 brood year. A correlation was found between the proportions of fall-run juveniles es-

Table 5. Yearly stock composition estimates for juvenile chum salmon collected between 58–63°N in the eastern Bering Sea during the summer/fall BASIS cruises. BAYES mean estimates are provided with standard deviations (SD), 95% credible intervals, median estimate, and Gelman and Rubin (1992) shrink factor. A 381-population baseline was used to estimate contributions from eight reporting groups. Reporting groups are as noted in Figs. 2 and 3.

Reporting group	Mean	SD	2.5%	Median	97.5%	Shrink
2003						
SE Asia	0.000	0.001	0	0	0.002	1.00
NE Asia	0.002	0.002	0	0.001	0.007	1.00
Kotzebue/Norton	0.484	0.032	0.422	0.484	0.547	1.00
Yukon Summer	0.377	0.036	0.305	0.377	0.447	1.01
Yukon Fall	0.116	0.016	0.086	0.115	0.148	1.01
Kuskokwim/Bristol	0.021	0.020	0	0.017	0.065	1.00
SW Alaska	0.001	0.002	0	0	0.007	1.01
GOA/PNW	0.000	0.001	0	0	0.003	1.00
2004						
SE Asia	0.000	0.001	0	0	0.002	1.00
NE Asia	0.031	0.009	0.016	0.031	0.051	1.00
Kotzebue/Norton	0.199	0.033	0.134	0.199	0.266	1.02
Yukon Summer	0.433	0.041	0.352	0.433	0.516	1.02
Yukon Fall	0.324	0.025	0.276	0.324	0.372	1.00
Kuskokwim/Bristol	0.007	0.012	0	0.001	0.041	1.01
SW Alaska	0.005	0.004	0	0.004	0.014	1.00
GOA/PNW	0.000	0.001	0	0	0.002	1.00
2005						
SE Asia	0.000	0.001	0	0	0.003	1.00
NE Asia	0.003	0.003	0	0.002	0.011	1.00
Kotzebue/Norton	0.172	0.037	0.102	0.171	0.247	1.00
Yukon Summer	0.655	0.048	0.558	0.656	0.746	1.01
Yukon Fall	0.138	0.024	0.094	0.137	0.186	1.01
Kuskokwim/Bristol	0.032	0.023	0	0.031	0.082	1.01
SW Alaska	0.001	0.001	0	0	0.005	1.00
GOA/PNW	0.000	0.001	0	0	0.003	1.00
2006						
SE Asia	0.000	0.001	0	0	0.002	1.00
NE Asia	0.001	0.001	0	0.000	0.005	1.00
Kotzebue/Norton	0.060	0.027	0.001	0.059	0.114	1.01
Yukon Summer	0.678	0.040	0.596	0.680	0.751	1.02
Yukon Fall	0.243	0.021	0.202	0.242	0.285	1.00
Kuskokwim/Bristol	0.018	0.022	0	0.008	0.074	1.02
SW Alaska	0.000	0.001	0	0	0.002	1.00
GOA/PNW	0.000	0.001	0	0	0.002	1.00
2007						
SE Asia	0.000	0.001	0	0	0.002	1.00
NE Asia	0.023	0.008	0.010	0.022	0.039	1.00
Kotzebue/Norton	0.176	0.044	0.099	0.174	0.266	1.03
Yukon Summer	0.585	0.048	0.489	0.585	0.674	1.03
Yukon Fall	0.187	0.020	0.150	0.186	0.227	1.01
Kuskokwim/Bristol	0.029	0.028	0	0.024	0.089	1.02
SW Alaska	0.000	0.001	0	0	0.003	1.00
GOA/PNW	0.000	0.001	0	0	0.002	1.00

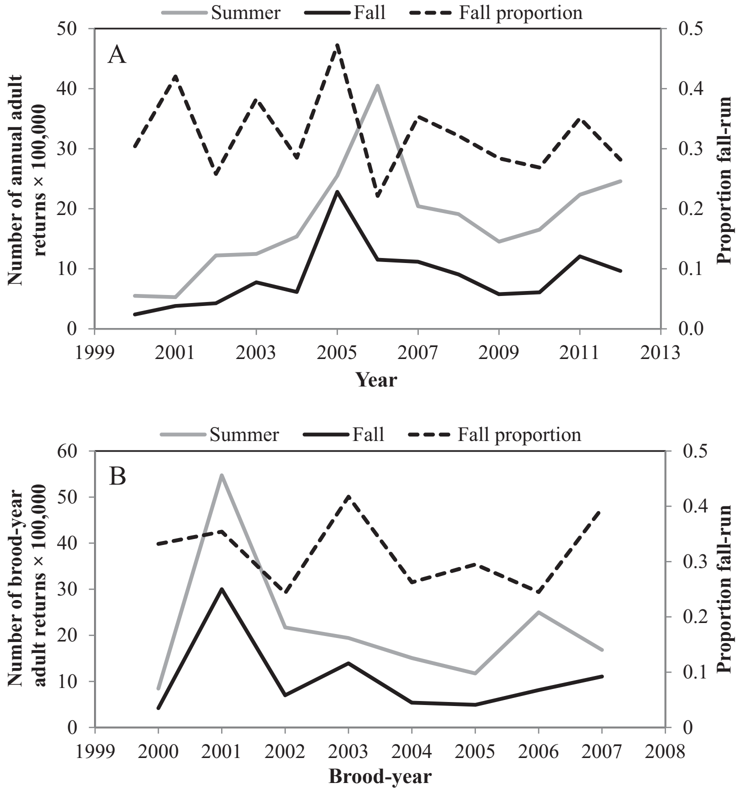

Fig. 4. Summer- and fall-run adult returns of chum salmon to the Yukon River; annual returns (A) and brood-year returns (B). Estimates of return are on the left y-axis and proportions of fall-run chum salmon are on the right y-axis.

timated from genetic analysis and the corresponding adult brood-year returns calculated from abundance estimates ($r = 0.94$, $p = 0.006$ at $\alpha = 0.05$; Fig. 5). This relationship was further supported by data for the 2001 brood year that was produced from an earlier study with allozyme loci (C. Kondzela, unpublished data).

DISCUSSION

The availability of multi-year collections of juvenile chum salmon from the eastern Bering Sea and the comprehensive genetic information of chum salmon populations throughout their geographic distribution (e.g., Beacham et al. 2009c) provided an opportunity to examine the distribution of western Alaskan chum salmon during their first summer/fall at sea. For the first time that we are aware of, our study investigated the relationship of the stock compositions of juvenile chum salmon collected at sea and the Yukon River adult chum salmon returns. Because the genetic diversity of coastal western Alaska chum salmon populations is low (DeCovich et al. 2012; Garvin et al. 2013) and therefore challenging to apply to mixed-stock analyses, we focused on the Yukon River, which has fall-run populations that are genetically distinct from the summer-run populations. Estimates of the proportions of the two life-history types in mixtures of juveniles were used to examine year-to-year differences in distributions in the Bering Sea during early marine residence, and to investigate the potential association of juvenile abundances with Yukon River adult returns.

The estimated stock proportions of juvenile chum salmon caught in the eastern Bering Sea during late summer/fall over a 5-year time period adds to our understanding of the distribution of western Alaska chum salmon during their first year in the ocean (Farley et al. 2004). Our results support a migration model whereby western Alaska juvenile chum salmon head primarily west and south across the eastern Bering Sea shelf during the summer/fall season (Farley et al. 2005). Contributions from each stock group of this highly migratory species were remarkably similar from year-to-year, especially given the inter-annual latitudinal shifts in juvenile chum salmon distribution across the eastern Bering Sea shelf, as well as the variation in the date that stations were sampled across years. Nearly all of the juvenile chum salmon were from the Coastal Western Alaska and Upper/Middle Yukon River stock groups, as was found in an earlier genetic analysis of samples from 2002 (C. Kondzela, unpublished data). Except in 2003, the highest proportion of juvenile chum salmon caught in the surveys was from the Yukon Summer populations (Table 5). In all years, the Yukon Summer component was higher than the Yukon Fall component. The contribution from Kotzebue/Norton Sound varied annually, and given the low abundance of many Norton Sound chum salmon popula-

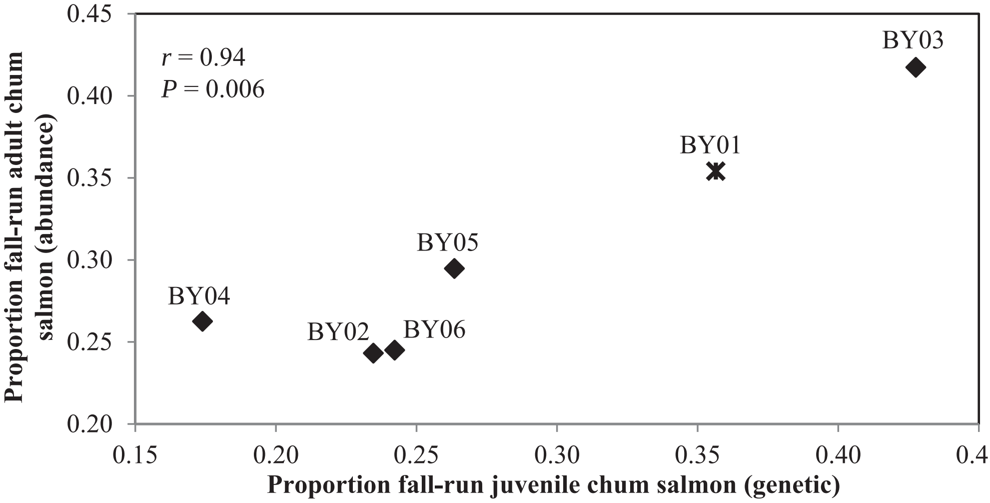

Fig. 5. The proportion of fall-run Yukon River juvenile chum salmon (relative to total Yukon) collected in the eastern Bering Sea between 58–63°N during 2002–2007 versus the brood-year adult returns. Microsatellite marker data indicated with diamonds and allozyme marker data with a star; each data point labeled by broodyear, e.g., BY04 represents the 2004 brood year (juveniles collected in 2005). Allozyme data was from C. Kondzela (unpublished).

tions in some years (Menard et al. 2009), surveys in the northeastern Bering Sea might help provide insight into the early marine residence of these populations. Although the presence of Kotzebue/Norton Sound and Northeast Asia origin chum salmon would not necessarily adversely impact analysis of the relative proportions of summer and fall chum salmon from the Yukon River, the yearly sample sets were limited to collections below 63°N in order to focus on Yukon River origin fish. Previous analyses (Farley et al. 2004) indicated that samples collected below 60°N contained Kuskokwim origin fish, although our analysis suggests that Kuskokwim/Bristol Bay origin fish were only a minor component as far south as 58°N and did not migrate northward during their first summer. This difference may simply reflect inter-annual variation of migration routes or an effect of sampling west of 166.75°W, an area potentially outside the migration route of the Kuskokwim origin chum salmon during the 2003–2007 surveys. A third possibility is that some of the Kuskokwim/Bristol Bay origin fish were misallocated to the Yukon Summer or Kotzebue/Norton Sound reporting groups (Table 3), although the effect would likely be similar across years and have little impact on the analysis of the relative proportions of the summer and fall run components.

On average, across the 5-year dataset, about one-third of the Yukon River juvenile chum salmon were from fall-run populations based on genetic stock estimates, much like the adult returns based on abundance estimates. Although no correlation was found between the estimated proportion of fall-run Yukon River juvenile chum salmon in the sample sets and the adult year classes that produced them, a significant correlation was found between the juveniles and the corresponding brood-year returns (Fig. 5). In the 2003 brood year, the departure of the relative survival of the two life-history types in the Yukon River provided contrast in the correlation analysis of the proportions of fall-run juveniles and brood-year returns. The significant correlation suggests that differences in the production and survival of the summer- and fall-run populations develop during the period of freshwater and early marine residence before late summer and early fall.

In most years, the abundance of fall-run fish is usually well-correlated with the abundance of summer-run fish (Fig. 4A), but infrequently, the fall-run proportion is substantially higher or lower than expected; for example, higher in 2005. The relative proportions of fall-run juvenile chum salmon provide insight into the relative strength of fall-run adult returns. For example, juvenile chum salmon produced from the 2001 and 2002 year classes have different impacts on the 2005 adult returns. There were few age-3 fall-run Yukon River chum salmon returns in 2005, so the juveniles produced from the 2002 year class did not contribute significantly to the 2005 adult returns. However, 94% of the fall-run return in 2005 was comprised of age-4 fish that were produced from the 2001 year class (juveniles sampled in 2002), which from an earlier genetic analysis (C. Kondzela, unpublished data) based on a different set of genetic markers had a relatively high proportion of fall-run fish (Fig. 5).

The proportion of fall-run juveniles that return as adults is spread across multiple years due to the age structure of chum salmon populations. Thus, the high proportion of fall-run juveniles from the 2003 year class (collected in 2004) contributed to adult returns in 2006 as age-3, in 2007 as age-4, in 2008 as age-5, and in 2009 as age-6. The age-3 and age-6 contributions were only 2–3% of the fall-run return in 2006 and 2009, but the high proportion of fall-run juveniles caught in 2004 is evident as age-4 fish, which comprised

76% of the 2007 fall-run return, and as age-5 fish, which comprised 56% of the 2008 fall-run return, the second highest proportion of age-5 fall-run returns in years 2000–2012.

To develop the relative abundance index for Yukon fall adult chum salmon, we relied on the abundance estimates of summer and fall-run components (Estensen et al. 2015). These run components are based on counts from multiple sources that are subject to varying degrees of uncertainty, which in turn affect the relative abundance index. One of the primary sources of uncertainty in abundance estimates is probably associated with estimating the summer and fall harvests due to the overlap of summer and fall runs in the lower river (Flannery et al. 2010). For example, summer-run chum salmon caught in the fall fisheries will be counted as fall chum, resulting in an overestimation of fall run abundance. However, from mixed-stock analyses of samples collected in the lower river, the numbers of summer-run chum salmon caught in the fall season is comparatively small, comprising 0–2% of the total Yukon return (B. Borba, unpublished data).

The proportion of annual and brood-year returns of fall-run adult chum salmon to the Yukon River during 2000–2012 had a cyclical pattern with higher proportions typically in odd-numbered years and lower proportions in even-numbered years (Fig. 4). This pattern appears to correspond to an alternate pattern of pink salmon abundance that is highest during even-numbered years in western Alaska populations (Bue et al. 2009; Menard et al. 2009; Estensen et al. 2015; Elison et al. 2015a,b). Additionally, Asian pink salmon populations are highest during odd-numbered years. During years of high pink abundance, interspecific competition in the ocean has been shown to reduce growth and lower survival of other species, including chum salmon (Ruggerone et al. 2003; Ruggerone and Nielsen 2004; Agler et al. 2013; Springer and van Vliet 2014).

CONCLUSION

We have shown from genetic analysis of juvenile chum salmon from the eastern Bering Sea that this early life-history stage has run proportions consistent with those of adult returns to the Yukon River. By the time juvenile chum salmon are caught on the continental shelf of the eastern Bering Sea in late summer/early fall, the relative proportion of summer and fall fish appears to have been determined for that brood year. This information may supplement the current management protocol that assumes a constant ratio of fall and summer abundance; however, the samples we analyzed were collected as one component of large, expensive, multiple-objective fishery and oceanographic surveys in the Bering Sea. It would be interesting to investigate a sampling protocol on a scale more practical to salmon management to determine whether a smaller vessel, fishing closer to shore near the Yukon River mouth (or even in the river), and over a shorter time period would provide similar results. Future investigations should incorporate ongoing advances in the genetic baselines, which may improve the accuracy of the stock composition estimates in the western Alaska region, particularly for the summer coastal stocks. Analyses of samples collected during more recent years (2009–2014) may further clarify the relationship between juvenile and adult chum salmon from the Yukon River.

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